Évaluation du potentiel de croissance des arbres feuillus et de leur sensibilité aux conditions climatiques

Thèse

Guillaume Moreau

Doctorat en sciences forestières
Philosophiæ doctor (Ph. D.)

Québec, Canada

Évaluation du potentiel de croissance des arbres feuillus et de leur sensibilité aux conditions climatiques

Thèse

Guillaume Moreau

Sous la direction de :

David Pothier
Alexis Achim

Résumé

En Amérique du Nord, la coupe de jardinage a été implantée en réponse à plusieurs décennies de mauvaises pratiques forestières ayant laissé de grandes superficies de peuplements feuillus dégradés et de faible vigueur. Or, l'application de la coupe de jardinage dans un contexte industriel a produit des résultats variés et parfois peu convaincants sur sa capacité à améliorer la vigueur générale des peuplements et à fournir un rendement soutenu en bois de haute valeur. L'objectif général de ce projet de recherche était d'améliorer les prévisions de la croissance et de la mortalité des arbres feuillus à partir d'une meilleure évaluation de leur potentiel de croissance sur pied et de leur sensibilité aux conditions climatiques. Nos résultats ont d'abord montré un effet marginal du taux de dégagement induit par la coupe de jardinage sur la croissance et le taux de survie des arbres résiduels. Ce résultat s'explique en partie par une concentration de la récolte des arbres à l'intérieur et aux abords des sentiers de débardage, laissant ainsi de larges zones non traitées dans les peuplements résiduels. Dans les années suivant l'application du traitement, uniquement 24 % des arbres ont connu une hausse de croissance significative, un pourcentage de réaction de croissance légèrement inférieur à celui induit par les perturbations naturelles au cours des décennies précédentes. Nos analyses ont également montré qu'une réduction marquée de la croissance sur plusieurs décennies précédait 88 % des événements de mortalité post-récolte, et que les prévisions de ces événements pouvaient être significativement améliorées en considérant les tendances de croissance 25 ans avant la coupe. De plus, la présence de défauts affectant la vigueur des arbres au moment de la coupe était positivement reliée à la probabilité de mortalité et négativement reliée à la probabilité d'avoir une hausse de croissance après la coupe. Par ailleurs, nos analyses ont montré qu'une évaluation visuelle de la densité du houppier est l'indicateur le plus efficace pour estimer la vigueur et le potentiel de croissance sur pied de l'érable à sucre. Finalement, nos analyses des relations entre la croissance et les conditions climatiques ont montré un lien fort entre l'occurrence des stress climatiques ponctuels et une diminution de la croissance de l'érable à sucre. Les épisodes de gel-dégel de forte intensité ont été particulièrement dommageables en provoquant des baisses abruptes de la croissance dans les deux régions étudiées. À l'inverse, les analyses provenant des tendances climatiques mensuelles ont indiqué une relation faible et instable dans le temps avec la croissance. Nos résultats indiquent que l'effet synergique d'une accumulation de plusieurs stress climatiques et d'épidémies d'insectes défoliateurs au début des années 1980 a induit un changement

important dans la dynamique de croissance de l’érable à sucre et sa réponse aux conditions climatiques mensuelles.

Table des matières

Liste des figures

Liste des tableaux

Remerciements

Je tiens à remercier sincèrement mon directeur de recherche, David Pothier, pour sa confiance et pour m’avoir donné la chance de poursuivre mes études graduées sur un sujet qui me passionne. Merci pour ta disponibilité et ta rigueur qui m’ont permis d’avancer rapidement et de me développer comme chercheur. Je veux également remercier mon co-directeur de recherche, Alexis Achim, qui a grandement contribué à ce projet et à ma formation. Merci pour ton ouverture, ton enthousiasme, ta créativité et pour toutes les opportunités que tu m’as données pour que je me développe comme chercheur. Ensemble, vous avez été d’un grand support dans mes travaux et votre camaraderie a rendu mon expérience fort agréable. J’ai eu énormément de plaisir à travailler avec vous. Je veux également vous remercier de m’avoir permis de dévier à quelques reprises d’un parcours académique traditionnel, en me permettant de réaliser des projets parallèles à ma thèse qui étaient très importants à mes yeux.

Ce projet de recherche n’aurait pas été possible sans la participation de notre partenaire industriel Domtar. J’aimerais remercier André Gravel, Patrick Cartier, Élise Jolicoeur, Éric Lapointe, Steeve Reynolds ainsi que Christian Guimont pour leur support et leur confiance. Vos conseils et votre aide technique ont grandement facilité ma progression.

Je souhaite remercier Ann Delwaide de m’avoir accompagné patiemment dans mes analyses de laboratoire et pour tous ses précieux conseils. Ton enseignement a fortement contribué à mon désir de faire un passage accéléré au doctorat. Merci également à Évelyne Thiffault de m'avoir partagé ton enthousiasme pour le monde de la recherche alors que je n’étais qu’un étudiant au premier cycle.

Un grand merci également à Éloïse Dupuis, Alexandre Morin-Bernard, Félix Poulin, Marie-Laure Lusignan, Émilie St-Jean et Édouard Moreau pour votre aide sur le terrain. Un merci tout spécial à mon ami Michel Poudrier pour son aide technique en programmation. Ce projet n’aurait pas été possible sans votre aide précieuse.

J’aimerais aussi remercier les membres de mon comité de thèse qui ont accepté d’examiner ce document, soit Christian Messier, Filip Havreljuk et Jean-Claude Ruel. Merci pour vos commentaires constructifs.

Enfin, je veux remercier mes parents et ma famille pour leur support inconditionnel dans mon cheminement académique. Jamais il ne m'aurait été possible d'atteindre un niveau d'accomplissement aussi élevé sans votre aide et sans vous avoir eu comme exemple. Je vous remercie du fond du cœur. Je termine en remerciant ma douce moitié, Catherine, pour son support et surtout, de me donner les meilleures raisons du monde de décrocher de mes recherches et de prendre des pauses du travail.

Merci tout le monde !

Avant-propos

Insertion d’articles

Cette thèse est composée de quatre chapitres rédigés en anglais et présentés sous forme d’articles scientifiques. En tant que candidat au doctorat et premier auteur, j'ai effectué la revue de littérature, établi les objectifs de recherche, réalisé et encadré l'échantillonnage sur le terrain, réalisé les analyses statistiques et l’interprétation des résultats et rédigé l’ensemble des articles scientifiques.

Chapitre 1

Moreau, G., Achim, A., & Pothier, D. (2020). Growth and survival dynamics of partially cut northern hardwood stands as affected by precut competition and spatial distribution of residual trees. *Forestry: An International Journal of Forest Research.* 93(1), 96-106 (*Soumis le 1 mars 2019, accepté le 26 juillet 2019, publié en ligne le 11 octobre 2019)*

Chapitre 2

Moreau, G., Achim, A., & Pothier, D. (2019). A dendrochronological reconstruction of sugar maple growth and mortality dynamics in partially cut northern hardwood forests. *Forest ecology and management*, *437*, 17-26. (*Soumis le 12 novembre 2018, accepté le 16 janvier 2018, publié le 22 janvier 2019)*

Chapitre 3

Moreau, G., Achim, A., & Pothier, D. (2020). Relevance of stem and crown defects to estimate tree vigour in northern hardwood forests. *Forestry: An International Journal of Forest Research*. (*Soumis le 4 septembre 2019, accepté le 27 janvier 2020, publié en ligne le 5 mars 2020*)

Chapitre 4

Moreau, G., Achim, A., & Pothier, D. (2020). An accumulation of climatic stress events has led to years of reduced growth for sugar maple in southern Quebec, Canada. *Ecosphere. (Soumis le 31 janvier 2020, accepté le 14 avril 2020)*

Coauteurs des chapitres

La rédaction de cette thèse de doctorat a été supervisée par David Pothier, directeur de thèse, et Alexis Achim, codirecteur de thèse. Ils sont les coauteurs de tous les chapitres puisqu'ils ont supervisé les travaux de recherche et ont participé à la rédaction des articles scientifiques.

David Pothier : Département des sciences du bois et de la forêt, Université Laval, 2405 rue de la Terrasse, Québec, Québec, Canada. G1V 0A6. Courriel : David.Pothier@sbf.ulaval.ca

Alexis Achim : Département des sciences du bois et de la forêt, Université Laval, 2405 rue de la Terrasse, Québec, Québec, Canada. G1V 0A6. Courriel : alexis.achim@sbf.ulaval.ca

Introduction

Les forêts feuillues de l'Amérique du Nord couvrent de grandes superficies du sud-est du Canada au nord-est des États-Unis et se situent principalement à proximité de zones densément peuplées, de la région des Grand-Lacs jusqu'à l'océan Atlantique (Bailey 1983). La proximité des usines de transformation et des marchés, ainsi que la grande valeur des bois feuillus pour les secteurs de transformation primaire donnent une importance économique considérable à la forêt feuillue (MFFP 2017). Uniquement au Québec, entre 2011 et 2017, la consommation totale de feuillus durs par les secteurs du déroulage, du sciage, des panneaux, des pâtes et papiers et du bois de chauffage était en moyenne de 6 665 000 m^3/an (MFFP 2017).

Le régime de perturbations naturelles de ces forêts est dominé par des perturbations partielles du couvert forestier, dont l'intervalle de retour relativement rapide (50-200 ans) produit une mosaïque de peuplements caractérisés par des structures irrégulières et inéquiennes (Lorimer & Frelich 1994; Seymour et al. 2002; Raymond et al. 2009). On retrouve au sein de ces structures complexes les attributs de forêts matures, tels que plusieurs cohortes d'arbres provenant de différentes perturbations plus ou moins récentes, une grande variation de la taille et de l'âge des arbres, ainsi qu'une distribution spatiale hétérogène de ces derniers au sein des peuplements (Raymond et al. 2009). Bien que dominées par l'érable à sucre (*Acer saccharum* Marsh.), ces forêts sont composées de plusieurs espèces d'arbres dont les caractéristiques écologiques telles que la longévité, la tolérance à l'ombre et la vitesse de croissance varient entre elles (Lorimer & Frelich 1994; Seymour et al. 2002). Cette irrégularité dans la composition forestière et la structure des peuplements engendre une dynamique de croissance et de mortalité complexe, résultant d'une répartition hétérogène des ressources entre les individus de différentes espèces et de leur efficacité à utiliser ces ressources (Pothier 2019).

Pour reproduire les effets du régime de perturbations naturelles, les peuplements feuillus sont principalement exploités à l'aide de la coupe de jardinage qui vise à maintenir la structure irrégulière ou inéquienne du peuplement, à promouvoir la régénération des espèces désirées, à améliorer la vigueur générale du peuplement et à fournir un rendement soutenu en bois de haute qualité (Arbogast 1957; Majcen 1996; Nyland 1998; Raymond et al. 2009). À chaque cycle de récolte, environ un tiers des arbres est abattu, libérant ainsi les arbres résiduels de certains de leurs concurrents directs. Au Québec, la coupe de jardinage a pris de l'ampleur au début des années 1990, succédant à la coupe à diamètre limite qui est reconnue pour avoir diminué le potentiel de production du bois de qualité par la dégradation des peuplements résiduels et la prolifération d'espèces indésirables (Guillemette et al. 2008). Bien que la coupe de jardinage ait donné des résultats prometteurs après son application dans des blocs expérimentaux (plus grand accroissement net dans les peuplements traités que dans les témoins), les résultats provenant de son application dans un contexte industriel ont été beaucoup moins convaincants (Majcen 1996; Bédard & Brassard 2002). Ces derniers résultats ont fait ressortir une productivité environ 40 % plus faible que celle anticipée en raison d'un taux de mortalité deux fois plus élevé que celui observé dans les dispositifs expérimentaux (Bédard & Brassard 2002). Plus récemment, on a également constaté une grande variation de la mortalité et de l'accroissement des arbres entre les régions et les conditions de croissance (e.g. Forget et al. 2007; Nolet et al. 2007; Fortin et al. 2008; Hartmann et al. 2009; Guillemette et al. 2008; Martin et al. 2014). Ce constat soulève plusieurs questions sur les facteurs qui prédisposent certains arbres à réagir positivement ou négativement à une coupe de jardinage. Bien que des études aient documenté les causes potentielles de mortalité des arbres résiduels (e.g. Caspersen 2006; Martin et al. 2014), la compréhension et la quantification de l'effet de ces facteurs sur la structure et la dynamique de croissance des peuplements résiduels restent à préciser.

En général, la création d'ouvertures dans le couvert forestier stimule la croissance des arbres situés à leur proximité en raison d'une diminution de la compétition et de l'augmentation de la disponibilité des ressources (Nowacki & Abrams 1997; Black & Abrams 2003; Jones & Thomas 2004). La réaction de croissance en diamètre devrait augmenter proportionnellement au degré d'ouverture du couvert forestier (Jones & Thomas 2004). Cependant, l'ouverture du couvert forestier dans le cadre de coupes de jardinage mécanisées peut aussi produire une compaction des sols et ainsi causer des dommages aux racines primaires des arbres, ce qui limite l'absorption d'eau et de nutriments (Hartmann et al. 2009). Ces dommages peuvent compromettre le développement des racines dans les années suivant la coupe, provoquer un stress hydrique et créer des portes d'entrée pour différents pathogènes (Hartmann et al. 2009). En plus de la compaction des sols, les coupes mécanisées peuvent aussi causer différents dommages aux arbres résiduels, variant du bris et de la perte de branches jusqu'à de larges abrasions sur le tronc et les racines (Nyland 1998; Hartmann et al. 2009). Ces blessures créent des portes d'entrée pour les pathogènes qui dégradent et annellent partiellement les arbres, ce qui réduit la croissance diamétrale.

En conséquence, la réaction de croissance des arbres résiduels à la suite des coupes peut être diminuée et leur taux de mortalité peut augmenter (Caspersen 2006; Hartmann et al. 2009; Martin et al. 2014). L'effet simultané des impacts positifs et négatifs des coupes de jardinage mécanisées rend difficilement prévisible la réaction de croissance des arbres, ce qui peut expliquer la grande variabilité des résultats obtenus à ce jour (Hartmann et al. 2009).

Les études ayant tenté de déterminer les causes de mortalité à la suite d'une récolte partielle ont principalement utilisé une approche post-mortem dans laquelle une cause « probable » était déduite d'un examen des caractéristiques physiques des arbres morts (Nolet et al. 2007; Martin et al. 2014; Guillemette et al. 2017). Puisque la mortalité est un phénomène complexe qui est généralement le résultat cumulatif de plusieurs causes, c'est-à-dire des facteurs incitatifs et des facteurs contributifs (Manion 1981), cette approche post-mortem peut facilement confondre les causes et les effets, en plus de n'identifier qu'une cause de mortalité. Par exemple, lorsque le chablis est identifié comme cause de mortalité, il est possible que l'arbre soit en réalité mort sur pied pour ensuite être renversé par le vent. Pour préciser cette approche post-mortem, l'utilisation de séries de croissance interdatées pourrait permettre d'étudier rigoureusement les patrons de croissance précédant la mortalité, de manière à déterminer avec précision les années de déclin de croissance ainsi que l'année de la mort des arbres. En effet, les récents progrès des méthodes dendrochronologiques ont fourni des observations précises sur les réactions de croissance et de mortalité des arbres à la suite de perturbations naturelles (Bigler & Bugmann 2004; Cailleret et al. 2017). Ces études ont démontré que la majorité des événements de mortalité sont associés à une période de réduction de croissance sur plus de 20 ans précédant la mort des arbres, de sorte que de meilleures prévisions de la mortalité peuvent être obtenues en considérant les tendances de croissance radiale à long terme (Bigler & Bugmann 2004; Cailleret et al. 2017). Pourtant, à notre connaissance, les tendances de croissance radiale à long terme n'ont jamais ou très peu été prises en compte par les études portant sur la dynamique temporelle et les causes de mortalité induites par des coupes de jardinage dans les forêts composées de feuillus nordiques (Hartmann & Messier 2008).

Un autre facteur d'incertitude pouvant expliquer une partie de la variation des résultats obtenus à la suite de coupes de jardinage est l'utilisation de systèmes de classification de la vigueur des arbres qui n'ont, encore à ce jour, que partiellement été validés de manière empirique. Ces systèmes de classification visent à estimer la vigueur des arbres pour guider les opérations de martelage en se basant sur les caractéristiques du houppier (Schomaker 2007), de l'écorce (OMNR 2004), des dommages pathologiques et mécaniques (OMNR 2004; Boulet 2007; Pelletier et al. 2016) et de la morphologie de l'arbre (Pelletier et al. 2016). La vigueur d'un arbre a été définie à la fois comme étant son potentiel de croissance (OMNR 2004; Pelletier et al. 2016) ou sa probabilité de mortalité durant la prochaine rotation de coupe (Boulet 2007).

Au Québec, le système de classification de la vigueur des arbres lors du martelage (Boulet 2007) a été mis au point en réaction à la croissance décevante des peuplements traités par des coupes de jardinage dans un contexte industriel (Bédard & Brassard 2002). Ce système de classification estime la vigueur des arbres pour ainsi former quatre priorités de récolte (M-S-C-R) lors du martelage précédant une coupe de jardinage (Boulet 2007).

i. **Mourir**: Tige très défectueuse, qui risque de se renverser, de se rompre ou de mourir sur pied avant la prochaine rotation (Priorité de récolte 1).

ii. **Survie** : Tige défectueuse en perdition dont le volume de bois risque de diminuer en raison de la carie, mais dont la survie n'est pas menacée avant la prochaine rotation (Priorité de récolte 2).

iii. **Conserver** : Tige peu défectueuse à conserver, dont le volume de bois marchand ne risque pas de se dégrader avant la prochaine rotation (Priorité de récolte 3).

iv. **Réserve** : Tige saine en réserve qui constitue le capital forestier de premier choix (Priorité de récolte 4).

Bien que ce système de classification soit appuyé par des observations préliminaires (Boulet & Landry 2015), certaines études empiriques ont conclu que la capacité du système à prévoir le risque de mortalité des arbres est globalement faible (Hartmann et al. 2008; Guillemette et al. 2015). En général, ces études ont mis en évidence que les arbres avec la plus haute priorité de récolte (M) ont bel et bien un risque de mortalité plus élevé que ceux des autres classes. Toutefois, les différences de risque de mortalité entre les autres classes de priorité de récolte (S, C et R) ne se sont pas statistiquement distinguées. Récemment, Moreau et al. (2018a) ont utilisé un indice de vigueur quantitatif fondé sur la production annuelle de bois par unité de surface foliaire, aussi appelé indice d'efficacité de croissance (Waring et al. 1980), pour valider le système de classification MSCR. Or, l'indice d'efficacité de croissance n’a pu être significativement relié aux classes de priorité de récolte MSCR (Moreau et al. 2018a). Cette absence de lien significatif indique que le système de classification par priorité de récolte est peu relié à la vigueur réelle des arbres et qu’il est donc peu probable que son application soit accompagnée par des gains importants de vigueur pour les peuplements traités par coupe de jardinage.

Par leur nature empirique, les études traditionnelles en sylviculture ont été construites de manière à observer les tendances de croissance à la suite de pratiques passées, afin d’ajuster les stratégies d’aménagement actuelles et futures. Cette approche fait le postulat que les conditions de croissance passées reflèteront avec précision le potentiel de croissance futur. Or, dans les dernières décennies, l’augmentation soutenue de la température annuelle ainsi que la sévérité et la fréquence des stress climatiques ont eu un impact direct sur la dynamique des écosystèmes forestiers (Bell et al. 2004; Iverson et al. 2008; Allen et al. 2010; Dai 2013; Zhang et al. 2018). En Amérique du Nord, on a observé un changement de composition forestière favorisant les espèces à croissance lente qui sont mieux adaptées aux stress climatiques, modifiant ainsi la dynamique de croissance et la captation de carbone (Zhang et al. 2018). Ces observations mettent en évidence certaines limites du postulat proposant que les conditions de croissance passées sont garantes de celles du futur, et pourraient expliquer une partie de la variation des résultats obtenus à la suite de coupes de jardinage. Étant donné qu’une augmentation des stress climatiques est attendue dans les prochaines années, les changements appréhendés de dynamique de croissance ajoute de l’incertitude au maintien de la productivité forestière à long terme (Zhang et al. 2018; SCAF 2018) et à l’efficacité de l’application des traitements sylvicoles. Afin d’anticiper l’effet des changements climatiques sur les écosystèmes forestiers et, ultimement, mettre en œuvre des mesures adaptatives à l’aménagement actuel, il apparaît impératif de raffiner notre compréhension de la vulnérabilité des espèces feuillues aux différents stress climatiques (Allen et al. 2015; D’Amato et al. 2013; Nolet & Kneeshaw 2018). Malgré ce constat, à ce jour, nous connaissons mal les relations entre la croissance de nos espèces feuillues et les conditions climatiques (Tardif et al. 2001; Bishop et al. 2015). De plus, l’effet des différents stress climatiques sur la dynamique de croissance des forêts feuillues n’a encore jamais été inclus dans des modèles de prévision en Amérique du Nord.

Démarche méthodologique

L’objectif général de ce projet de recherche est d’améliorer les prévisions de la croissance et de la mortalité des arbres feuillus à partir d’une meilleure évaluation de leur potentiel de croissance sur pied et de leur sensibilité aux conditions climatiques. L’approche proposée par cette étude vise à améliorer l’évaluation visuelle des arbres pour refléter adéquatement leur potentiel de croissance en établissant des liens étroits entre leurs caractéristiques morphologiques, leur vigueur et leur sensibilité aux conditions climatiques. Les données utilisées pour l’ensemble de ce projet proviennent de 36 placettes échantillons permanentes (PEP) couvrant deux régions du sud du Québec, soit l’Estrie et la Beauce. Le projet de recherche est divisé en quatre chapitres distincts.

Le premier chapitre de la thèse a comme objectifs spécifiques i) d’évaluer l’impact de la distribution spatiale des arbres produite par le passage de la machinerie durant la coupe de jardinage sur la réaction de croissance et le taux de survie et des arbres résiduels et ii) d’évaluer l’importance de l’environnement compétitif avant et après la coupe sur la réaction de croissance et le taux de survie. Un modèle de prévision de la probabilité de récolte, de l’accroissement et de la mortalité des arbres en fonction de leur répartition spatiale au moment du traitement a été mis au point. Un total de 23 PEP a été échantillonné afin de reconstruire l’environnement de croissance de 455 arbres, dont 97 ont été récoltés et 68 sont morts suivant l’application du traitement.

L’objectif du second chapitre est d’évaluer l’effet des tendances de croissance antérieures sur le taux de mortalité et la réaction de croissance des arbres à la suite d’une coupe de jardinage. Plus précisément, ce chapitre a testé les hypothèses de recherche suivantes : i) la mortalité post-récolte est généralement précédée par un déclin de croissance progressif durant les décennies précédant la coupe (> 20 ans), plutôt que par une chute marquée de la croissance suivant l’application du traitement, et ii) une croissance radiale limitée durant une longue période avant la coupe (> 20 ans) va diminuer la probabilité d’avoir une hausse de croissance à la suite d’une coupe de jardinage. L’étude des tendances de croissance antérieures a été faite à l’aide de 112 séries de croissance inter-datées réalisées sur des érables à sucre (86 vivants et 26 morts) et couvrant une période de 65 ans, de manière à caractériser les patrons de croissance pré-récolte et à identifier les caractéristiques morphologiques (i.e. taille, vigueur) qui prédisposent certains arbres à avoir une hausse de croissance ou à mourir à la suite d’une coupe de jardinage.

Le troisième chapitre de la thèse vise à identifier les défauts apparents du tronc et du houppier des arbres qui sont significativement reliés à leur vigueur actuelle. Pour ce faire, nous avons réalisé une analyse des relations entre deux indices de vigueur reconnus et une gamme complète de caractéristiques du tronc et du houppier répertoriés dans trois systèmes de classification de la vigueur utilisés en Amérique du Nord. Un total de 336 érables à sucre et 84 bouleaux jaunes ont été échantillonnés. Les analyses statistiques ont été faites avec parcimonie, de manière à identifier l'assemblage de défauts le plus simple pour estimer la vigueur actuelle des arbres.

L'objectif du quatrième chapitre est de quantifier l'effet des conditions climatiques sur la dynamique de croissance de l'érable à sucre. Ainsi, ce chapitre vise à i) quantifier de manière empirique l'effet de deux types d'événements climatiques sévères (sécheresse et gel-dégel) sur la dynamique de croissance de l'érable à sucre, et ii) comparer l'effet de ces événements climatiques sévères à celui des tendances climatiques mensuelles. Une chronologie de référence a été construite pour chacune des deux régions couvertes par notre jeu de données (l'Estrie et la Beauce) et l'effet du climat sur la croissance a été analysé sur une période de plus de 50 ans.

Les résultats de ce projet de recherche devraient permettre de mieux comprendre la dynamique de croissance des arbres à la suite d'une coupe de jardinage mécanisée et ainsi améliorer l'évaluation visuelle des arbres de façon à refléter adéquatement leur potentiel de croissance au moment de la récolte. Cette approche devrait aider à maximiser la production de bois de qualité en forêt feuillue en conservant les forts contributeurs à la croissance globale des peuplements. De plus, nos résultats devraient permettre de mieux comprendre l'impact des conditions climatiques sur la dynamique de croissance de l'érable à sucre, une étape essentielle pour intégrer l'effet potentiel des changements climatiques sur la croissance à long terme de nos peuplements feuillus.

1. Chapitre 1

Growth and survival dynamics of partially cut northern hardwood stands as affected by precut competition and spatial distribution of residual trees

1.1. Abstract

Modelling growth and survival dynamics after partial harvesting must take account of the heterogeneous spatial pattern of residual trees that results from the presence of machinery trails. We used data from 23 permanent sample plots in northern hardwood stands to reconstruct the growing environment of individual trees before and after partial harvesting. We modelled harvest probability, growth response and survival probability using a complementary set of explanatory variables that was assembled to reflect the spatial distribution of trees and skid trails prior to and after harvest. Results showed that the distribution of harvested trees was concentrated in skid trails and in their close vicinity. However, this spatial pattern had no significant effect on either the post-cut basal area increment (BAI) or the survival of residual trees. BAI and survival of individual trees were both mostly related to the competitive environment prior to harvest, while post-cut changes in competitive environment had only a marginal effect on growth and survival dynamics. We conclude that selection cuts did not substantially increase the growth and survival of residual trees, likely because tree removal was mostly concentrated near skid trails, where the negative effects of machinery access were highest.

1.2. Résumé

Un total de 23 placettes échantillons permanentes ont été échantillonnées afin de reconstruire l’environnement de croissance avant et après l’application d’une coupe de jardinage. La probabilité de récolte, la réaction de croissance et la probabilité de survie ont été modélisées en utilisant un assemblage de variables reflétant la distribution spatiale des arbres et des sentiers de débardage. Nos résultats ont montré que le prélèvement des arbres a été concentré à l’intérieur et aux abords des sentiers de débardage. La croissance et la survie des arbres résiduels étaient principalement liées à l’environnement compétitif avant la coupe. À l’inverse, la diminution de l’environnement compétitif induit par la coupe n'avait qu'un effet marginal sur la croissance et la survie des arbres résiduels. Nous concluons que les coupes de jardinage n'ont pas augmenté la croissance et la survie des arbres en raison d’une récolte concentrée à l’intérieur et aux abords des sentiers de débardage.

1.3. Introduction

The natural disturbance regime in northern hardwood forests is driven by small canopy gaps created by the death of one to several dominant trees (Lorimer & Frelich 1994). Natural senescence, wind, pathogens and insect herbivory are the main mortality agents whose average return interval of 50-200 years generally results in multi-cohort, uneven-aged stands dominated by shade-tolerant species (Seymour et al. 2002). To mimic this natural mortality regime, northern hardwood stands are mainly managed using selection cuts. In recent decades, these have been applied as part of the 'selection' silvicultural system that aims to maintain the stand's uneven-aged structure, to promote the regeneration of desired species, to improve the overall stand vigour, and to provide a sustained yield of high-quality timber (Arbogast 1957; Majcen 1996; Nyland 1998). At each harvest cycle, about one third of the trees are removed and most residual trees should at least be partly released from direct competitors.

Several studies have been conducted to understand the factors that influence growth and mortality dynamics after such selection cuts. In general, gap creation stimulates the radial growth of residual trees by reducing competition and improving resource availability (Nowacki & Abrams 1997; Jones & Thomas 2004; Dyer et al. 2010). However, gaps created by mechanized selection cuts may also be associated with soil disturbance and compaction, in addition to damage to the roots and trunk of residual trees (Grigal 2000; Seablom & Reed 2005; Thorpe et al. 2008). Such effects may increase mortality and mitigate the growth response of surviving trees following selection cuts (Caspersen 2006; Thorpe et al. 2008; Hartmann et al. 2009; Martin et al. 2014). The concurrent positive and negative influences of harvest gaps yield uncertainty regarding the net stand-level response to selection cuts.

Because all trees are harvested in trails used for the machinery access, residual trees are typically clustered, which in turn leads to an uneven distribution of resources among them (Boivin-Dompierre et al. 2017). Consequently, tree growth responses are also likely to follow a spatial pattern that depends on trail width and spacing (e.g. Hartmann et al. 2009; Boivin-Dompierre et al. 2017). Information about the spatial distribution of trees and skid trails within a stand would thus be useful to help predict the growth of residual trees after selection cutting. In northern hardwood forests, only a few studies have used the spatial distribution of trees relative to skid trails as predictors of the tree growth response after selection cuts, and they were all conducted in the same study site (e.g. Hartmann et al. 2008; Hartmann &

Messier 2008; Hartmann et al. 2009). While Hartmann et al. (2008) and Hartmann & Messier (2008) found no relationship between the growth response of sugar maple trees and the distance to a skid trail, Hartmann et al. (2009) showed a negative impact of the machinery passage on tree growth as far as 12 m from skid trails. In contrast, after mechanized group-selection openings whose sizes varied from 50 to 400 m^2, Jones and Thomas (2004) and Dyer et al. (2010) found higher annual diameter increment for trees located at the gap edge. Because the negative impact of harvesting operations mainly influences trees close to skid trails, post-cut mortality is also likely to follow a similar spatial pattern in years following partial harvest (Thorpe et al. 2008). In a boreal forest, the proximity to a skid trail was found to have a major impact on the cumulative mortality of residual black spruce (*Picea mariana* (Mill.) B.S.P.) trees during the first decade after harvest (Thorpe et al. 2008). However, such spatial mortality dynamics have yet to be quantified in northern hardwood forests.

In addition to the spatial pattern produced by mechanized partial harvesting, the growth response of trees could be affected by other factors such as stem size (Jones & Thomas 2004; Jones et al. 2009) and their social status within the canopy prior to harvest (Latham & Tappeiner 2002; Hartmann et al. 2009; Dyer et al. 2010). Indeed, trees occupying a dominant canopy position prior to the cut were likely under less competitive pressure, and therefore growing faster, than subordinate trees. Consequently, a selection cut may not produce major changes in light availability for large, dominant trees, a fact that could limit their growth response (Dyer et al. 2010) and the effect on their survival probability. Conversely, trees that were subject to intense competition for light before selection cutting could respond markedly to the treatment due to the noticeable improvement in their competitive environment (Black & Abrams 2003). However, these growth trends among trees of different social status and competitive environment have rarely been considered, presumably because information about competition between trees before harvest is rarely available.

In this study, we used data from 23 permanent sample plots (PSP) that were established in different northern hardwood stands to reconstruct the growing environment of individual trees before and after selection cutting. Our main objective was to evaluate the effect of the spatial distribution of trees relative to skid trails at time of harvest on their post-cut growth and survival dynamics. To consolidate our analysis, we modelled harvest probability, growth response and survival probability using a complementary set of candidate explanatory variables. The specific objectives of the study were to: i) assess the impact of the spatial pattern produced by selection cuts on the tree growth response and post-cut survival and ii) evaluate the importance of the pre- and post-cut competitive environments on the growth response and survival of individual trees to selection cuts. Obtaining improved knowledge about growth and survival of trees and their spatial distribution patterns after mechanized selection cutting is of operational and ecological interest, and is key to the long-term sustainability of northern hardwood forests managed under the selection silvicultural system.

1.4. Material and methods

1.4.1. Sampling sites

The study area was located on private woodlots owned by Domtar Corporation in southern Quebec, Canada (45°31'-45°57'N, 71°23'-70°33'W) and encompasses both the eastern sugar maple-American basswood and the eastern sugar maple-yellow birch bioclimatic subdomains (Saucier et al. 2009). The first subdomain is characterized by mean annual temperatures between 4 and 5 °C and mean annual precipitation between 1000 and 1150 mm, with a growing season of 165 to 180 days. The second subdomain is characterized by mean annual temperatures between 2.5 and 4 °C and mean annual precipitation between 915 and 1100 mm, with a growing season of 145 to 165 days (Saucier et al. 2009). The topography of both subdomains is characterized by hills and slopes and the main surface deposits are shallow or deep tills (Grondin et al. 2007). The sampling sites were located in uneven-aged northern hardwood stands dominated by sugar maple *(Acer saccharum* Marsh.), followed by yellow birch (*Betula alleghaniensis* Britt.) and red maple (*Acer rubrum* L.), with minor components of American beech (*Fagus grandifolia* Ehrh.), black cherry (*Prunus serotina* Ehrh.), basswood (*Tilia americana* L.), hornbeam (*Ostrya virginiana* (Mill.) K. Koch), balsam fir (*Abies balsamea* (L.) Mill.), red spruce (*Picea rubens* Sargent) and Eastern hemlock (*Tsuga canadensis* (L.) Carr.).

1.4.2. Sample plots and treatments

From 1998 to 2003, 23 circular permanent sample plots (PSPs) of 400 m^2 were established randomly in stands representative of the regional site conditions, at least one year prior to the application of selection cuts. Within each of these PSPs, all trees with a diameter at breast height (DBH) > 9.0 cm were tagged. The selection cuts aimed at harvesting trees uniformly in a single operation and were conducted between 2002 and 2007. The long-term disturbance history of stands was unknown but there were no signs of cuts from previous years such as old stumps. Before cutting, stands were characterized by a mean density of

523 trees/ha, a mean basal area of 26 m^2/ha, and a mean DBH of 26 cm (Table 1). The mean harvest rate in PSPs was 30 % (± 15 %) of the basal area. Trees were removed using feller-buncher harvesters working with a forwarder, a cable skidder or a grapple skidder. Skidding trails had a maximum width of 4 m and were spaced about 20 m apart from edge to edge. The selection cuts aimed to remove senescent trees and trees of low vigour from all species and DBH classes while maintaining an uneven-aged structure in the residual stand. Tree marking was conducted in eight of the 23 stands before harvest, in which cases it was applied according to a classification developed by Majcen et al. (1990). This classification assigns trees a survival probability until the next scheduled harvest based on pathological symptoms, mechanical damage and other visible defects. Then, based on a visual inspection of the stem, the classification system also assigns a quality grade that segregate trees with sawlog potential from trees with only pulpwood potential. This classification was referred to as the 'VQ' system in Delisle-Boulianne et al. (2014). In the 15 remaining stands, the selection of stems to be harvested was done by experienced harvester operators.

Table 1.1 Pre-harvest descriptive characteristics of trees (mean ± standard deviation, minimum - maximum) according to species group from the 23 permanent sample plots for stems with DBH > 9 cm. Pre-harvest values are estimated based on previous survey and diameter measurement of stumps and dead trees. BA is the basal area.

Species group	DBH (cm)	BA (m^2/ha)	Tree density (stems/ha)
Sugar maple	25 ± 11 (9 – 76)	16 ± 10 (1 - 31)	224 ± 113 (15 – 365)
Yellow birch	18 ± 8 (9 – 43)	4 ± 4 (0 – 13)	71 ± 83 (0 – 281)
Red maple	23 ± 9 (10 - 43)	2 ± 5 (0 – 5)	31 ± 64 (0 – 233)
Other Hardwoods	27 ± 11 (10 – 52)	3 ± 3 (0 – 11)	35 ± 29 (0 – 105)
Softwoods	18 ± 6 (9 – 29)	1 ± 1 (0 – 5)	14 ± 25 (0 - 86)
Total in all PSP	23 ± 10 (9 – 76)	26 ± 7 (15 - 38)	513 ± 149 (300 – 875)

1.4.3. Data collection

The PSPs were inventoried periodically at a mean interval of five years with an additional survey being systematically conducted during the year that immediately followed the application of the selection cuts. At each survey, the species and DBH of all trees with a DBH > 9.0 cm were recorded. During the summer of 2016, we collected additional information in all 23 plots to reconstruct the pre- and post-harvest competitive environments of all trees within each PSP. To do so, we georeferenced the position of all trees that 1) were alive both at the time of the selection cuts and at the last measurement in 2016, 2) had died after the selection cut, and 3) were harvested (based on the location of their stump). To be able to quantify the competitive environment of trees at the edge of our PSPs, we also georeferenced live trees, dead trees and stumps within a 6-m strip around the perimeter of each plot. The Cartesian coordinates of each tree and stump were determined by measuring their distance (± 0.1 m) and azimuth relative to the plot centre using a hypsometer and a compass.

The same method was used to localize and map the skid trails that were closest to each plot. Skid trails were delimited based on a set of criteria proposed by Hartmann et al. (2009), i.e. i) the presence of openings in the forest canopy, ii) the presence of wounds at the base of trees, iii) the presence of ruts, iv) the presence of stumps, v) the absence of obstacles, and vi) the presence of saplings belonging to species that are usually associated with higher levels of light and soil disturbance. Only clearly identifiable trails were considered for further analysis. The GIS software ArcGIS 9.2 (Esri GIS and Mapping Software, Redlands, CA) was used to compute the distance of each tree to the closest skid trail section.

During the summer of 2016, we also remeasured the DBH (± 0.1 cm) of all trees with a DBH > 9.0 cm as well as the diameter of each stump at a height of 30 cm above the ground (DSH). To estimate the DBH of trees that were harvested during selection cutting operations, we developed relationships between DSH and DBH using measurements made on 384 trees of all species and randomly selected from four DBH classes (9.0-19.0, 19.1-29.0, 29.1-39.0, and ≥ 39.1). Finally, the radial growth history was assessed from increment cores sampled on all live trees at a height of 1 m above ground and oriented towards the plot centre. The sample cores were glued to wooden blocks before they were air dried and gradually sanded to allow a clear identification of the latewood boundaries. Annual rings were then measured for a period of 10 years before and after selection cut with a Velmex micrometer (± 0.002 mm).

1.4.4. Competition index

The level of competition around each tree was calculated using the distance-dependent competition index (CI) proposed by Hegyi (1974):

$$CI = \Sigma_{i=1}^{n} \; d_i/(d \times dist_i) \qquad [1]$$

where d_i is the DBH (mm) of the i^{th} neighbour tree located at a distance of $dist_i$ (m) from the subject tree, and d is the DBH of the subject tree. All values were computed from the inventory conducted during the year that followed each selection cut. Estimates of DBH values immediately after cut for trees located in the 6-m buffer strip around each plot were produced to adjust the pre- and post-cut CI calculation in each plot. This was achieved using a linear model relating the DBH measured immediately after cut (DBH_0) and that measured in 2016 (DBH_1) for the sample trees located within the plots. The prediction equation (R^2 = 0.93) was:

$$DBH_0 = 0.91DBH_1 - 1.42T + 2.22 \qquad [2]$$

where T is the number of years between the application of the selection cut and 2016. If the estimated DBH of trees that were located in the 6-m strip around each plot was lower than 9 cm at the time of the cut, this entry was simply removed from the dataset that was used to calculate CI. To determine the radius to calculate CI (from 2 to 6 m) that was best related to tree growth, we used a mixed-effects linear model with a plot-level random effect. Based on the Akaike's information criterion (AIC), the mixed-effect model that best explained growth included the competition index that was computed over a 6-m radius. This radius was thus used in all subsequent analyses. To estimate the level of competition around each tree before harvest, we used the same method but also included in the calculations all trees that had died since the selection cut, including all harvested trees. For stumps located within the PSP, the DBH at the time of cutting (DBH_0) was estimated by Eq. 2 using the last DBH measurement before cutting (DBH_1) and the number of years between the last survey and the year of cutting (T).

In addition to the competition index calculated before (CI_{bc}) and after (CI_{ac}) cutting, two additional measures of competition were developed for further analyses. The release index

(*RI*) was firstly defined as the difference between CI_{bc} and CI_{ac}, and secondly the relative release index (*RRI*) was defined as input variables:

$$RRI = (CI_{bc} - CI_{ac})/CI_{bc} \qquad [3]$$

1.4.5. Modelling harvest probability

The modelling process was performed using 455 sample trees of which 97 were harvested at the time of the selection cuts, 68 had died since their application, and 290 remained alive between selection cuts and 2016. Harvest probability was modelled at the tree level using a mixed effects logistic regression with a plot-level random effect. Only trees harvested outside skid trails were included in this model because the harvest of these trees is independent of the obligatory passage of the machinery, and results solely from the choice of the tree marker and/or the operator. Moreover, because the trees harvested in the skid trails would have been assigned a null distance, the inclusion of these trees in the model would have clearly led to the conclusion that harvesting was clumped. The candidate explanatory variables were the DBH at time of harvest, CI_{bc}, the distance of trees to the nearest skid trail section, and tree species. Some of the species were poorly represented and so could not be individually taken into account in the model. Consequently, we used the following species groups: i) sugar maple (n = 263), ii) yellow birch (n = 102), iii) red maple (n = 46), iv) softwoods (balsam fir, red spruce, black spruce and Eastern hemlock, n = 19), and v) other hardwoods (American beech, black cherry, basswood and hornbeam, n = 42). The type of treatment (with or without tree marking) and its interaction with the other candidate variables were also included in the model.

1.4.6. Modelling the radial growth response

The radial growth response of individual trees to selection cuts was expressed through BAI_{10} (dm^2 yr^{-1}), and was also statistically modelled using a mixed-effects linear model with a plot-level random effect. In addition to the four competition indices described above, the distance to the nearest skid trail and the species group (five levels) were submitted to the models as candidate explanatory variables. The level of correlation between CI_{bc} and CI_{ac} prevented their use in the same model. Also, to rigorously evaluate the importance of the pre-cut competitive environment on the tree growth response, we did not include tree DBH as a candidate variable in the analysis because of its strong correlation with CI_{bc} (r = -0.57). A square-root transformation was applied to BAI_{10} to produce a normal distribution of the dependent variable.

1.4.7. Modelling survival probability

The occurrence of mortality events after selection cutting was deduced using the periodic PSP surveys. At each survey, all dead trees were identified although the exact time of death since cutting could only be approximated. Several methods were developed to consider such interval-censored data using survival functions (Cox and Oakes 1984). These functions make it possible to treat a mortality event as a binomial variable that takes a value of 1 if a tree died and a value of 0 if a tree survived over a given time interval (e.g. Fortin et al. 2008; Guillemette et al. 2008). Survival probability was modelled at the tree level using the Cox proportional hazards model with the plot included as a frailty random term. This model describes the probability of an event or its hazard (the mortality of the tree) if the subject survived up to that particular time point (the next PSP survey). We also included the following candidate explanatory variables in the model: the four competition indices described above (i.e. CI_{bc}, CI_{ac}, *RI*, and *RRI*), the distance to the nearest skid trail section and the species group. Once again, we did not include tree DBH in the analysis because of its strong correlation with CI_{bc}.

1.4.8. Model selection

To determine the best prediction models, all candidate variables were included successively in each prediction model while always avoiding the inclusion of highly correlated predictors. The resulting models were systematically compared to an intercept-only model (null model). The selection of the best growth, survival and harvest models was based on AIC value and AIC weight. If no model was clearly better (i.e., with an AIC weight over 90 %), a model averaging procedure was performed to compute unconditional 95 % confidence intervals for parameters of interest (Mazerolle 2006). Variable parameters with confidence intervals excluding zero were considered as good predictors (Mazerolle 2006). The delta AIC, the marginal and the conditional coefficient of determination (R^2) were also computed, but used only to help describe the models. In the case of the survival model, we computed the pseudo-R^2 related to the Cox survival analysis, which was based on the improvement in likelihood between the fixed fitted model and a model without predictor variables (null model) (see Therneau & Lumley 2014). Multiple comparisons were made on species groups when this variable was significant in the models. Preliminary analyses indicated that there was a logarithmic relationship between tree growth response and the variables CI_{bc} and CI_{ac}. Consequently, a log transformation was applied to these variables to keep a linear relationship, facilitate model fitting and meet the regression model assumptions. All statistical analyses were performed in the R statistical programming environment (Version 3.5.1, R Core Team, 2018). We used the *lme* function of the *nlme* package (Pinheiro et al. 2017) to develop our linear mixed effects models. The *coxph* function of the *survival* package (Therneau & Lumley 2014) was used for the Cox proportional hazards model while the *glmer* function of the *lme4* package (Bates et al. 2015) was used for the mixed effects logistic regression. Model selection based on AIC and multi-model inferences were performed using the AICcmodavg package (Mazerolle, 2017). Multiple comparisons were performed using the *pairwise-survdiff* function of the *survival* package (cox proportional hazards models) and the *glht* function of the *multcomp* package (Hothorn et al. 2019). To avoid multi-collinearity, the variance inflation factor (VIF) was calculated between candidate variables (with VIF < 10 as the threshold to exclude a variable from the model) using *vif* function of the *car* package (Zuur et al. 2010). In the case of mixed models, we tested the variance homogeneity, the normality of residuals, the presence of outliers and the over-dispersion to ensure that regression assumptions were met. Finally, the proportional hazard assumption was tested using the *cox.zh* function of the *survival* package to ensure that regression assumptions were met for the cox proportional hazards models.

1.5. Results

1.5.1. Harvest probability

The logistic model used to predict harvest probability included 472 trees among which 97 were harvested and 375 were left standing. The DBH ($p < 0.0001$), CI_{bc} ($p = 0.003$), species group ($p= 0.007$) and the distance to the nearest skid trail ($p = 0.012$) all had statistically significant effects on harvest probability. There were no significant effects of the treatment type or of any interactions among variables. The best model (AIC weight of 0.99) included only the DBH, the distance to the nearest skid trail and species group (Table 1.2, model 4). According to this model, the harvest probability was directly related to increasing DBH (Figure 1.1a) and with a decreasing distance to the nearest skid trail (Figure 1.1b). Multiple comparisons between species groups indicated that the harvest probability of sugar maple was significantly lower than that of other species (Figure 1.1ab). The difference in harvest probability between sugar maple and the other species groups was highest for trees close to skid trails and progressively decreased with increasing distance to the trail (Figure 1.1b). The harvest probability decreased faster for larger than smaller trees as the distance of the skid trail increased (Figure 1.1c).

Table 1.2 Model selection results for the five best regression models predicting the harvest probability in selection cuts. DIST is the distance to nearest skid trail, CI_{bc} is the competition index computed immediately before selection cutting, AIC is the Akaike Information Criteria, Δi is the delta AICc (difference in AIC with the best model), W_{ti} is the AIC weight, R^2_{MR} is the marginal coefficient of correlation and R^2_{CN} is the conditional coefficient of correlation. All models included an intercept among the fixed effects as well as a plot-level random intercept. Note that the competition index before cut (CI_{BC}) could not be included in models containing DBH because of the high collinearity between the two variables.

Model	Variables	AIC	Δi	Wti	R^2_{MR}	R^2_{CN}
5	**DBH + DIST + Species group**	**433.86**	**0.00**	**0.99**	**0.13**	**0.13**
4	DBH + DIST	443.38	9.52	0.01	0.09	0.10
3	DBH	447.19	13.33	0.00	0.07	0.09
2	CI_{bc} + DIST + Species group	466.06	32.20	0.00	0.07	0.08
1	CI_{bc} + Species group	466.79	32.93	0.00	0.06	0.07
0	Intercept only	479.86	46.00	0.00	-	-

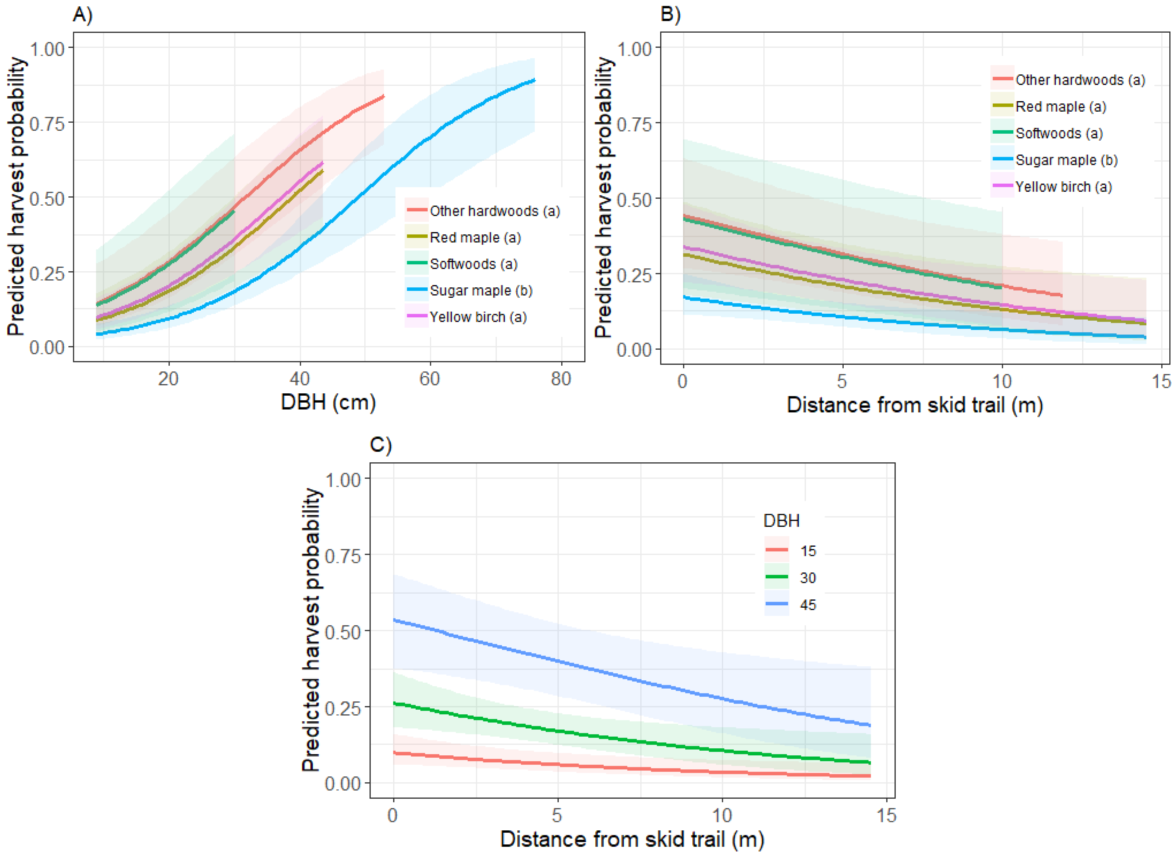

Figure 1.1 Effects of A) DBH and B) distance to nearest skid trail on mean predicted harvest probabilities for all species group (other covariates were kept constant at their mean values). (a) and (b) indicated groups with significantly different harvest probability based on the multiple comparison analysis. C) Mean predicted harvest probabilities of DBH classes as

function of distance to nearest skid trail. Confidence intervals predictions (shaded area) were calculated with α = 0.05

1.5.2. *Growth response*

The predictor variables that were significantly related to the tree growth response to selection cutting were CI_{bc} (*p* < 0.001) and CI_{ac} (*p* < 0.001). There was a marginally significant effect of *RRI* (*p* = 0.054), while the distance to the nearest skid trail (*p* = 0.50), the species group (*p* = 0.45) and the release index (*p* = 0.24) had clear non significant effects. The best model included CI_{bc} and *RRI* as predictors (Table 1.3, model 5) with an AIC weight of 0.60 and a conditional R^2 of 0.34. The addition of the *RRI* to the best model increased its parsimony but had only week effect on the R^2. Multi-model inferences indicated that the unconditional confidence intervals of only one parameter (CI_{bc}) excluded zero (Table 1.4). This result indicates that although *RRI* was part of the model with the lowest AIC, this variable did not contribute much to explain the variation in sugar maple growth. According to model 4, the tree growth response increased with decreasing competition before the cut (Fig. 1.2). An examination of the RRI values showed that 42 % of the trees in the database did not experience a release (RI and RRI value of 0), which implies that no change in competitive environment occurred in a 6-m radius after harvest.

Table 1.3 Model selection results for the five best regression models predicting the basal area growth response of trees during a 10-year period following selection cuts. BAI_{10} is the mean annual basal area increment for the 10 years prior to cutting, CI_{ac} is the competition index computed immediately after selection cutting, CI_{bc} is the competition index computed immediately before selection cutting, DIST is the distance to nearest skid trail, RRI is the relative release index and RI is the release index. AIC is the Akaike Information Criteria, Δi is the delta AIC (difference in AIC with the best model), Wti is the AIC weight, R^2_{MR} is the marginal coefficient of correlation and R^2_{CN} is the conditional coefficient of correlation. All models included an intercept among the fixed effects as well as a plot-level random intercept.

Model	Variables	AIC	Δ_i	Wt_i	R^2_{MR}	R^2_{CN}
5	**ln (CI_{bc}) + RRI**	**198.71**	**0.00**	**0.37**	**0.27**	**0.34**
4	ln (CI_{bc})	200.34	1.63	0.16	0.26	0.33
3	ln (CI_{bc}) + RI	200.45	1.74	0.16	0.27	0.33
2	ln (CI_{bc}) + RI + DIST	200.62	1.91	0.14	0.27	0.24
1	ln (CI_{ac}) + RRI	202.22	3.51	0.06	0.26	0.32
0	Intercept only	284.05	85.35	0.03	-	-

Table 1.4 Model-averaged parameter estimates and their 95 % confidence interval (CI) computed for the basal area increment and the survivals models. Parameter estimates in bold correspond to terms for which CI excluded 0. Note that the intercept term code for species group is yellow birch. Only the terms from the five best models are presented. CI_{ac} is the competition index computed immediately after selection cutting, CI_{bc} is the competition index computed immediately before selection cutting, RRI is the relative release index, RI is the release index and DIST is the distance to nearest skid trail.

Models predicting basal area increment			
Term	Estimate	CI lower	CI upper
$\boldsymbol{CI_{bc}}$	**-0.24**	**-0.45**	**-0.04**
$\boldsymbol{CI_{ac}}$	-0.04	-0.22	0.15
RRI	0.10	-0.24	0.44
RI	0.01	-0.05	0.06
DIST	0.00	-0.01	0.01
Models predicting tree survival			
Term	Estimate	CI lower	CI upper
$\boldsymbol{CI_{bc}}$	**0.22**	**0.14**	**0.31**
$\boldsymbol{CI_{ac}}$	**0.23**	**0.15**	**0.32**
RRI	-1.20	-2.75	0.36
DIST	-0.05	-0.14	0.34
RI	-0.20	-0.59	0.19
Species group			
Sugar maple	**-1.39**	**-1.96**	**-0.81**
Other hardwoods	0.04	-0.82	0.89
Red maple	-0.86	-1.74	0.07
Softwoods	-0.56	-1.62	0.50

1.5.3. Post-cut survival model

Independent variables significantly related to the probability of tree survival after selection cutting included CI_{bc} ($p < 0.001$), CI_{ac} ($p < 0.001$) and species group ($p < 0.001$). The *RRI* also had a marginally significant effect on this variable ($p = 0.071$). The best model with an AIC weight of 0.36 included CI_{bc}, RRI and the species group (model 5, Table 1.5), but three other models were plausible with $\Delta_i < 2$ (Table 1.5). Multi-model inferences indicated that the unconditional confidence intervals of the parameters associated with CI_{bc} and species group excluded zero, but not the other variables (Table 1.4). Consequently, *RRI* cannot be considered as a good predictor of post-cut tree survival. Tree survival probability decreased with increasing CI_{bc} (Fig. 1.3a). Multiple comparisons between species groups showed that the mean survival probability in years following selection cutting decreased faster for yellow birch, other hardwoods and softwoods than for sugar and red maples (Fig. 1.3b).

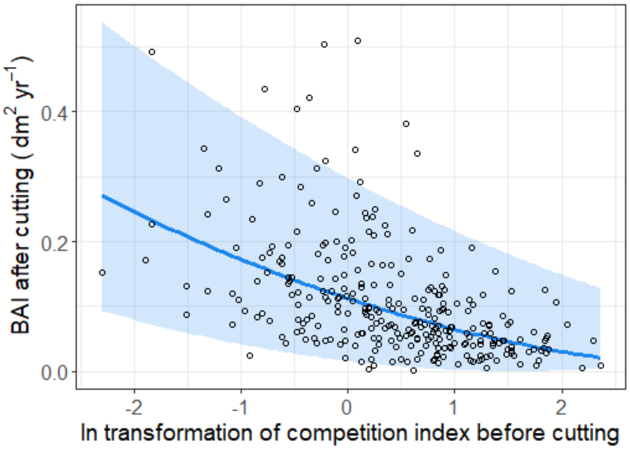

Figure 1.2 Mean predicted annual basal area increment during the 10-year after cutting (BAI_{10}) as a function of the ln transformation of the competition index before cutting ln(CI_{bc}). Confidence intervals of BAI_{10} predictions (shaded area) were calculated with α = 0.05.

Table 1.5 Model selection results for the five best regression models predicting the probability of tree survival following selection cutting. CI_{ac} is the competition index computed immediately after selection cutting , CI_{bc} is the competition index computed immediately before selection cutting, RRI is the relative release index, RI is the release index, DIST is the distance to nearest skid trail, AIC is the Akaike Information Criteria, Δi is the delta AIC (difference in AIC with the best model), Wti is the AIC weight and R2 is the coefficient of determination adapted for survival analysis. All models included an intercept among the fixed effects as well as a plot-level random intercept

Model	Variables	AIC	Δ_i	Wt_i	R^2
5	**CI_{bc} + RRI + Species group**	**724.04**	**0.00**	**0.32**	**0.14**
4	CI_{bc} + RRI + Species group + DIST	724.51	0.47	0.26	0.13
3	CI_{ac}+ RRI + Species group	725.41	1.38	0.16	0.14
2	CI_{ac}+ RRI + Species group + DIST	725.92	1.88	0.13	0.13
1	CI_{bc} + RI + Species group + DIST	727.36	3.32	0.06	0.13
0	Intercept only	768.11	44.71	0.00	-

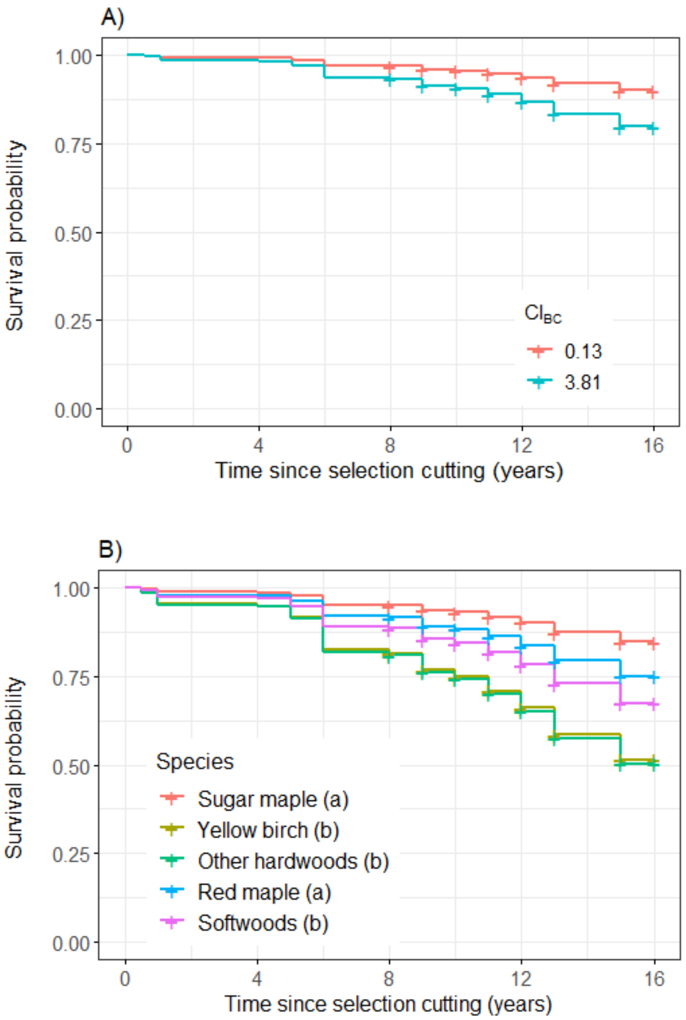

Figure 1.3 Effects of A) the competition index before cutting and B) species group on the mean predicted survival probabilities (in all simulations, other covariates were kept constant at their mean values). In A) 0.13 and 3.81 are the values of the 25th and 75th percentiles of the competition index before cutting, respectively. In B), (a) and (b) indicated groups with significantly different survival probability based on the multiple comparison analysis.

1.6. Discussion

1.6.1. Post-cut tree spatial pattern and growth response

Our results confirmed the existence of a strong spatial pattern among harvested trees, whereby gaps are created by skid trails along which tree removal is concentrated. The higher harvest probability near skid trails is consistent with observations of Genet & Pothier (2013) and Boivin-Dompierre et al. (2017), who studied spatial patterns of harvest after partial cutting in boreal forest stands. Practically, such a pattern can be explained by the greater ease with which trees near skid trails can be harvested (Genet & Pothier 2013). Because mechanical harvesters cannot reach larger trees without cutting smaller ones along their path (Delisle-Boulianne 2013), trees far from a skid trail that would otherwise be harvested may indeed be left standing to avoid the undesired harvest of vigorous trees. The additional harvest of such trees could consequently increase removal above the desired threshold for selection cuts, which is generally limited to a third of the initial basal area. As observed by Delisle-Boulianne et al. (2014) and Fortin (2014), the species group was also a good predictor of harvest probability. This can be explained by the fact that American beech, which made 63 % of the ''other hardwoods'' group, is highly vulnerable to the beech bark disease while balsam fir, which dominated the “softwoods” group, is susceptible to develop early stem decay. Therefore, both of these species are generally harvested intensively to increase the likelihood of maintaining high quality stands between two selection cuts (Pothier et al. 2013; Delisle-Boulianne et al. 2014). The higher harvest probability of yellow birch compared to sugar maple was less expected. It may be attributable to a high proportion of non-vigorous yellow birch trees, or to a marked preference of the wood processing industry for yellow birch during the harvest period.

The observed spatial pattern among harvested trees had no significant effect on the growth of residual trees, at least during our 10-year period of observation after selection cutting. Several factors may explain such a weak growth response to openings created by skid trails and nearby harvested trees. Even if trees near skid trails are more likely to experience a reduction in competition that may bear positive effects on growth rate (Jones & Thomas 2004; Dyer et al. 2010), machinery trafficking in these trails can also alter soil physical properties and cause damage to the root system of residual trees (Grigal 2000; Hartmann et al. 2008; 2009). As the majority of its fine roots are located in the organic layer and the upper 12 cm of the mineral soil (Fisk et al. 2004), sugar maple is vulnerable to soil disturbance and compaction. Accordingly, negative impacts on tree growth can occur in strips as large as 12 m along skid trails and for up to 10 years after selection cutting in northern hardwood stands (Hartmann et al. 2009). Growth, crown health, survival and seed production in sugar maple are strongly responsive to variation in soil conditions and nutrient availability (Huggett et al. 2007; Moore & Ouimet 2006; Moore & Ouimet 2010; Long et al. 2011). Hartmann et al. (2009) observed that the growth of northern hardwood species is mostly affected by competitive interactions involving resource depletion by neighbours of all sizes, which include light, but also the uptake of soil nutrients from smaller competitors. The alteration of soil physical properties and of root systems due to the passage of the machinery could thus have played an important role in limiting the benefits of canopy openings around skid trails.

Post-cut growth rate predictions were better when considering the pre-cut rather than the post-cut competitive environment. This indicates that the selection cuts monitored in this study actually had little effect on the post-cut growth rate of residual trees. As observed in previous studies, the post-cut competitive environment was also a highly significant predictor ($p<0.0001$) when taken in isolation (e.g. Hartmann et al. 2008; Boivin-Dompierre et al. 2017; Moreau et al. 2019). However, in this study, this effect was explainable by the fact that the pre- and post-cut competition indices were highly correlated ($r = 0.94$). The competitive environments of the studied stands were hardly altered by the selection cuts, as also evidenced by the fact that the competition around only 58 % of the residual trees was reduced (within a 6-m radius) following the selection cuts. This limited impact is attributable to the concentration of harvesting in and around skid trails. In turn, the concentration of released trees around skid trails, where the negative effects of the machinery passages on growth response are highest (Hartman et al. 2009), may explain the weak predictive ability of the relative release index. In North America, weak growth responses to partial harvests were also observed for several softwood species (Bose et al. 2018a). For example, in stands dominated by red spruce (*Picea rubens* Sarg.) and balsam fir (*Abies balsamea* (L.) Mill.), an increase in tree growth was observed only seven years after thinning (Bose et al. 2018a). The authors explained this lagged response by a period of preferred allocation to below-ground biomass in response to the stress induced by the higher wind regime in the thinned stands. In our case, the negative impact of machinery trafficking on the root system of released residual trees (Hartmann et al. 2009) and the need to increase the strength anchorage to face the higher wind loading (Bose et al. 2018a) may explain the low stem growth response of trees in the first 10 years after cutting.

1.6.2. Post-cut survival

Similarly to the growth response, the post-cut survival probability of residual trees was not significantly related to the distance to the nearest skid trail. This result is consistent with that of Moreau et al. (2019) who observed that only a small proportion of sugar maple tree mortality could be directly associated with the effects of harvesting operations. When it occurred, such post-cut mortality may especially affect trees that were already weakened before selection cutting (Hartmann & Messier 2008). The survival probability of yellow birch, other hardwoods and softwoods was observed to decrease faster over time than that of sugar and red maples. The low survival probability of yellow birch may be related to the lower shade tolerance of the species compared to sugar and red maples (Fortin et al. 2008; Martin et al. 2014). Even if tree DBH was not directly included in our survival model, the strong correlation between the competition index and DBH suggests that smaller yellow birch trees are more likely to suffer from competition for light (Fortin et al. 2008), thereby decreasing their survival probability. In addition, more small-size yellow birch trees were present in the stands than sugar and red maples (Table 1.1), which may also explain the lower mean survival probability of yellow birch. In the case of other hardwood species, beech bark disease, an important mortality agent of American beech (Gavin and Peart 1993), can explain their higher mortality rate, while that of coniferous species is likely related to the vulnerability of balsam fir to post-cut windthrow (Fortin et al. 2008; Martin et al. 2014).

Predictions of post-cut survival probability were significantly improved by considering the pre-cut instead of post-cut competitive environment. This result suggests that tree mortality is often caused by the competitive pressure on the subject tree before selection cutting, an effect that seems difficult to counteract, as suggested by the weak predictive ability of the relative release index. This increase in relative release index may be more important for suppressed trees whose vigour can deteriorate with an increasing duration of the suppression period (Baral et al. 2016). Suppressed sugar maple trees without vigour-affecting defects are able to respond positively to gap exposure, thereby increasing their survival probability (Moreau et al. 2019). However, for this to have an effect at the stand scale, the competitive environment of a sufficient proportion of residual trees would need to be altered by the selection cut (Bose et al. 2018b).

1.6.3. The importance of pre-harvest environment

Consideration of the pre-cut competitive environment is not commonly included in studies of the growth response and survival of trees to selection cutting (e.g. Kiernan et al. 2009; Hartmann et al. 2009; Martin et al. 2014; Boivin-Dompierre et al. 2017). Yet, ignoring it makes it impossible to segregate the effects of the pre-cut competition from that of the competition release induced by the harvest. More specifically for this study, because the post-cut competitive environment was a highly significant variable in both growth and survival models ($p < 0.0001$), ignoring pre-cut competition would have led us to conclude wrongly that our subject trees significantly responded to the silvicultural treatment. Coupling *a posteriori* reconstruction of the competition index before treatment with our relative release index showed an interesting potential for the purpose of quantifying the effect of partial harvesting on tree growth and survival. Even though the use of distance-dependent competition indices requires time-consuming measurements in the field, these efforts may be justified by better predictions of growth of post-cut residual trees, especially for shade-tolerant trees from the understory (Kuehne et al. 2019). Nevertheless, other factors than pre-cut environment can have an important impact on both post-cut growth and survival of trees. Tree size, social status and age, as well as the presence of stem defects indicative of low tree vigour have also been identified as important factors affecting post-cut growth (Fortin et al. 2008; Martin et al. 2014; Bose et al. 2018b; Moreau et al. 2019). For example, the post-cut growth release and mortality probability of sugar maple trees with vigour-affecting stem defects were, respectively, 6 times lower and 16 times higher than those of vigorous, defect-free sugar maple trees (Moreau et al. 2019).

1.6.4. Silvicultural implications

Results from this study provide evidence that mechanized selection cutting induces a systematic spatial competition pattern whereby canopy openings are concentrated in skid trails and along narrow strips on either sides, thus leaving large untreated areas in the stand. The marginal effect of the relative release index on tree growth and survival suggests that at least a small proportion of residual trees responded positively to the reduction of neighborhood competition induced by the selection cut over 10 years. This is in line with the higher annual diameter increment that was observed at the edge of mechanized group-selection openings in similar northern hardwood stands (Jones and Thomas 2004; Dyer et al. 2010). To expand the positive release effects on tree growth and survival to a larger proportion of the stand, the harvesting design could include secondary trails, in which only harvesters are allowed to circulate. These secondary trails could be used to harvest higher proportions of low-vigour trees that increase inter-tree competition but make little contribution to the overall stand productivity. Indeed, our results suggest that the harvest of slow-growing, low-vigour trees is more important than the improved growth of residual trees to increase the long-term productivity of northern hardwood stands. Secondary trails can be directly attached to primary trails or, alternatively, be located parallel between two primary trails as in the case of ghost trails (Boivin-Dompierre et al. 2017). By doing so, the proportion of harvested trees located far from primary trails, along which the negative effects of repeated machinery passages are highest (Brais & Camiré 1998; Williamson & Neilson 2000; Miller et al. 2004; Hartmann et al. 2009), should increase and thus lead to a positive growth response of residual trees.

The proportion of released trees after selection cutting could also be improved by increasing the harvest rate. For example, increasing the harvest rate from 30 to 50 % of the initial basal area would make the application of the selection cut resemble that of an irregular shelterwood (Raymond et al. 2009). Similarly to selection cutting, the irregular shelterwood system is considered as a suitable treatment to regenerate forests under a disturbance regime varying from low to intermediate intensities (Raymond et al. 2009). This system provides the flexibility required to locally increase the harvest of trees bearing vigour-affecting defects, and thus increase the number of released trees. However, a higher harvest rate could lead to deviations in stand structure and regeneration composition compared to selection cutting. Indeed, while selection cuts aim to maintain a balanced uneven-aged structure that favours shade-tolerant species, irregular shelterwoods lead to a larger variety of stand structures that can promote lesser shade-tolerant species (Raymond et al. 2009). Since some variation in stand structure is permitted according to the principles of ecosystem-based management (Seymour et al. 2002; Raymond et al. 2009), it appears relevant to consider the irregular shelterwood system in the management strategy of northern hardwood forests (Kern et al. 2017).

1.7. Conclusion

Results from this study highlight the importance of considering the pre-cut competitive environment and the degree of release induced by the removal of neighbourhood trees at time of harvest to understand both growth and survival dynamics after selection cutting. Ignoring the pre-harvest competition environment could lead to erroneous conclusions concerning the impact of the treatment on the growth response and survival of residual trees. An *a posteriori* reconstruction of the competition index before treatment to estimate a relative release index showed an interesting potential to this end. The positive impact of selection cuts on the growth and survival of residual trees over ten years was probably limited by the concentration of harvesting in and around skid trails, where the negative effects of machinery passage on the tree growth response are highest. Therefore, to increase the long-term net productivity of partially cut northern hardwood stands, we recommend 1) prioritizing the harvest of low-vigour trees, 2) using machinery with maximum boom reach and the implementation of secondary trails with limited machinery passage, and 3) considering irregular shelterwood cuts with higher harvest rates in the management strategy wherever appropriate.

Overall, the weak response of residual trees to selection cutting presented in this study was observed over a large area of southern Quebec that encompasses various site and stand conditions. Nevertheless, practical applications of our recommendations should be accompanied by further testing and validation of our results in other parts of the northern hardwood range. Future applications of selection cutting would benefit from a better understanding of the effects of the cutting pattern and selection of trees to harvest on the growth response of residual trees.

1.8. Acknowledgements

This research was funded by a Discovery Grant to David Pothier from the Natural Sciences and Engineering Research Council of Canada (NSERC), the Fonds de recherche du Québec – Nature et technologies (FRQNT), and Domtar Corporation. We would like to thank Eloïse Dupuis, Alexandre Morin-Bernard and Félix Poulin for their help with the fieldwork and to the staff from Domtar for their support on the project.

1.9. References

Arbogast, C. (1957). Marking guides for northern hardwoods under the selection system. USDA Forest Service, Paper No. 56, 20 pp.

Baral, S. K., Danyagri, G., Girouard, M., Hébert, F., & Pelletier, G. (2016). Effects of suppression history on growth response and stem quality of extant northern hardwoods following partial harvests. *Forest Ecology and Management*, 372, 236–246.

Bates, D., M. Maechler, B. Bolker, & S. Walker. (2015). lme4: linear mixed-effects models using Eigen and S4. R package version 1.1-8.

Black, B.A., & Abrams, M.D., (2003). Use of boundary-line growth patterns as a basis for dendroecological release criteria. *Ecological Applications*, 13, 1733–1749.

Boivin-Dompierre, S., Achim, A., & Pothier, D. (2017). Functional response of coniferous trees and stands to commercial thinning in eastern Canada. *Forest Ecology and Management*, 384, 6–16.

Bose, A. K., Weiskittel, A., Kuehne, C., Wagner, R. G., Turnblom, E., & Burkhart, H. E. (2018a). Does commercial thinning improve stand-level growth of the three most commercially important softwood forest types in North America?. *Forest Ecology and Management*, 409, 683-693.

Bose, A. K., Weiskittel, A., Kuehne, C., Wagner, R. G., Turnblom, E., & Burkhart, H. E. (2018b). Tree-level growth and survival following commercial thinning of four major softwood species in North America*. Forest ecology and management*, 427, 355-364.

Brais, S., & Camire, C. (1998). Soil compaction induced by careful logging in the claybelt region of northwestern Quebec (Canada). Canadian Journal of Soil Science, 78(1), 197-206.

Caspersen, J.P., 2006. Elevated mortality of residual trees following single-tree felling in northern hardwood forests. *Canadian Journal of Forest Research*, 36, 1255–1265.

Cox D.R., & Oakes D. 1984 Analysis of survival data, Chapman and Hall, London - New York, 201 S. *Biometrical Journal*, 29. 114-114.

Delisle-Boulianne S, (2013). Mise au point d’un modèle de prélèvement par tiges individuelles pour simuler les coupes de jardinage en Outaouais. Université Laval, Québec, Canada. Mémoire de maîtrise. 27 pp.

Delisle-Boulianne, S., Fortin, M., Achim, A., & Pothier, D. (2014). Modelling stem selection in northern hardwood stands: assessing the effects of tree vigour and spatial correlations using a copula approach. *Forestry: An International Journal of Forest Research*, *87*(5), 607-617.

Dyer, J.H., Gower S.T., Forrester, J.A., Lorimer, C.G., Mladenoff, D. J., & Burton, J.I. (2010). Effects of selective tree harvests on aboveground biomass and net primary productivity of a second-growth northern hardwood forest. *Canadian Journal of Forest Research*, 40, 2360–2369.

Fisk, M.C. Fahey, T.J., Groffman, P.M., & Bohlen, P.J (2004). Earthworm invasion, fine-root distributions, and soil respiration in north temperate forests. *Ecosystems*, 7, 55–62.

Fortin, M., Bédard, S., DeBlois, J., & Meunier, S. (2008). Predicting individual tree mortality in northern hardwood stands under uneven-aged management in southern Québec, Canada. *Annals of Forest Science*, 65(2), 1.

Fortin, M. (2014). Using a segmented logistic model to predict trees to be harvested in forest growth forecasts, *Forest systems, 23, 139-152*

Gavin, D. G., & Peart, D. R. (1993). Effects of beech bark disease on the growth of American beech (Fagus grandifolia). *Canadian Journal of Forest Research*, 23(8), 1566-1575.

Genet, A., & Pothier, D. (2013). Modeling tree spatial distributions after partial harvesting in uneven-aged boreal forests using inhomogeneous point processes. *Forest Ecology and Management,* 305, 158–166.

Grigal, D. F. (2000). Effects of extensive forest management on soil productivity. *Forest Ecology and Management*, 138(1-3), 167-185.

Grondin, P., Jean, N., & Hotte, D. (2007). Intégration de la végétation et de ses variables explicatives à des fins de classification et de cartographie d'unités homogènes du Québec méridional, *Ministère des Ressources naturelles et de la Faune*, Direction de la recherche forestière. Mémoire de recherche No 150, pp. 62

Guillemette, F., Bédard, S., & Fortin, M. (2008). Evaluation of a tree classification system in relation to mortality risk in Québec northern hardwoods. *The Forestry Chronicle*, 84, 886–899.

Hartmann, H., Wirth, C., Messier, C., & Berninger, F. (2008). Effects of above-and belowground partial harvest disturbance on growth and water status of residual sugar maple. *Tree physiology,* 28(12), 1851-1862.

Hartmann, H., Beaudet, M., & Messier, C. (2008). Using longitudinal survival probabilities to test field vigour estimates in sugar maple (Acer saccharum Marsh.). *Forest Ecology and Management*, 256(10), 1771-1779.

Hartmann, H., & Messier, C. (2008). The role of forest tent caterpillar defoliations and partial harvest in the decline and death of sugar maple. *Annals of Botany*, 102, 377–387.

Hartmann, H., Beaudet, M., Mazerolle, M.J., & Messier, M. (2009). Sugar maple (Acer saccharum Marsh.) growth is influenced by close conspecifics and skid trail proximity following selection harvest. *Forest Ecology and Management,* 258, 823–831.

Hegyi, F.(1974). A simulation model for managing jack pine stands. In: Growth Models for Tree and Stand Simulation. *Royal College of Forestry,* Stockholm, Sweden, pp. 74–90.

Hothorn, H., Bretz, F., Westfall, P. (2019). multcomp. R package version 1.4-10

Huggett, B.A., Schaberg, P.G., Hawley, G.J., & Eager, C. (2007). Long-term calcium addition increases growth release, wound closure, and health of sugar maple (Acer saccharum) trees at the Hubbard Brook Experimental Forest. *Canadian journal of forest research,* 37, 1692-1700

Jones, T.A., & Thomas, S.C. (2004). The time course of diameter increment responses to selection harvests in Acer saccharum. *Canadian journal of forest research*, 34, 1525–1533.

Jones, T. A., Domke, G. M., & Thomas, S. C. (2009). Canopy tree growth responses following selection harvest in seven species varying in shade tolerance. *Canadian journal of forest research*, 39(2), 430-440.

Kern, C. C., Burton, J. I., Raymond, P., D'Amato, A. W., Keeton, W. S., Royo, A. A., ... & Willis, J. L. (2017). Challenges facing gap-based silviculture and possible solutions for mesic northern forests in North America. *Forestry: An International Journal of Forest Research*, 90(1), 4-17.

Kiernan, D.H., Bevilacqua, E., & Nyland, R.D. (2009). Individual-tree diameter growth model for sugar maple trees in uneven-aged northern hardwood stands under selection system. *Forest Ecology and Management*, 256,1579–1586.

Kuehne, C., Weiskittel, A.R., & Waskiewicz, J. (2019). Comparing performance of contrasting distance-independent and distance-dependent competition metrics in predicting individual tree diameter increment and survival within structurally-heterogeneous, mixed-species forests of Northeastern United States. *Forest Ecology and Management*, 433, 205–216.

Latham, P. & Tappeiner, J., (2002). Response of old-growth conifers to reduction in stand density in western Oregon forests. *Tree Physiology.*, 22, 137–146.

Long, R.P., Horsley, S.B. & Hall, T.J. (2011). Long-term impact of liming on growth and vigor of northern hardwoods. *Canadian Journal of Forest Research*, 41,1295–1307.

Lorimer, C. G., & Frelich, L. E. (1994). Natural disturbance regimes in old-growth northern hardwoods: implications for restoration efforts. *Journal of Forestry*, 92(1), 33-38.

Majcen Z., Richard, Y., Ménard, M., Grenier, Y. (1990). Choix des tiges à marquer pour le jardinage d’érablières inéquiennes, Guide technique, *Ministère de l’Énergie et des Ressources du Québec*, Direction de la recherche forestière, Mémoire No. 96

Majcen, Z. (1996). Coupe de jardinage et coupe de succession dans cinq secteurs forestiers. Accroissement quinquennal en surface terrière et état de la régénération, *Ministère des Ressources naturelles et de la Faune du Québec*, Direction de la recherche forestière, Mémoire No. 70

Martin, A. R., Caspersen, J. P., Fuller, M. M., Jones, T. A., & Thomas, S. C. (2014). Temporal dynamics and causes of postharvest mortality in a selection-managed tolerant hardwood forest. *Forest ecology and management*, 314, 183-192.

Mazerolle, M.J. (2006). Improving data analysis in herpetology: using Akaike's Information Criterion (AIC) to assess the strength of biological hypotheses. *Amphibia-Reptilia,* 27, 169–180.

Mazerolle, M.J. (2017). AICcmodavg: Model selection and multimodel inference based on (Q)AIC(c). R package version 2.0-3.

Miller, R.E., Colbert, S.R., & Morris, L.A. (2004). Effects of heavy equipment on physical properties of soils and on long-term productivity: a review of literature and current research. *National Council for Air and Stream Improvement Technical Bulletin No. 887*.

Moore, J. D., & Ouimet, R. (2006). Ten-year effect of dolomitic lime on the nutrition, crown vigor, and growth of sugar maple. *canadian Journal of Forest research*, 36(7), 1834-1841.

Moore, J. & Ouimet, R. (2010). Effects of two Ca fertilizer types on sugar maple vitality. *canadian Journal of Forest research*, 40, 1985–1992

Moreau, G., Achim, A., & Pothier, D. (2019). A dendrochronological reconstruction of sugar maple growth and mortality dynamics in partially cut northern hardwood forests. *Forest ecology and management*, 437, 17-26.

Nowacki, G.J., & Abrams, M.D. (1997). Radial-growth averaging criteria for reconstructing disturbance histories from presettlement-origin oaks. *Ecological Monographs*, 67, 225–249.

Nyland, R.D. (1998). Selection system in northern hardwoods. *Journal of Forestry*, 96, 18-21.

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., Heisterkamp, S., Van Willigen, B., & Maintainer, R. (2017). Package 'nlme'. *Linear and nonlinear mixed effects models*, version, 3.

Pothier, D., Fortin, M., Auty, D., Delisle-Boulianne, S., Gagné, L. V., & Achim, A. (2013). Improving tree selection for partial cutting through joint probability modelling of tree vigor and quality. *Canadian journal of forest research*, 43(3), 288-298.

Raymond, P., Bédard, S., Roy, V., Larouche, C., & Tremblay, S. (2009). The Irregular Shelterwood System : Review, Classification, and Potential Application to Forests Affected by Partial Disturbances. *Journal of Forestry*, 107, 405–413.

Saucier, J.-P., Grondin, P., Robitaille, A., Gosselin, J., Morneau, C., Richard, P.-J.-H., Brisson, J., Sirois, L., Leduc, A., Morin, H., Thiffault, E., Gauthier, S., Lavoie, C. & Payette, S. (2009). Écologie forestière. Manuel de foresterie, 2e édition. *Ordre des ingénieurs forestiers du Québec*, Éditions Multimondes, Québec, pp.165-316.

Seablom, T. J., & Reed, D. D. (2005). Assessment of factors contributing to residual tree damage from mechanized harvesting in northern hardwoods. *Northern Journal of Applied Forestry*, 22(2), 124-131.

Seymour, R. S., White, A. S., & Philip, G. D. (2002). Natural disturbance regimes in northeastern North America—evaluating silvicultural systems using natural scales and frequencies. *Forest Ecology and Management*, 155(1-3), 357-367.

Therneau, T. M., & Lumley, T. (2014). Package ‘survival’. Survival analysis Published on CRAN, 2, 3.

Thorpe, H. C., Thomas, S. C., & Caspersen, J. P. (2008). Tree mortality following partial harvests is determined by skidding proximity. *Ecological Applications*, 18(7), 1652-1663.

Weber, P., Bugmann, H., Fonti, P., & Rigling, A. (2008). Using a retrospective dynamic competition index to reconstruct forest succession. *Forest Ecology and Management*, 254(1), 96-106.

Williamson, J. R., & Neilsen, W. A. (2000). The influence of forest site on rate and extent of soil compaction and profile disturbance of skid trails during ground-based harvesting. *Canadian Journal of Forest Research*, 30(8), 1196-1205.

Zuur, A. F., Ieno, E.N., Elphick, C.S. (2010). A protocol for data exploration to avoid common statistical problems. *Methods in Ecology and Evolution*. 1, 3–14.

2. Chapitre 2
A dendrochronological reconstruction of sugar maple growth and mortality dynamics in partially cut northern hardwood forests

2.1. Abstract

We investigated the growth and mortality dynamics of 22 northern hardwood stands with well-known disturbance histories in southern Quebec, Canada. The main objective of this study was to evaluate the effect of short- and long-term growth trends on both the probability of mortality and the radial growth response of trees following partial cutting. This was first achieved by identifying growth release episodes and characterizing growth patterns prior to tree death from entire tree-ring series of 86 live and 26 dead sugar maple (*Acer saccharum* Marsh.) trees. Using mixed-effects logistic regression, we quantified the effects of short- and long-term growth trends, as well as external variables such as neighbourhood competition and tree vigour status on the probability of mortality and growth release events. Results showed that long periods of continuous growth decline or long periods of slow radial growth after a severe decrease occurred in 88 % of dead trees. These growth patterns were associated with a progressive decline in tree vigour that was mostly initiated by drought and insect defoliations during the 1980s, thereby supporting the relevance of studying long-term tree-ring chronologies to deduce causes of post-harvest mortality. Our model showed that predictions of post-cut mortality events could be significantly improved by considering long-term radial growth trends (25 years before cutting) in individual trees. In terms of growth response, 24 % of live trees had a release event occurring after the selection cut, which is slightly lower than the response induced by natural disturbance in previous decades. None of the tested long-term growth variables were significantly related to the occurrence of growth release events. Consequently, suppressed sugar maple trees appear to maintain their capacity to respond positively to gap creation, regardless of the length of the suppression period. We conclude that while long-term radial growth trends are strongly related to mortality probabilities, the growth release potential of trees is negatively impacted by the presence of defects affecting tree vigour (e.g. fungal infections and cambial necroses) and positively related to the removal of neighbouring trees, rather than to prior growth trends.

2.2. Résumé

Nous avons étudié la dynamique de croissance et de mortalité de 22 peuplements feuillus dont l'historique des perturbations était bien documenté dans le sud du Québec, Canada. L'objectif principal de cette étude était d'évaluer l'effet des tendances de croissance antérieures sur le taux de mortalité et la réaction de croissance des arbres suivant une coupe de jardinage. Les résultats ont montré que 88 % des événements de mortalité étaient précédés d'une longue période de déclin de croissance. De ce fait, la prédiction des événements de mortalité pouvait être significativement améliorée en considérant les tendances de croissance 25 ans avant la coupe. Concernant la réaction de croissance, 24 % des arbres résiduels ont connu une hausse de croissance significative après la coupe. Les tendances de croissance antérieures n'étaient pas significativement liées à la probabilité d'avoir une hausse de croissance dans les années suivant la coupe de jardinage.

2.3. Introduction

Northern hardwood forests cover large areas in North America (Delisle-Boulianne et al. 2014) and are dominated by sugar maple (Acer saccharum Marsh.), a shade-tolerant species adapted to frequent small-scale disturbance events (Seymour et al. 2002). The resulting uneven-aged stands are mainly harvested using mechanized partial cuts that aim to promote the regeneration of shade-tolerant species, the growth of residual trees, and a sustained yield in high-quality timber (Majcen 1996; Nyland 1998). Although the objectives and theoretical effects of mechanized partial cuts are well defined, there are considerable variations in tree mortality and growth responses among regions and site conditions (Bédard & Brassard 2002; Forget et al. 2007; Fortin et al. 2008; Hartmann et al. 2009; Martin et al. 2014). These variations raise several questions about the factors that predispose trees to increase significantly their growth or to die following a partial cut. Studying growth and mortality dynamics induced by mechanized partial cuts could help improve their application in northern hardwood forests in order to maximize post-treatment productivity.

Tree-ring chronologies are well-suited for reconstructing forest dynamics, as demonstrated by the detailed insights on growth and mortality responses to disturbance events that have been provided by recent advances in dendrochronological analyses (Bigler & Bugmann, 2004; Black & Abrams, 2004; Black et al. 2009; Cailleret et al. 2016, 2017). For example, these analyses have shown that most tree mortality events are associated with reduced growth during periods exceeding 20 years prior to tree death (Vanoni et al. 2016; Cailleret et al. 2017). This suggests that predictions of mortality events could be improved by considering long-term radial growth trends in individual trees, thereby supporting the relevance of studying long-term tree-ring chronologies (Cailleret et al. 2017).

Despite these observations, few studies have taken into account long-term radial growth patterns in the temporal dynamics of postharvest mortality within northern hardwood forests (but see Hartmann & Messier 2008). The multiple causes of post-harvest tree mortality include pre- or post-harvest fungal infections (Guillemette et al. 2008), windthrow that can occur along the skid trails (Forget et al. 2007), as well as damage directly caused by tree felling and machinery trafficking (Martin et al. 2014). Repeated machinery passage can notably increase the rate of tree mortality in years following partial harvest (Caspersen 2006; Martin et al. 2014) as it can produce soil disturbance and compaction as well as damage to the roots and trunk of residual trees

(Caspersen 2006; Hartmann et al. 2009; Martin et al. 2014). However, these causes of mortality may not be detected when inferred through a post-mortem approach whereby a likely cause was deduced from an examination of the physical characteristics of dead trees (e.g., Forget et al. 2007; Martin et al. 2014; Guillemette et al. 2017). Yet, such a post-mortem approach can lead to erroneous conclusions because it can easily confuse causes and effects, in addition to identifying only a single cause of death. For example, for an overturned or snapped tree, the deduced cause of windthrow could have been preceded by another cause that was not apparent at the time of sampling, such as repeated insect defoliation events (Hartmann & Messier, 2008).

While dendrochronological analyses can be helpful in predicting tree mortality, they can also be used to quantify the growth response of trees surrounding dead trees through the study of growth release pulses (i.e., Nowacki & Abrams, 1997; Black et al. 2009; Stan & Daniels, 2010; Trotsiuk et al. 2012; Després et al. 2017). Growth release pulses are defined as abrupt increases in radial growth, which are measured as a percentage growth change that occurs during a given time period and which exceeds a minimum threshold (Black & Abrams 2003). The boundary-line release criteria method, which was developed by Black & Abrams (2003, 2004) and Black et al. (2009), scales each release event by its maximum release potential, which is specific to each species and determined by prior growth rates. This method could thus be used to determine accurately and objectively which trees respond to partial cutting with a significant radial growth increment (Webster & Jensen 2007). In addition, this method allows the inclusion of past growth trends as candidate variables to explain the growth release potential of trees. For example, trees with limited radial growth during a 10-year period before a partial disturbance event have much higher growth release potential than trees with fast radial growth during the same period (Black and Abrams 2004). In contrast, trees showing long-term suppressed growth may have a reduced capacity to respond positively to the same partial disturbance event (Baral et al. 2016).

The main objective of this study was to evaluate the effect of short and long-term growth trends on sugar maple tree mortality and growth response following partial cutting. These growth trends were then related to external variables such as neighbourhood competition, tree vigour status and site disturbance history to determine their causes. We first hypothesized that post-harvest mortality is generally preceded by a progressive decline in tree vigour, which is characterized by a progressive decline in radial growth in decades prior to the partial cut (i.e.,>20 years), rather than by a marked drop in the first few years following partial cutting. Our second hypothesis stated that limited radial growth over a long period (> 20 years) before harvest decreases the likelihood of a growth release event occurring after a partial cut.

2.4. Material and methods

2.4.1. Sampling sites and disturbance history

Sampling was conducted in private woodlots that are owned by Domtar Corporation in southern Quebec, Canada (45◦31’-45◦57’N, 71◦23’-70◦33’W). This area encompasses both the eastern sugar maple-American basswood (*Tilia americana* L.) and the eastern sugar maple-yellow birch (*Betula alleghaniensis* Britt.) bioclimatic subdomains (Saucier et al. 2009). The first subdomain is characterized by a growing season of 165 to 180 days, a mean annual temperature between 4 and 5 °C, and mean annual precipitation between 1000 and 1150 mm. The second one is characterized by a growing season of 145 to 165 days, a mean annual temperature between 2.5 and 4 °C, and mean annual precipitation between 915 and 1100 mm (Saucier et al. 2009). The topography of both subdomains is characterized by hills and slopes shaped by the foothills of the Appalachian Mountains and the main surface deposits are shallow to deep tills (Grondin et al. 2007). The sampling sites were located in uneven-aged northern hardwood stands mainly composed of sugar maple, with minor components of yellow birch, red maple (Acer rubrum L.), American beech (*Fagus grandifolia* Ehrh.), balsam fir (*Abies balsamea* [L.] Mill.) and red spruce (*Picea rubens* Sarg.). During the first half of the 1980s, this area was affected by severe drought and insect defoliations, which reduced the overall growth and vigour of sugar maple stands during the following decade (Payette et al. 1996). However, these stands have gradually recovered from these disturbances during the 1990s (Payette et al. 1996).

2.4.2. Sample plots and treatments

From 1998 to 2003, 22 circular permanent sample plots of 400 m^2 were established in as many different stands as possible at least one year prior to a selection cut. All trees with a diameter at breast height (DBH) > 9.0 cm were tagged. Selection cuts were conducted between 2002 and 2007 in all stands. These selection cuts aimed at removing low-vigour and low-quality trees of all species while maintaining an uneven-aged structure in the residual stand. Prior to cutting, merchantable tree volume averaged 190 dm^3, while mean stand basal area was around 26 m^2 ha^{-1}. The applied selection cuts aimed to harvest 35 %

of the basal area using feller-buncher harvesters that were equipped with a forwarder, a cable skidder, or a grapple skidder. Skidding trails had a maximum width of 4 m and were spaced about 20 m apart.

2.4.3. Data collection

The permanent sample plots were inventoried periodically at a mean interval of five years. Species and DBH of trees with a DBH > 9.0 cm were recorded in each survey. In 19 of the 22 plots, tree vigour was evaluated one year before or after the selection cuts according to a classification system that was developed by Majcen et al. (1990 – Table 2.1). This classification system was deemed suitable for evaluating whether or not trees were likely to survive until the next scheduled partial harvest (i.e., 25 years), based upon pathological symptoms, mechanical damage and other visible defects (Delisle-Boulianne et al. 2014). Vigorous trees with good survival probabilities are those without major defects, i.e., well-developed crowns and foliage, and the absence of large dead or dying branches. In contrast, weak or non-vigorous trees with low survival probabilities are those that were affected by major defects such as wood decay, damaged crowns, large dead or dying branches, unhealed cracks, fungal infections, or cambial necroses.

During the summer of 2016, we collected additional information in all 22 plots. Using a diameter tape, we first measured DBH (± 0.1 cm) of all stems > 9.0 cm in each plot and within a 6-m buffer around their edges. Second, we measured the distance (± 0.1 m) and the azimuth of each tree relative to the plot centre using a hypsometer and a compass. The Cartesian coordinates of each tree were then mapped using trigonometric functions. Third, we extracted an increment core from all live trees at a height of 1 m above the ground surface and oriented toward the plot centre. Finally, we sampled a wood disc from all standing dead trees (n = 30) at a height of 1 m aboveground.

2.4.4. Tree-ring chronology

Increment cores that were sampled from all live trees were glued to wooden blocks before they were air-dried and sanded. Discs that were sampled from dead trees were also air-dried and sanded. Annual rings were measured with a Velmex micrometer (± 0.002 mm). We constructed a master standardized chronology (Figure 2.1), using increment cores with clearly identifiable rings from a subsample of 38 dominant sugar maple trees that were randomly distributed in our study plots. The master chronology was constructed and evaluated using the program COFECHA (Holmes 1983) to add highly correlated tree-ring series (r-values > 0.3) and was subsequently compared with those from a previous study on sugar maple from the same area (Payette et al. 1996). Chronologies from both studies had matching years of growth depression, which were thus used as marker years for cross-dating trees that had not been used to construct the master chronology. To reduce the difference between the number of live and dead sampled trees (Salas-Eljatib et al. 2018), we used all 30 discs that were taken from dead trees, while randomly selecting 90 cores among the sample plots and distributed roughly uniformly among DBH values that ranged from 9.1 to 52 cm for further analyses. Cross-dating of each tree-ring chronology was statistically evaluated with COFECHA (Holmes 1983). At the end of the process, any series that showed weak correlation to the master chronology and no concordance with the marker years were removed from the sample to ensure that only well cross-dated series were retained for further analysis. Based upon the visual examination of marker years and correlations with the master chronology, the final dataset consisted of 86 live trees and 25 dead trees. The live and dead trees where always treated separately in two distinct categories for further analysis.

Table 2.1 Definitions of defects characterizing low-vigour trees according to the classification system of Majcen et al. (1990) as adapted by Guillemette et al. (2008).

Defect	Definition	Survival probability
Wound of mechanical origin	Any part of the bole where the bark has been removed by a mechanical process. The sapwood is exposed and is affected or not by significant decay.	Low when >50 cm^2 (DBH 10–28 cm); >150 cm^2 (DBH 20–28 cm); >300 cm^2 (DBH ≥ 30 cm)
Wound of biological origin	Any part of the bole where the bark has been removed and the sapwood exposed as a result of biotic agent (e.g. bird-peaking, beaver)	Same as above
Decay	Presence of decay in a knot, crack, seam or wound	Low
Proportion of dead crown	The proportion of crown (%) dead due to dieback or lost due to crown breakage. The death of lower branches due to natural pruning of the bole is not included.	Low when >30%
Lean	3 categories: ≤10°, >10° and ≤45°, and >45	Low when >45°
Roots cut	The presence of roots having been cut by logging equipment	Low when >30% of the roots were cut
Uprooting	Living tree uprooted due either to windthrow or logging	Low
Fungus or canker	The presence of a fungus or canker on the bole	Low

2.4.5. Release events and boundary-line method

To identify release events in each cross-dated tree-ring series, we used the boundary-line method that was developed by Black & Abrams (2003; 2004) and Black et al. (2009). Release events are defined as abrupt pulses in radial growth that occurred during a given time period, which are generally caused by the death of competing trees (Lorimer & Frelich 1989). The boundary-line method consists of scaling each potential release event relative to the expected maximum growth change, which in turn is defined according to the prior growth rate. The method considers that the release potential of a tree is strongly dependent upon its prior growth rate (in relative terms), with greater release potential for previously suppressed trees (Black & Abrams 2003). In accordance with Black et al. (2009), who recommended that 50000 ring measurements are necessary to develop a boundary line for a given species, we used 50250 ring-width measurements from the sugar maple ring-series dataset that had been assembled by Payette et al. (1996). This dataset comes from eight sites that were located in the same area as our 22 permanent sample plots.

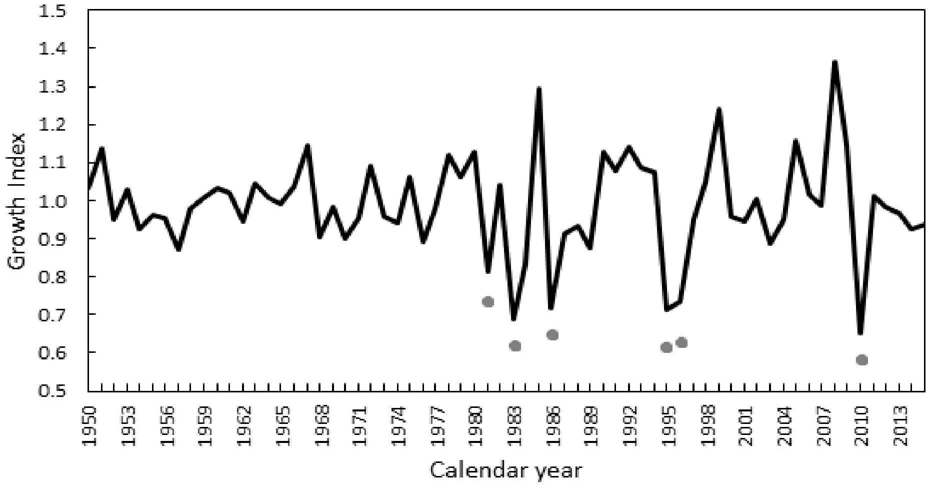

Figure 2.1 Age-standardized master chronology from the mean radial growth of 38 dominant sugar maple trees (r = 0.90). Main marker years are identified by grey dots (1981, 1983, 1986, 1995-1996 and 2010)

The first step in developing the boundary line was to calculate the percent-growth change (PGC) for every year in each tree-ring series using the running mean method (Nowacki & Abrams 1997):

$$PGC = \frac{M_2 - M_1}{M_1} X100 \qquad [1]$$

where M_1 corresponds to the mean radial growth for the 10-year period prior to the year of interest, and M_2 is the mean radial growth over the subsequent 10 years. We then plotted the values of PGC that were calculated for each calendar year in our series against the value of M_1. The second step was to calculate an average of the 10 highest positive PGC values within each 0.25-mm class of M_1. Different functions were then used to relate the average of the 10 highest PGC values to M1. The function with the highest R^2 was a negative exponential function. The equation ($R^2 = 0.97$) was:

$$PGC = 862.35e^{-0.897M_1} \qquad [2]$$

Growth changes that fell within 50 to 100 % of the boundary-line for a given M_1 were classified as major releases, while those falling within 20.0 to 49.9 % were classified as moderate releases (Fig. 2.2). All growth changes below 20 % of the boundary line were not considered as actual releases (Black & Abrams 2003).

Finally, because the boundary-line method used the average radial growth for the 10-year period before and after a given year of interest, we were unable to calculate PGC for the last 10 years of each series. Consequently, the PGC over a 10-year period could not be used to detect release events that occurred after 2005. To identify release events until 2009, the time period before and after the year of interest used to calculate the PGC was gradually decreased from 10 to 6 years after 2005. Decreasing the number of years from 10 to 6 did not have much effect on the PGC variation, but it allowed the identification of two additional release events. To limit the potential identification of false releases that were detected, every release event was subjected to visual inspection, as recommended by Nagel et al. (2013).

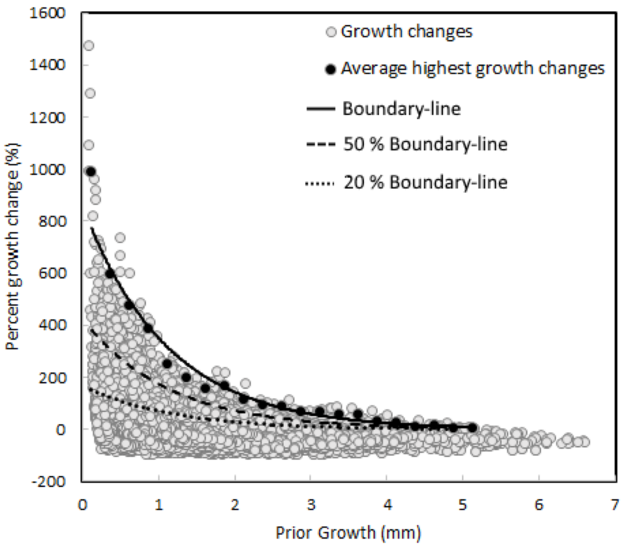

Figure 2.2 Percent growth changes (PGC) measured during 10-year periods after a given year of interest as a function of the 10-year radial growth measured before this given year for sugar maple trees located in southern Quebec, Canada. The boundary line was drawn using a negative exponential function. The averages of the 10 highest PGC values within each 0.25-mm class of mean radial growth for the 10-year period before the year of interest are identified by black dots. All growth changes below 20 % of the boundary line were not considered as actual releases.

2.4.6. Competition index

The level of competition around each tree in our sample plots was calculated using a distance-dependent competition index (CI) that was proposed by Hegyi (1974):

$$CI = \Sigma_{i=1}^{n} d_i/(d \times dist_i) \qquad [3]$$

where d_i is the DBH (mm) of the ith neighbouring tree located at a distance $dist_i$ (m) from the subject tree, and d is the DBH of the subject tree. All values were computed from the inventory that had been performed immediately after selection cutting, except for trees located in the 6-m buffer strip around each plot. For these latter trees, the DBH immediately after cutting was estimated using a linear model relating the DBH measured immediately after cutting (DBH_0) and that measured in 2016 (DBH_1) for the sample trees located within the plots. The prediction equation (R^2 = 0.93) was:

$$DBH_0 = 2.22 + 0.91DBH_1 - 1.42T \qquad [4]$$

where T is the number of years between the application of the selection cut and 2016. Equation 3 was then used to determine the competition radius (from 2 to 8 m) that was best related to tree growth, based upon the Akaike's information criterion (*AIC*). To do this, we used a linear mixed-effects model with a plot-level random intercept:

$$(BAI_{10})^{0.5} = b_0 + b_1 CI_r + \beta_j \qquad [5]$$

where BAI_{10} (dm^2) is the tree basal area increment of an individual tree for the first 10 years after cutting, CI_r is the distance-dependent index that was calculated with different radii r (Eq. 3), and β_j is the random effect of plot j.

2.4.7. Modelling release and mortality probabilities

Mortality and release probabilities were modelled at the tree level using mixed effects logistic regression, with plot included as a random term. Three types of growth variables were entered into the models: i) the growth-level variable, i.e., basal areal increment (BAI, dm^2), and the average radial growth (AG, mm) that was calculated for periods of 5, 10 and 25 years before selection cutting; ii) the growth trend variables (GT), i.e., the sign of the slope of linear regressions that were fitted to the annual radial growth values over a period of 5 years before cutting; and iii) mean sensitivity (MS), i.e., the average growth variability over periods of 5 and 10 years before cutting. The sensitivity S_t at year *t* was defined as:

$$S_t = \left|\frac{(RW_t - RW_{t-1})}{(RW_t)}\right| \qquad [6]$$

where RW_t is the radial growth measured at year *t*, and RW_{t-1} is the radial growth measured at year *t-1*. The growth sensitivity index therefore represents the susceptibility of trees to annual climatic variability (Fritts 1976) and has been recognized as a good indicator of tree vigour (Ogle et al. 2000; Suarez et al. 2004; Hartmann et al. 2008). In addition to the growth variables, DBH, the competition index (CI) and tree vigour class (2 levels i.e. low or high, see Table 1) were incorporated into the models as candidate explanatory variables. The degree of correlation between the competition index and DBH prevented their simultaneous use in the list of models that were tested. A log-transformation was applied to the average radial growth to permit model convergence.

The modelling process started with manual stepwise selection of the best growth-level variable (simple regression model). Only one growth-level variable at a time was included in both mortality and release models. Selection of the best model was based upon Akaike's information criterion, corrected for small sample sizes (*AICc*). All remaining variables were then successively included, while avoiding highly correlated predictors. Models were systematically compared to an intercept-only model (null model).

Preliminary analyses indicated that tree vigour class was strongly related to the probabilities of release and mortality. Consequently, further modelling efforts only took into account the data from the 19 plots within which the tree vigour status had been monitored. This applied to 66 live sample trees and 15 dead ones. All statistical analyses were performed in the R statistical programming environment (Version 3.5.1, R Core Team, 2018). We used the *lme* function of the *nlme* package (Pinheiro et al. 2017) for linear mixed-effects models, while the *glmer* function of the *lme4* package (Bates et al. 2015) was used for mixed-effects logistic regression. Homoskedasticity, variance inflation factors (VIF) between the candidate variables (Zuur et al. 2010), normality of residuals, the presence of outliers, and over-dispersion were tested to ensure that regression assumptions were met.

2.5. Results

2.5.1. Mortality patterns

Cross-dating of dead trees indicated that their mortality occurred between 1996 and 2015. Most of the tree-ring series that were analyzed for this study showed a severe growth depression in the early 1980s (e.g., Figure 2.1), followed by multiple decrease events thereafter. For trees that died after selection cuts, these growth decreases often led to a continuous growth decline that ceased only with tree death. Three different ring series patterns were observed prior to tree death (Figure 2.3). The first pattern, which applied to 48 % of dead trees, was associated with long periods of continuous growth decline, interspersed with small pulses of radial growth that ended with tree death (Figure 2.3, triangular series). The second pattern was observed on 40 % of dead trees and was associated with very long periods of slow radial growth after a severe decline, i.e., > 15 years with radial growth < 1 mm yr^{-1} before death (Figure 2.3, diamond series). The third pattern applied to 12 % of dead trees (Figure 2.3, square series), whereby death was preceded by a short and abrupt growth decline in years following selection cutting (≤ 6 years).

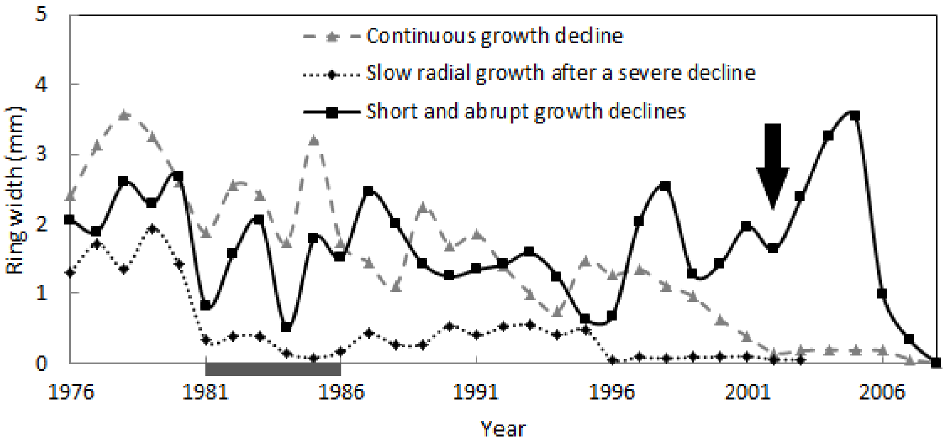

Figure 2.3 Three different ring series patterns that were observed prior to tree death: i) long periods of continuous growth decline interspersed with small pulses of radial growth that ended with tree death, ii) long periods of slow radial growth after a severe decline, and iii) short and abrupt growth decline in years following selection cutting. The arrow indicates the year of the partial cut (2002). The shaded area on the x-axis indicated the period of drought and insect defoliations that occurred from 1981 to 1986 (Payette et al. 1996).

2.5.2. Post-cut mortality model

The mixed-effect model described in eq. 3 had its lowest AICc value when an 8-m radius was used to compute the competition index, which was retained in subsequent analyses. Estimated variances of the plot random effects that were included in the mortality model did not significantly differ from 0 (α = 5 %). Consequently, only fixed effects were used for the rest of our modelling effort. Among the growth variables that were tested to help predict the probability of tree mortality after selection cutting, log-transformed average growth over the 25 years preceding selection cuts was the most significant variable (p = 0.0003) and yielded the univariate model with the lowest AICc (Table 2, Model 5). According to the evidence ratio (ratio of AICc weight with the best model), extending the window of observation from 10 to 25 years for this variable improved model fit more than three-fold. Tree vigour class (p = 0.001), the growth trend over a 5-year period before selection cutting (p = 0.024), the mean sensitivity over the 5 years preceding selection cuts (p = 0.052), and the competition index (p = 0.027) were introduced one after another to form the final multiple regression model with the lowest AICc (Table 2.2, Model 10). According to model 10 (Table 2.2), mean mortality probabilities decreased abruptly with an increasing radial growth over the 25 years preceding the selection cut (Figure 2.4a). In contrast, mean mortality probabilities increased sharply with increasing mean sensitivity index (Figure 2.4b) and increasing competition index (Figure 2.4c). Moreover, the mean mortality probability was 16 times higher in non-vigorous than in vigorous trees (Figure 2.4d). Finally, mortality probabilities of non-vigorous trees that were characterized by negative pre-cut growth trends were 25 times higher than those of non-vigorous trees with positive growth trends (Figure 2.4e).

2.5.3. Release events

Most of the live trees that we examined (76 %) showed at least one release event between 1950 and 2009, but only 23 % had more than one. Among these release events, moderate releases (95 %) were much more common than major releases (5 %) and this proportion remained the same for periods before and after cutting. Overall, release events were more frequent during the 1990s and the first part of the 2000s at the beginning of which the selection cuts had been applied (Figure 2.5a). Only 24 % of live trees had a release event occurring after selection cutting (Figure 2.5a). For these trees, the time interval between the cut and the release event varied between 1 and 3 growing seasons.

Table 2.2 Statistics of the 5 best simple and multiple regression models predicting the probability of tree mortality following selection cutting. AICc is the Akaike Information Criteria, corrected for small sample sizes, with delta AICc (Δi), model Likelihood (Mk) and AICc weight (Wti). All models included an intercept among the fixed effects. Models in boldface type are the best models. AG: Average growth, BAI: basal areal increment, GT: Growth trend, MS: Mean sensitivity, IND: Competition index

	Variables	AICc	Δ_i	Mk	Wt_i
Simple regression models					
5	**log(AG 25 years)**	**62.86**	**0.00**	**1.00**	**0.56**
4	log(AG 10 years)	65.12	2.26	0.32	0.18
3	BAI 25 years	66.29	3.43	0.18	0.10
2	log(AG 5 years)	67.22	4.35	0.13	0.06
1	BAI 10 years	67.48	4.62	0.09	0.05
0	Intercept only	81.78	18.91	0.00	0.00
Multiple regression models					
10	**log(AG 25 years) + Vigour class + GT + MS(5 years) + CI**	**38.83**	**0.00**	**1.00**	**0.38**
9	log(AG 25 years) + Vigour class + GT + MS(5 years) + DBH	40.49	1.44	0.48	0.18
8	log(AG 25 years) + Vigour class + GT + MS(10 years) + CI	40.66	1.61	0.45	0.17
7	log(AG 25 years) + Vigour class + GT + DBH	41.30	2.59	0.23	0.01
6	log(AG 25 years) + Vigour class + GT + MS(10 years) + DBH	42.15	3.11	0.21	0.00
0	Intercept only	80.95	42.12	0.00	0.00

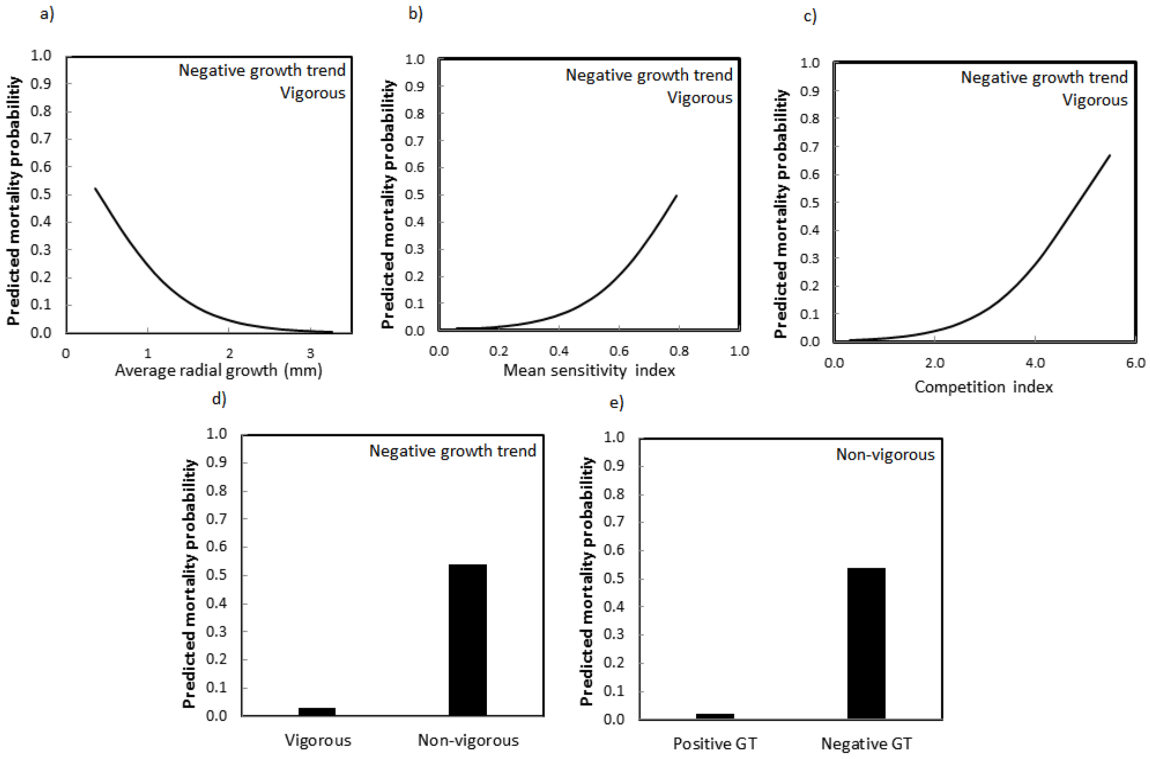

Figure 2.4 Effects of explanatory variables on mean predicted mortality probabilities (other covariates are kept constant at the mean values) a) average radial growth (25 year-period), b) mean sensitivity index (5 year-period), c) competition index, d) vigour class, e) growth trend (GT).

A low proportion of the dead trees that we examined (36 %) had an occurrence of at least one release event from 1950 to 2009, with only 16 % showing multiple release events. All observed releases were of moderate intensity and none occurred after selection cutting (Figure 2.5b).

2.5.4. Post-cut release occurrence model

The logistic model that was used to predict release occurrence compared 18 trees with a release event after selection cuts to 48 live trees without any evidence of a release event during the same period. Again, the estimated variances of the plot random effects included in the model did not significantly differ from 0 ($\alpha = 5$ %), so only fixed effects were used in subsequent steps. Among the variables that were tested to explain the occurrence of a release event, no growth variables were significant. Tree vigour class ($p = 0.0348$) had significant effects and the competition index ($p = 0.0540$) had marginal effects. Also, with a P value of 0.08, there was inconclusive evidence that DBH had an effect on release probabilities. The best model included both tree vigour class and the competition index (Table 2.3, model 5), with an AICc weight of 0.76. Comparing with the second best model that included only vigour class, inclusion of the competition index increased the fit of the model by more five-fold. According to this model, the growth release probability decreased with increasing competition index (Figure 2.6a) and was about six times higher in vigorous than in non-vigorous trees in the same competitive environment (Figure 2.6b).

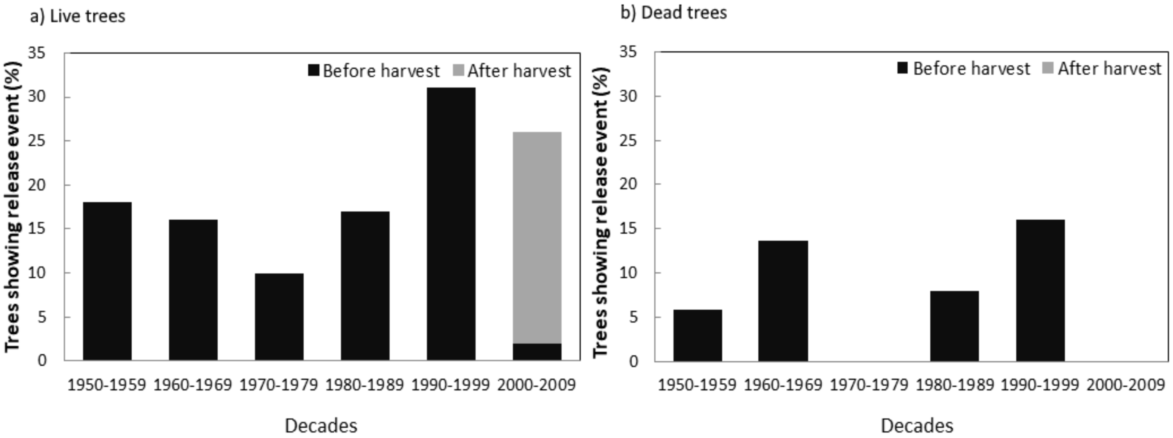

Figure 2.5 Percentage of (a) live trees (n=86) and (b) dead trees (n=25) for which release events were detected in each decade since 1950.

Table 2.3 Statistics of the best models predicting the probability of growth release occurrence following selection cutting. AICc is the Akaike Information Criterion, corrected for small sample sizes, with delta AICc (Δ_i), model Likelihood (Mk) and the AICc weight (Wt_i). All models included an intercept and a random plot effect. The model in boldface type is the best model. CI: competition index

Model	Variables	AICc	Δ_i	Mk	Wt_i
5	**Vigour class + CI**	**70.01**	**0.00**	**1.00**	**0.76**
4	Vigour class	73.34	3.33	0.18	0.14
3	CI	75.05	5.04	0.08	0.06
2	Vigour class + DBH	77.27	7.26	0.02	0.02
1	DBH	79.41	9.41	0.00	0.00
0	Intercept	81.45	11.44	0.00	0.00

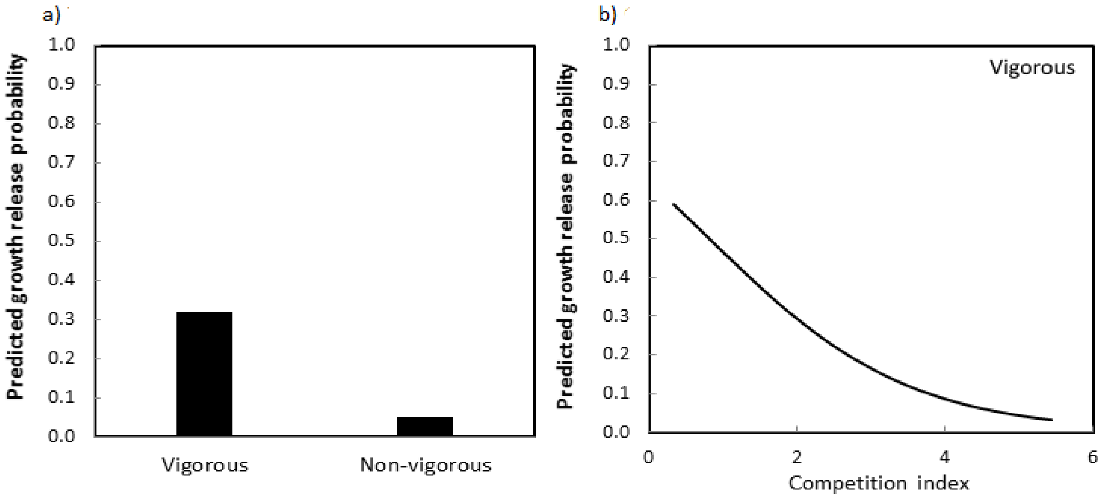

Figure 2.6 Effects of competition index a) and tree vigour at the time of selection cut; b) on mean predicted growth release probabilities after selection cutting. In both panels, the average value of the covariate was used to calculate the values of the variable that was presented.

2.6. Discussion

2.6.1. Mortality patterns

The main objective of this study was to evaluate the effect of short- and long-term growth trends on post-harvest mortality and tree growth responses to partial cutting. To do so, we characterized growth patterns prior to tree death and we identified growth release episodes from entire tree-ring series of sugar maple trees from stands for which the disturbance history was well documented. Overall, long periods of continuous growth decline or long periods of slow radial growth after a severe decrease were observed in respectively 48 % and 44 % of dead trees. These growth patterns generally caused a progressive decline in tree vigour that was mostly initiated by the synergetic influence of drought and insect defoliations that occurred from 1981 to 1986 (Payette et al. 1996). These results supported our first hypothesis that stated that post-harvest mortality is preceded by a progressive decline in vigour, which was initiated decades before the partial cut, rather than by a marked drop in the first few years following the application of the treatment. Long-term growth decrease is normally associated with depletion of carbon reserves and with a gradual decline in hydraulic performance that affects the survival probabilities of trees (Cailleret et al. 2017). Overall, only 12 % of mortality events were preceded by such a rapid growth decline in the first few years following selection cutting. In this case, trees likely died as a result of intense stress caused by soil disturbance and compaction, as well as damage to tree roots, trunk and the crown, which occurred during partial cut operations (Caspersen 2006; Martin et al. 2014).

2.6.2. Post-cut mortality model

Our results showed that predictions of post-cut mortality events can be significantly improved by considering long-term radial growth trends in individual trees. A prolonged period of slow radial growth was shown to increase the risk of tree mortality markedly, thereby providing additional support for our first hypothesis. Shorter-term radial growth variables, such as tree growth-trend and growth sensitivity over a 5-year period, were also effective in increasing the performance of the mortality model, as has been observed in other studies (Bigler & Bugmann 2004, Hartmann et al. 2008, Cailleret et al. 2016). Growth trend is a complementary growth variable because it allows the identification of trees undergoing a growth decrease period at the moment of harvest. Growth trend may also help identify trees that are susceptible of dying after a short and abrupt growth decline, despite growing at a relatively high rate at the time of harvest. Higher sensitivity to annual climatic variability in years prior to harvest, which is expressed by higher inter-annual growth variability, was also expected to be linked with increased post-cut mortality risk. Climate-related variables, such as temperature and water availability, represent important determinants of carbon acquisition and growth rate (Fatichi et al. 2014; Lempereur et al. 2015). Carbon resources that are allocated to radial growth may come from photosynthates that are acquired over the past several years (Lane et al. 1993; Gaudinski et al. 2009). Carbon reserves are a key resource for trees undergoing stress, as they are used to moderate the effects of variation in carbon production (Gaudinski et al. 2009). Carbohydrate reserves are particularly important for hardwood species, such as sugar maple, because they must produce new foliage each spring to activate the photosynthetic process. Consequently, wood production in sugar maple is strongly dependent upon the growing conditions that prevailed during previous years and the carbon resource reserves that were accumulated during this same period (Lane et al. 1993). Higher sensitivity to annual climatic variability, therefore, may reflect a lack of reserves accumulated in past years, thereby reflecting low tree vigour.

The tree vigour classification system that was developed by Majcen et al. (1990) is an important predictor of the occurrence of mortality after selection cutting, with non-vigorous trees having a mortality probability about 16 times higher than vigorous trees. Tree classification systems have been used for several years in northern hardwood forests and only vary slightly from one region to another across Northeastern North America (OMRN

2004; Boulet 2007; Schomaker 2007). These systems use apparent pathological, morphological and mechanical defects on tree stems and crowns to estimate tree vigour and harvesting priorities. For example, mechanical and pathological wounds can reduce tree growth and increase risks of mortality (Guariguata 1998; Ickes et al. 2003) by using carbon resources to compartmentalize the affected cells. These carbon resources are no longer available for tree growth, and the walling-off of energy-storing tissues can magnify this effect (Shigo 1985). For their part, crown-related variables that are included in tree classification systems (e.g., crown ratio) are considered as indirect measures of tree photosynthetic capacity (Leites et al. 2009) and have previously been related to tree growth and survival probabilities (Leites et al. 2009; Morin et al. 2015; Boivin-Dompierre et al. 2017). Cankers and other fungal or bacterial infections can affect tree radial growth (Kaitera et al. 1995; Cherubini et al. 2002) and increase mortality probability (Guillemette et al. 2008) by decreasing photosynthetic potential (Hansen et al. 2000) or by killing part of the cambium and impeding water and nutrient absorption (Davis et al. 1997; Joseph et al. 1998; Mallet & Volney 1999).

2.6.3. Release event identification and modelling

Because many natural disturbance events occurred during the first part of the 1980s (Payette et al. 1996), we expected to observe a large number of growth release events in surviving trees by the end of this particular decade. Yet, the highest frequency of growth release events was observed during the 1990s. This delayed response may be explained by a longer than expected recovery period after disturbance stresses before surviving trees were able to take advantage of canopy openings that are created by the death of neighbours. After selection cutting, the occurrence of release events was slightly less frequent than that observed during the preceding decade. This suggests that the intensity of natural disturbances during the 1980s was likely higher than that induced by selection cutting during the 2000s. While selection cuts generally improve the light availability of residual trees, harvest operations can also produce root, stem and crown damage, which can offset the potential benefits of reduced competition (Hartmann et al. 2009). In addition, the passage of machinery requires wide trails within which every tree is harvested. In the present case, these trails led to a removal of 17 % of the basal area, while the treatment removed nearly 35 %. This left only 18 % of the basal area to be removed from trees outside the trails, most often in narrow strips along these trails. Such localized tree removal within and near skid trails can prevent the extension of the positive effects of partial cutting to all residual trees

(Boivin-Dompierre et al. 2017). The fact that we observed an increasing probability of growth release events with decreasing tree competition suggests that localized tree removal along skid trails may have reduced the potential number of trees with a positive growth response.

None of the long-term growth variables that were tested was significantly related to the occurrence of growth release events. This is contrary to our second hypothesis, which stated that limited radial growth during a long period prior to harvest decreases the subsequent likelihood of a growth release event. This result suggests that the growth release potential of trees is attributable mainly to sudden events, such as the mortality or removal of neighbouring trees, rather than to prior growth trends. Consequently, suppressed sugar maple trees still have the capacity to respond positively to gap creation, regardless of the length of the suppression period. In contrast, Baral et al. (2016) found that long periods of suppression reduced the growth response of sugar maple trees to partial harvesting. However, the study did not measure the growth reaction of trees in terms of percent-growth change, but in basal area increment (cm^2 yr^1). Indeed, a suppressed tree with low radial growth is likely to have a lower increment, even following a release event, compared to a dominant tree with a fast growth rate. In our study, trees exhibiting post-cut growth release after being suppressed were relatively small (DBH < 32 cm), which is consistent with the generally higher growth response that is observed in young, small trees after partial cutting compared to large, older trees (Lorimer & Frelich 1989). Trees that have not developed any defects affecting tree vigour during a growth suppression period that has been induced by high neighbourhood competition will retain their ability to respond positively to gap exposure. Conversely, trees affected by defects that are related to tree vigour during the same growth suppression period will have a lower growth release potential, and a higher probability of mortality in years following the selection cut. This is supported by the results of Baral et al. (2016), who associated the reduced growth response of suppressed trees to partial cutting to a greater probability to being damaged by defects affecting tree vigour.

2.6.4. Silvicultural implications: assessing vigour for tree marking

These results highlight the complex growth dynamics of sugar maple trees and the challenges that are related to the silvicultural management of northern hardwood forests. Tree-ring chronologies indicated that declining sugar maple trees are likely to be unproductive for a long period before dying. Even if declining trees are unproductive, they still contribute to increasing competition among neighbouring trees, which is likely to decrease stand growth and increase mortality losses. To limit the loss of productivity that is associated with the maintenance of such trees between two selection cuts, we recommend continuing the use of a tree vigour classification system to guide tree marking decisions. In addition to identifying moribund trees, such vigour classification systems can help identify trees that are likely to have a positive growth response to selection cutting, thereby increasing stand productivity and product value. Our results suggest that in the case of sugar maple, a simple binary classification system (i.e. high-vigour or low-vigour trees according to criteria presented in Table 2.1) is a good predictor of post-harvest mortality and the ability of sugar maple trees to respond positively to a selection cut. Such a simple classification system has the advantage of improving the tree marking process without affecting its quality (Delisle-Bouliane et al. 2014; Cecil-Cockwell & Caspersen 2015; Moreau et al. 2018).

2.7. Conclusion

In recent years, dendrochronological approaches have been successfully applied to investigate mortality and growth responses to natural disturbance events (e.g., Bigler & Bugmann 2004; Fraver & White 2005; Black et al. 2009; Hartmann et al. 2008; Cailleret et al. 2016, 2017; Després et al. 2017). This study confirms that predictions of post-cut mortality are significantly improved by considering long-term radial growth trends in individual trees. Tree-ring chronologies showed that post-harvest mortality is mostly preceded by a progressive decline in vigour, which is marked by progressive growth decrease in the decades prior to partial cutting. These results confirmed the relevance of studying long-term tree-ring chronologies to predict post-harvest mortality and to deduce causes of post-harvest tree death. In years following partial cutting, only 24 % of live trees responded with a growth release event. This growth response is slightly lower than that which has been induced by natural disturbances in previous decades. None of the short- or long-term growth variables that were tested could explain the occurrence of growth release events. Suppressed sugar maple trees retain the capacity to respond positively to gap creation, regardless of the length of the suppression period, and to short-term growth trends. In order to maximize the productivity of managed northern hardwood stands, further research is required to better understand the factors that can help stimulate a growth reaction in years following partial cutting.

2.8. Acknowledgements

This research was funded by a Discovery Grant to David Pothier from the Natural Sciences and Engineering Research Council of Canada (NSERC), the Fonds de recherche du

Québec – Nature et technologies (FRQNT), and Domtar Corporation. We also thank Ann Delwaide for her help in the dendrochronological laboratory, to Eloïse Dupuis, Alexandre Morin-Bernard and Félix Poulin for their help with the fieldwork and to the staff from Domtar for their support on the project. We are grateful to William F.J. Parsons for reviewing and making valuable comments on the manuscript.

2.9. References

Baral, S. K., Danyagri, G., Girouard, M., Hébert, F., & Pelletier, G. (2016). Effects of suppression history on growth response and stem quality of extant northern hardwoods following partial harvests. *Forest Ecology and Management*, 372, 236–246.

Bates, D., M. Maechler, B. Bolker, & S. Walker. (2015). lme4: linear mixed-effects models using Eigen and S4. R package version 1.1-8.

Bédard, S., & Brassard, F. (2002). Les effets réels des coupes de jardinage dans les forêts publiques du Québec en 1995 et 1996, *Ministère des Ressources naturelles du Québec*, Direction de la recherche forestière, Sainte-Foy, Québec, Canada, 15 p.

Bigler, C., & Bugmann, H. (2004). Predicting the time of tree death using dendrochronological data. *Ecological Applications*, 14, 902–914.

Black, B.A., & Abrams, M.D., (2003). Use of boundary-line growth patterns as a basis for dendroecological release criteria. *Ecological Applications*, 13, 1733–1749.

Black, B.A., & Abrams, M.D., (2004). Development and application of boundary-line release criteria. *Dendrochronologia*, 22, 31–42.

Black, B.A., Abrams, M.D., Rentch, J.S., & Gould, P.J. (2009). Properties of boundary-line release criteria in North American tree species. *Annals of Forest Science,* 66, 205-205.

Boivin-Dompierre, S., Achim, A., & Pothier, D. (2017). Functional response of coniferous trees and stands to commercial thinning in eastern Canada. *Forest Ecology and Management*, 384, 6–16.

Boulet, B. (2007). Défauts et indices de la carie des arbres: Guide d'interprétation, 2^{e} éd. Les Publications du Québec, Québec, pp. 317

Boulet, B., & Landry, G. (2015). La carie des arbres: Fondements, diagnostic et application, 3^{e} éd. Les publications du Québec, Québec, pp. 347

Cailleret, M., Bigler, C., Bugmann, H., Camarero, J. J., Cufar, K., Davi, H., ... & Suarez, M. L. (2016). Towards a common methodology for developing logistic tree mortality models based on ring-width data. *Ecological Applications*, *26*(6), 1827-1841.

Cailleret, M., Jansen, S., Robert, E. M., Desoto, L., Aakala, T., Antos, J. A., ... & Čada, V. (2017). A synthesis of radial growth patterns preceding tree mortality. *Global change biology*, *23*(4), 1675-1690.

Caspersen, J.P., 2006. Elevated mortality of residual trees following single-tree felling in northern hardwood forests. *Canadian Journal of Forest Research*, 36, 1255–1265.

Cecil-Cockwell, M. J. L., & Caspersen, J. P. (2015). A simple system for classifying sugar maple vigour and quality. *Canadian Journal of Forest Research*, 45, 900-909

Cherubini, P., Fontana, G., Rigling, D., Dobbertin, M., Brand, P., & Innes, J.L. (2002). Tree-life history prior to death: Two fungal root pathogens affect tree-ring growth differently. *Journal of Ecology*, 90, 839–850.

Davis, D.D., Torsello, M.L., & McClenahen, J.R. (1997). Influence of *Cryphonectria parasitica* basal cankers on radial growth of scarlet oak in Pennsylvania. *Plant Disease*, 81,369–373.

Delisle-Boulianne, S., Fortin, M., Achim, A., & Pothier, D. (2014). Modelling stem selection in northern hardwood stands: assessing the effects of tree vigour and spatial correlations using a copula approach. *Forestry: An International Journal of Forest Research*, *87*(5), 607-617.

Després, T., Asselin, H., Doyon, F., Drobyshev, I., & Bergeron, Y. (2017). Gap dynamics of late successional sugar maple–yellow birch forests at their northern range limit. *Journal of Vegetation Science,* 28, 368–378.

Fatichi, S., Leuzinger, S., & Körner, C. (2014). Moving beyond photosynthesis: From carbon source to sink-driven vegetation modeling. *New Phytologist*, 201,1086–1095.

Forget, E., Nolet, P., Doyon, F., Delagrange, S., & Jardin, Y. (2007). Ten-year response of northern hardwood stands to commercial selection cutting in southern Quebec, Canada. *Forest Ecology and Management*, 242, 764–775.

Fortin, M., Bédard, S., DeBlois, J., & Meunier, S. (2008). Predicting individual tree mortality in northern hardwood stands under uneven-aged management in southern Québec, Canada. *Annals of Forest Science*, 65(2), 1.

Fraver, S., & White, A.S. (2005). Identifying growth releases in dendrochronological studies of forest disturbance. *Canadian Journal of Forest Research*, 35, 1648–1656.

Fritts, H.C. (1976). Tree Rings and Climate. Academic Press, London, UK. 567 pp.

Gaudinski, J.B., Torn, M.S., Riley, W.J., Swanston, C., Trumbore, S.E., Joslin, J.D., Majdhi, H., Dawson, T.E., Hanson, P.J. (2009). Use of stored carbon reserves in growth of temperate tree roots and leaf buds: Analyses using radiocarbon measurements and modeling. *Global Change Biology*, 15, 992–1014.

Grondin, P., Jean, N., & Hotte, D. (2007). Intégration de la végétation et de ses variables explicatives à des fins de classification et de cartographie d’unités homogènes du Québec méridional, *Ministère des Ressources naturelles et de la Faune*, Direction de la recherche forestière. Mémoire de recherche No 150, pp. 62

Guariguata, M.R. (1998). Response of forest tree saplings to experimental mechanical damage in lowland Panama. *Forest Ecology and Management*, 102, 103–111.

Guillemette, F., Bédard, S., & Fortin, M. (2008). Evaluation of a tree classification system in relation to mortality risk in Québec northern hardwoods. *The Forestry Chronicle*, 84, 886–899.

Hansen, E.M., Stone, J.K., Capitano, B.R., Rosso, P., Sutton, W., Winton, L., Kanaskie, A., & McWilliams, M.G. (2000). Incidence and impact of Swiss needle cast in forest plantations of Douglas-fir in coastal Oregon. *Plant Disease*, 84, 773-778.

Hartmann, H., Beaudet, M., & Messier, C. (2008). Using longitudinal survival probabilities to test field vigour estimates in sugar maple (Acer saccharum Marsh.). *Forest Ecology and Management*, 256(10), 1771-1779.

Hartmann, H., & Messier, C. (2008). The role of forest tent caterpillar defoliations and partial harvest in the decline and death of sugar maple. *Annals of Botany*, 102, 377–387.

Hartmann, H., Beaudet, M., Mazerolle, M.J., & Messier, M. (2009). Sugar maple (Acer saccharum Marsh.) growth is influenced by close conspecifics and skid trail proximity following selection harvest. *Forest Ecology and Management,* 258, 823–831.

Hegyi, F.(1974). A simulation model for managing jack pine stands. In: Growth Models for Tree and Stand Simulation. *Royal College of Forestry,* Stockholm, Sweden, pp. 74–90.

Holmes, R.L., (1983). Computer assisted quality control in tree-ring dating and measurement. *Tree-Ring Bulletin*, 43, 69–78.

Ickes, K., Dewalt, S.J., & Thomas, S.C. (2003). Resprouting of woody saplings following stem snap by wild pigs in a Malaysian rain forest. *Journal of Ecology*, 9, 222–233.

Joseph, G., Kelsey, R.G., & Thies, W.G. (1998). Hydraulic conductivity in roots of ponderosa pine infected with black-stain (*Leptographium wageneri*) or annosus (*Heterobasidion annosum*) root disease. *Tree Physiology*, 18, 333–339.

Kaitera, J., Isaenva, L., & Jalkanem, R. (1995). Long-term damage on Scots pine caused by Gremmeniella abientina near a nickel smelter in the Kola peninsula. *European journal of forest pathology*, 25(6-7), 391-399.

Lane, C. J., Reed, D. D., Mroz, G. D., & Liechty, H. O. (1993). Width of sugar maple (Acer saccharum) tree rings as affected by climate. *Canadian Journal of Forest Research*, 23(11), 2370-2375.

Leites, L.P., Robinson, A.P., & Crookston, N.L. (2009). Accuracy and equivalence testing of crown ratio models and assessment of their impact on diameter growth and basal area increment predictions of two variants of the Forest Vegetation Simulator. C*anadian Journal of Forest Research*, 39, 655–665.

Lempereur, M., Martin-St-Paul, N.K., Damesin, C., Joffre, R., Ourcival, J.-M., Rocheteau & A., Rambal, S. (2015). Growth duration is a better predictor of stem increment than carbon supply in a Mediterranean oak forest: Implications for assessing forest productivity under climate change. *New Phytologist*, 207, 579–590.

Lorimer, C.G., & Frelich, L.E. (1989). A methodology for estimating canopy disturbance frequency and intensity in dense temperate forests. *Canadian Journal of Forest Research*, 19, 651–663.

Majcen Z., Richard, Y., Ménard, M., & Grenier, Y. (1990). Choix des tiges à marquer pour le jardinage d'érablières inéquiennes, Guide technique, *Ministère de l'Énergie et des Ressources du Québec*, Direction de la recherche forestière, Mémoire No. 96

Majcen, Z. (1996). Coupe de jardinage et coupe de succession dans cinq secteurs forestiers. Accroissement quinquennal en surface terrière et état de la régénération, *Ministère des Ressources naturelles et de la Faune du Québec*, Direction de la recherche forestière, Mémoire No. 70

Mallet, K.I., & Volney, W. J. A. (1999). The effect of *Armillaria* root disease on lodgepole pine tree growth. *Canadian Journal of Forest Research*, 29, 252–259.

Martin, A. R., Caspersen, J. P., Fuller, M. M., Jones, T. A., & Thomas, S. C. (2014). Temporal dynamics and causes of postharvest mortality in a selection-managed tolerant hardwood forest. *Forest ecology and management*, 314, 183-192.

Moreau, E., Bédard, S., Moreau, G., & Pothier, D. (2018). Relationships between tree vigor indices and a tree classification system based upon apparent stem defects in northern hardwood stands. *Forests*, 9(10), 588.

Morin, R. S., Randolph, K. D. C., & Steinman, J. (2015). Mortality rates associated with crown health for eastern forest tree species. *Environmental Monitoring and Assessme*nt, 187, 1–11

Nagel, T. A., Svoboda, M., & Kobal, M. (2013). Disturbance, life history traits, and dynamics in an old-growth forest landscape of southeastern Europe. *Ecological Applications*, 24, 663–679.

Nowacki, G.J., & Abrams, M.D. (1997). Radial-growth averaging criteria for reconstructing disturbance histories from presettlement-origin oaks. *Ecological Monographs*, 67, 225–249.

Nyland, R.D. (1998). Selection system in northern hardwoods. *Journal of Forestry*, 96, 18-21.

Ogle, K., Whitham, T.G., & Cobb, N.S. (2000). Tree-ring variation in Pinyon predicts likelihood of death following severe drought. *Ecology*, 81, 3237-3243.

Ontario Ministry of Natural Ressources. (2004). Ontario tree marking guide, Ver. 1.1. *Ontario Ministry of Natural Ressources*, 252 pp.

Payette, S., Fortin, M.J., & Morneau, C. (1996). The recent sugar maple decline in southern Quebec : probable causes deduced from tree rings. *Canadian Journal of Forest Research*, 26, 1069–1078.

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., Heisterkamp, S., Van Willigen, B., & Maintainer, R. (2017). Package 'nlme'. *Linear and nonlinear mixed effects models*, version, 3.

Pothier, D., Fortin, M., Auty, D., Delisle-Boulianne, S., Gagné, L. V., & Achim, A. (2013). Improving tree selection for partial cutting through joint probability modelling of tree vigor and quality. *Canadian journal of forest research*, 43(3), 288-298.

R Development Core Team, 2018. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria, http://www.R-Landsc. Ecol. 21, 596–605.

Robitaille, G., Boutin, R., & Lachance, D. (1995). Effects of soil freezing stress on sap flow and sugar content of mature sugar maples (Acer saccharum). *Canadian journal of forest research*, 25(4), 577-587.

Salas-Eljatib, C., Fuentes-Ramirez, A., Gregoire, T. G., Altamirano, A., & Yaitul, V. (2018). A study on the effects of unbalanced data when fitting logistic regression models in ecology. *Ecological Indicators*, 85, 502–508.

Saucier, J.-P., Grondin, P., Robitaille, A., Gosselin, J., Morneau, C., Richard, P.-J.-H., Brisson, J., Sirois, L., Leduc, A., Morin, H., Thiffault, E., Gauthier, S., Lavoie, C. & Payette, S. (2009). Écologie forestière. Manuel de foresterie, 2e édition. *Ordre des ingénieurs forestiers du Québec*, Éditions Multimondes, Québec, pp.165-316.

Schomaker, M. (2007). *Crown-condition classification: a guide to data collection and analysis (Vol. 102)*. US Department of Agriculture, Forest Service, Southern Research Station.

Shigo, A.L., (1985). Wounded forests, starving trees. *Journal of Forestry*. 83, 668–673.

Stan, A.B., & Daniels, L.D. (2010). Growth releases of three shade-tolerant species following canopy gap formation in old-growth forests. *Journal of Vegetation Science*, 21,74–87.

Suarez, M.L., Ghermandi, L., & Kitzberger, T. (2004). Factors predisposing episodic drought induced tree mortality in *Nothofagus* – site, climatic sensitivity and growth trends. *Journal of Ecology*, 92, 954–966.

Trotsiuk, V., Hobi, M. L., & Commarmot, B. (2012). Age structure and disturbance dynamics of the relic virgin beech forest Uholka (Ukrainian Carpathians). *Forest Ecology and Management*, 265, 181-190.

Vanoni, M., Bugmann, H., Nötzli, M., & Bigler, C., (2016). Drought and frost contribute to abrupt growth decreases before tree mortality in nine temperate tree species. *Forest Ecology and Management*, 382,51–63.

Webster, C. R., & Jensen, N. R. (2007). A shift in the gap dynamics of *Betula alleghaniensis* in response to single-tree selection. *Canadian Journal of Forest Research*, 37(3), 682-689.

Zuur, A. F., Ieno, E.N., & Elphick, C.S. (2010). A protocol for data exploration to avoid common statistical problems. *Methods in Ecology and Evolution*. 1, 3–14.

3. Chapitre 3

Relevance of stem and crown defects to estimate tree vigour in northern hardwood forests

3.1. Abstract

The visual assessment of tree vigour before partial cutting is a key element of the long-term sustainability of managed hardwood forests. Several classification systems have been developed and applied to perform this task during the tree-marking process. They segregate trees in different vigour classes based on the presence and severity of stem and crown defects. Yet, the relevance of using these defects to assess tree vigour has rarely been empirically validated. In this study, we analysed the relationships between quantitative vigour indicators and a full range of individual defects using 336 sugar maple and 84 yellow birch trees. Among the tested defects, the tree crown density showed the best ability to identify slow growing, non-vigorous sugar maple trees, regardless of their size. However, none of the stem-related defects, such as bark aspect, the presence of cambial necrosis or conks and stromata were strongly related to our quantitative vigour indicators. For yellow birch, none of the stem defects and crown conditions were found to be related to our vigour indicators. We conclude that, pending longitudinal studies that will provide a full empirical validation of classification systems, crown density should be used to assess recent growth and vigour of sugar maple trees and guide tree marking.

3.2. Résumé

Nous avons réalisé une analyse des relations entre deux indices de vigueur quantitatifs basé sur la croissance et une gamme complète de défauts répertoriés dans trois systèmes de classification de la vigueur utilisés en Amérique du Nord. Un total de 336 érables à sucre et 84 bouleaux jaunes ont été échantillonnés. Parmi les défauts testés, la densité du houppier était l’indicateur le plus efficace pour identifier les arbres non vigoureux, quelle que soit leur taille. À l’inverse, les défauts de la tige tels que l’aspect de l’écorce, la présence de nécrose du cambium et de sporophores n’étaient pas de bons prédicteurs des indices de vigueur quantitatifs. Pour le bouleau jaune, aucun des défauts testés n’était lié à nos indicateurs de vigueur. Nous concluons que la densité du houppier devrait être utilisée pour guider les opérations de marquage dans les érablières.

3.3. Introduction

Northern hardwood forests cover a large area of North America, which is generally located near an important and lucrative market for wood-products. Sugar maple (*Acer saccharum* Marsh.) and yellow birch (*Betula alleghaniensis* Britt.) trees are particularly sought after as a raw material for products such as veneer, flooring and furniture (Havreljuk et al. 2013). In recent decades, the demand for wood products has led to the application of partial cuts characterised by the harvesting of large-diameter trees with high-quality stems. Such practices, now referred to as 'high-grading', have often resulted in degraded stands characterized by low proportions of vigorous, large-diameter trees (Nyland 1998; Raymond et al. 2009).

To help rehabilitate high-graded forest stands, and thus recover their productivity, the selection cutting system has been widely implemented using tree marking rules that prioritize the removal of non-vigorous trees (Nyland 1998). To guide tree marking decisions, several classification systems have been developed to estimate tree vigour based on crown or bark characteristics (Schomaker 2007; OMNR 2004), pathological symptoms and mechanical damage (Boulet 2007), or tree form (Pelletier et al. 2016). Current classification systems typically segregate trees into several vigour classes based on various individual stem attributes. Tree vigour has been defined either based on the growth potential of trees (OMNR 2004; Pelletier et al. 2016) or the risk of mortality during the next cutting cycle of 25 years (Boulet 2007).

Most attempts to validate classification systems empirically have led to the conclusion that numerous vigour classes were unnecessary to achieve the desired accuracy (Fortin et al. 2008; Guillemette et al. 2008; Hartmann et al. 2009; 2015; Cecil-Cockwell & Caspersen 2015; Moreau et al. 2018a). Among these studies, Moreau et al. (2018a) demonstrated that for both sugar maple and yellow birch trees, a four-class vigour system was only weakly related to quantitative tree vigour indices such as the growth efficiency index (Waring et al. 1981; Christiansen et al. 1987; Waring 1987) and other indicators of radial growth (Pedersen 1998; Bigler & Bugmann 2003; Duchesne et al. 2003; Hartmann et al. 2009).

The complexity of such classification systems is most often related to the large range of individual defects that hardwood species are prone to develop in their lifetime, and that must therefore be evaluated (Cecil-Cockwell & Caspersen 2015). Although several of these defects are caused by pathogens (e.g., Boulet 2007), their use to asses tree vigour has yet to be empirically validated. Without such validation, trees may be incorrectly classified based on the presence/absence of defects that are unrelated to their growth potential or mortality probability. It also makes it difficult to separate stem defects related to tree vigour and those that are more related to tree quality, i.e. the volume and value of products that can be recovered from each tree (Pothier et al. 2013; Cecil-Cockwell & Caspersen 2015; Power & Havreljuk 2018). Potential lags between the appearance of the defects and their effects on tree growth and mortality imply that empirical validations of such systems should be based on longitudinal data. However, long-term surveys are rarely available in practice, especially where classification systems have evolved over time.

In the absence of longitudinal data, another approach to gain immediate knowledge on the visual assessment of tree vigour consists of relating the presence of apparent defects to well-established quantitative tree vigour indices that are based on recent growth (Bigler & Bugmann 2003; Hartmann et al. 2009; Waring et al. 1980; Mitchell et al. 1983; Waring & Pitman 1985; Pedersen et al. 1998; Coops et al. 2009; Moreau et al. 2018a). The use of such quantitative vigour indices can be considered appropriate for this task given that tree vigour decline is a slow process by which little change may be observed over a decade (Moreau et al. 2018a). The approach advocated in this study is based on the premise that in cases where the study of recent growth rings indicates a loss of vigour, the defects related to this decline should still be present on the tree at the end of the observation period.

The general objective of this study was thus to identify the stem and crown defects that are significantly related to the current vigour of sugar maple and yellow birch trees. To achieve this, we empirically quantified the relationships between defects commonly used in North American classification systems and two types of well-established quantitative tree vigour indices. In addition, multi-model selection was conducted to determine parsimoniously the simplest defect assemblages that can be used to accurately assess tree vigour. To our knowledge, such a parsimonious analysis has never been performed to examine how tree vigour varies along a full range of individual stem and crown defects that can be easily identified. Gaining knowledge on the visual assessment of tree vigour is necessary to help improve tree marking rules, which are key to rehabilitate high-graded northern hardwood forests managed under silvicultural system reliant on partial cuts.

3.4. Materials and methods

3.4.1. Sampling sites

The study area was located on private woodlots owned by Domtar Corporation in southern Quebec (45°31'-45°57'N, 71°23'-70°33'W). This area lies within the eastern sugar maple-American basswood and the eastern sugar maple-yellow birch bioclimatic subdomains (Saucier et al. 2009). The first subdomain is characterized by mean annual temperatures between 4 and 5 °C and mean annual precipitation between 1000 and 1150 mm, with a growing season of 165 to 180 days (Saucier et al. 2009). The second one is characterized by mean annual temperatures between 2.5 and 4 °C and mean annual precipitation between 915 and 1100 mm, with a growing season of 145 to 165 days (Saucier et al. 2009). The main surface deposits are shallow or deep tills of glacial origin and the topography is characterized by hills and gentle slopes (Grondin et al. 2007). The sampling sites were located in uneven-aged northern hardwood stands dominated by sugar maple *(Acer saccharum* Marsh.), followed by yellow birch (*Betula alleghaniensis* Britt.) red maple (*Acer rubrum* L.) with minor components of American beech (*Fagus grandifolia* Ehrh.), balsam fir (*Abies balsamea* (L.) Mill.) and red spruce (*Picea rubens* Sarg.).

3.4.2. Sample plots and data collection

From 1998 to 2003, 35 circular permanent sample plots (PSPs) of 400 m^2 in area were established randomly in northern hardwood stands representative of regional site conditions. Within each PSP, all trees with a diameter at breast height (DBH) > 9.0 cm were tagged and the PSPs were inventoried periodically at a mean interval of five years. Species and DBH of trees with a DBH > 9.0 cm were recorded at each survey. During the summer of 2016, we remeasured the DBH (± 0.1 cm) of each tree within the 35 PSPs and we extracted an increment core from all sugar maple and yellow birch trees at a height of 1 m above the ground surface and oriented toward the plot center. The increment cores were air-dried and sanded to allow a clear identification of the final cell layer. Annual ring widths were then measured with a Velmex micrometer (± 0.002 mm).

Additional information on previously cored trees were collected during the summer of 2018. First, we remeasured the DBH (± 0.1 cm) of all sampled trees. Second, based on three complementary tree classification systems used in northern hardwood forests across North America (i.e. OMNR 2004; Boulet 2007; Schomaker 2007), we identified all stem and crown defects present on all sugar maple and yellow birch trees. The tree vigour classification of

Boulet (2007) relies on the presence/absence of pathological symptoms and mechanical damage grouped into different categories of stem-related defect: (1) conks and stromata (i.e., fungal fruiting bodies); (2) cambial necrosis; (3) stem deformations and injuries; (4) stem base and root defects; (5) stem and bark cracks; (6) woodworms (i.e., insect entry holes) and sap wells; and (7) forks and pruning defects. The crown health indicators from Schomaker (2007) were: (1) crown dieback (CDBK), i.e. the recent mortality of branches with fine twigs, which begins at the terminal portion of a branch and proceeds inward toward the trunk; (2) crown density (CDEN), i.e. the proportion of the projected crown outline that contains biomass, which includes branches, foliage and reproductive structures (see Figure 3.1); and (3) crown vigour class (CVC), i.e. the visual assessment of the crown vigour using the uncompacted live crown ratio, the presence of damaged foliage and recent crown dieback as criteria to define a three-level categorical variable (high, moderate, and poor vigour). For their part, both CDBK and CDEN were estimated in 5 % increments. Finally, we determined the bark aspect of each tree according to the Ontario Tree Marking Guide (OMNR 2004). This classification system uses the firmness of the bark as well as characteristics of bark fissures and ridges to assess tree vigor (see OMNR 2004 for further details). The bark aspect was expressed as a three-level categorical variable, i.e. rough (low vigour), intermediate (medium vigour), and smooth bark (high vigour). In total, all these characteristics were measured on 336 sugar maple and 84 yellow birch trees.

3.4.3. Vigour indices

Tree vigour can be quantitatively estimated from growth indices, which are considered as good indicators of tree health and long-term probability of mortality (Duchesne et al. 2003; Bigler & Bugmann 2003). Theoretically, stemwood production is one of the last priorities of tree resource allocation (Waring 1987). On the one hand, low stemwood production should indicate that most of the acquired carbon is used to sustain higher priority allocations, which implies a weak overall tree vigour. On the other hand, high stemwood production suggests that tree carbon resources far exceed priority allocations, thereby indicating strong overall tree vigour (Waring 1987). We therefore computed two types of growth indices that have been widely used to estimate tree vigour, i.e. an index based solely on the stem's basal area growth (Duchesne et al. 2003; Bigler & Bugmann 2003; Hartmann et al. 2009; Moreau et al. 2019) and the growth efficiency index (Waring et al. 1980; Mitchell et al. 1983; Waring & Pitman 1985; Pedersen et al. 1998; Coops et al. 2009; Moreau et al. 2019). Given that sugar maple growth decline is known to extend over several years and even up to several decades before tree death (Moreau et al. 2019), the growth indices were calculated over a ten-year period. Indeed, during such a 10-year period, tree vigour, as assessed based on the presence/absence of apparent defects, was observed to remain stable for 80 % of vigorous and 95 % of non-vigorous sugar maple and yellow birch trees (Moreau et al. 2018a). Radial growth was averaged over the entire 10-year period to reduce the potential effects of episodic events into the vigour indices (Moreau et al. 2018a). The first vigour index corresponds to the mean annual basal area increment (BAI) from 2008 to 2018. Tree-level BAs in 2018 and 2016 were computed using the DBH values from repeated measurements, then we subtracted 2016 values from 2018 values to obtain BA increments for the period 2016-2018. Annual tree-rings from the increment cores sampled in 2016 were then used to compute individual BAI from 2016 to 2008. Tree-level BAI ($dm^2 \, yr^{-1}$) values from 2008 to 2018 were obtained by summing the two measurements and then dividing by the number of years. The second vigour index, known as the growth efficiency index (GE), corresponds to stemwood mass increment per unit leaf area, and was also calculated over the same period. The annual production of stemwood mass was calculated as in Moreau et al. (2018a):

$$\Delta W_s = \frac{\beta_1\left(D_{2018}^{\beta_2} - D_{2008}^{\beta_2}\right)}{10} \qquad [1]$$

where ΔW_s is the dry weight of stemwood produced annually (kg), D_{2018} is tree DBH in 2018 (cm), D_{2008} is tree DBH in 2008 (cm), β_1 takes the value of 0.1315 for sugar maple and 0.1932 for yellow birch, while the value of β_2 is 2.3129 for sugar maple and 2.1569 for yellow birch (Lambert et al. 2005). The leaf area of each tree was estimated with the following equation (Moreau et al. 2018b):

$$LA = \beta_1 CSA^{\beta_2} \qquad [2]$$

where LA is tree leaf area (m^2), CSA is crown surface area (m^2) calculated with crown height and its mean quadratic radius (see Moreau et al. 2018b for details), β_1 is 1.121 for sugar maple and 1.021 for yellow birch, and β_2 is 0.981 for sugar maple and 1.035 for yellow birch. The GE ($g \, m^2 \, yr^{-1}$) of each tree was then calculated using the average stemwood mass produced annually (ΔWs), divided by the tree leaf area (LA):

$$GE = \Delta W_s / LA \qquad [3]$$

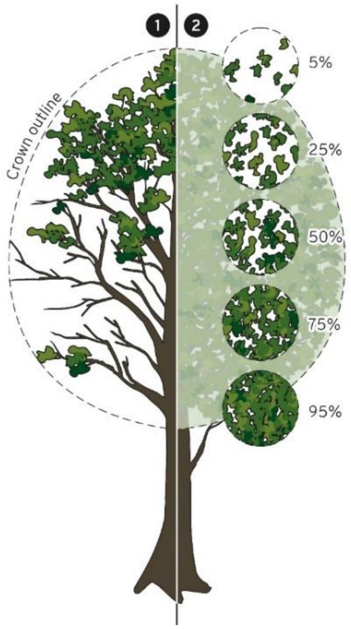

Figure 3.1 Method for determining the crown density (CDEN), i.e. the amount of crown branches, foliage, and reproductive structures that blocks light visibility through the projected crown outline. The first step consists of reconstructing the crown outline by visualizing a normal, expected crown, that encompass the branch tips of the subject tree. The projected crown outline includes dead and broken branches, which are then considered as a percentage of crown missing. The second step consists of estimating the foliage density i.e. the amount of light intercepted by the remaining live portion of the crown. Based on these two assessments, the percentage of the projected crown outline that blocks sunlight is estimated in 5 % increments. For more details, see Schomaker (2007).

3.4.4. Mixed linear models

To examine the relationships between stem and crown defects and the two quantitative vigour indices, we fitted mixed linear models with a plot-level random effect using the *lme* function of the *nlme* package (Pinheiro et al. 2017) in the R statistical programming environment (Version 3.5.1, R Core Team, 2018). Three types of independent variables were tested: (1) size-related variables, i.e. DBH in 2018, leaf area (LA) and relative height (RH), defined as the height of the tree of interest divided by the average height in the PSP, (2) crown condition values estimated from the system of Schomaker (2007), i.e. CDBK, CDEN, CVC, and (3) stem-related variables, i.e. the stem-defect categories from Boulet (2007) and the bark aspect from OMNR (2004). To fit the model, size-related variables, CDBK and CDEN were treated as continuous data, CVC and bark aspect as three-level categorical data (high, moderate, and poor vigour), and the stem-defect as two-level categorical data (presence/absence). The growth efficiency index was ln-transformed (using natural logarithm) to ensure the normality of residuals. Model assumptions (homogeneity of variance, normality of residuals and the presence of outliers) were validated with a graphical analysis of the residuals. To avoid multi-collinearity, the variance inflation factor (VIF) was calculated between candidate variables with VIF < 5 as the threshold to exclude a variable from the model (Zuur et al. 2010).

3.4.5. Modelling process

Preliminary analyses indicated that sugar maple had significantly ($P < 0.05$) lower BAI and greater GE values than yellow birch trees. Consequently, the two species were treated separately for further analyses. Considering the large amount of candidate explanatory variables, a manual stepwise procedure was performed in three distinct steps to find the best univariate, bivariate and multivariate models. First, only one size-related variable at a time was included in models to select the best univariate model. The resulting models were systematically compared to an intercept-only model (null model). The selection of the best model was based upon Akaike's information criterion (AICc). Second, only one crown-related variable at a time was added to the best univariate model to select the best bivariate model. The interaction between two candidate explanatory variables was systematically included in the models. In the third step, 18 models composed the final multivariate model selection: the null model, the best univariate and bivariate models, eight models composed of the best bivariate model with only one additional stem-related variable at the time and finally, seven additional models were produced by sequentially adding all remaining stem-related variables to the multivariate model. Bark aspect was added first in the multivariate model because it has been shown to reflect the growth potential of sugar maple and yellow birch trees (Gauthier & Guillemette 2018). Fungal infections and crack defects were added second and third because they were previously related to stem quality (Havreljuk et al. 2014). The remaining stem-related variables were added to the models according to their risk (from highest to lowest) of decreasing tree vigour based on Boulet (2007). When the AIC weight of any model was lower than 90 %, a model averaging procedure was performed to compute unconditional 95 % confidence intervals for parameters of interest (Mazerolle 2006). Only variable parameters with confidence intervals excluding zero were considered as good predictors (Mazerolle 2006). To help describe the models, we also computed the delta AIC, the conditional coefficient of determination (R^2) and the P-value of the candidate variables. Model selection based on AICc and multi-model inferences were performed using the AICcmodavg package (Mazerolle 2017).

3.5. Results

The frequency of all categorical defects was generally well distributed across diameter classes (Table 3.1). The number of sampled trees decreased with increasing diameter class, which is what would be expected given the typical negative exponential distribution of uneven-aged stands (Table 3.1). Overall, 74 % of the sample trees had at least one stem defect, 30 % had two stem defects and 8 % had more than two defects. The most abundant stem defects for both sugar maple and yellow birch were stem deformations and injuries and the presence forks and pruning defects, while the least abundant were conks and stromata and the presence of woodworms and sap wells (Table 3.1). The occurrence of stem defects on trees seemed to be independent as they were not correlated with each other. However, the proportion of trees with poor crown condition tended to increase with an increasing number of stem defects. For example, while only 2.5 % of trees without stem defects had a crown density lower than 50 %, this proportion increased to 13 % for trees with one stem defect and then to 40 % for trees with more than two stem defects. Similarly, the number of stem defects increased with increasing bark roughness. Nevertheless, only weak correlations were observed among variables representing stem and crown defects, which resulted in an absence of multi-collinearity during the modelling process.

3.5.1. Sugar maple

The best univariate model explaining the variation of both BAI and GE included tree DBH as an independent covariate (Table 3.2, model 1; Table 3.3, model 1). In the second step, the addition of crown density and its interaction with DBH yielded the best bivariate models for both BAI and GE (Table 3.2, model 4; Table 3.3, model 4). Because the interaction between DBH and crown density was highly significant ($p < 0.0001$) for both BAI and GE, this term was retained and thus included in further modelling steps. Although not being part of the best bivariate model, the interaction term between DBH and both crown dieback and crown vigour had also significant relationship with BAI ($p < 0.0001$) and GE ($p < 0.05$). In the third step, the addition of the bark aspect, the presence of conks and stromata and stem and bark cracks decreased the AICc slightly and increased the coefficient of determination (R^2) of the best bivariate model for BAI (Table 3.2, models 7-9). However, multi-model inferences indicated that the unconditional confidence intervals of only one parameter (the interaction between DBH and crown density) excluded zero (Table 3.4). This result indicates that none of these stem-related variables contribute much to explaining the variation in sugar maple growth. For GE, no stem-related defect induced a decrease of the AICc of the best bivariate model or had significant parameters (Table 3.3). Despite this, the inclusion of the bark aspect, the presence of stem base and root defects, woodworms and sap wells and forks and pruning defects yielded plausible multivariate models with $\Delta_i < 2$ (Table 3.3, models 8-11). Multi-model inferences indicated that the unconditional confidence intervals of the parameters associated with the interaction between DBH and the crown density excluded zero, unlike any other variables (Table 3.4). Consequently, none of these stem-related variables can be considered as good predictors of the sugar maple GE. Based on the best models and the observed data, the BAI and GE of sugar maple trees increased with increasing DBH and crown density (Figure 3.2). Unlike BAI that increased steadily from the lowest to the highest DBH class, GE values increased with DBH up to the 40-49 DBH class and remained constant thereafter (Figure 3.2b). For trees with a crown density below 50 %, BAI and GE values were consistently low for all DBH classes (Figure 3.2).

Table 3.1 Number of sugar maple and yellow birch trees sampled in the 35 PSPs by diameter class and categorical defect categories: CS, conks and stromata; CN, cambial necrosis; DI, stem deformation and injuries; BR, stem base and root defects; CK, stem and bark cracks; WS, and root defects, CK: Stem and bark cracks, WS: Woodworms and sap wells, FP: Forks and pruning defects, Bark$_{1-3}$: Bark character from high vigour (1) to low vigour (3), CVC$_{1-3}$: Crown vigour class from high vigour (1) to low vigour (3).

Sugar maple

DBH (cm)	Total	CS	CN	DI	BR	CK	WS	FP	Bark$_1$	Bark$_2$	Bark$_3$	CVC$_1$	CVC$_2$	CVC$_3$
9.0-19.9	123	3	29	37	4	7	5	12	19	97	7	41	79	3
20.0-29.9	104	9	21	21	14	17	8	18	17	17	3	34	69	1
30.0-39.9	72	8	13	16	11	14	4	13	18	18	5	26	46	0
40.0-49.9	27	3	2	4	1	7	1	6	2	2	4	15	12	0
> 50.0	10	1	1	3	2	1	1	4	3	3	4	3	7	0
Total	336	24	66	81	32	46	19	53	59	137	23	119	213	4

Yellow birch

DBH (cm)	Total	CS	CN	DI	BR	CK	WS	FP	Bark$_1$	Bark$_2$	Bark$_3$	CVC$_1$	CVC$_2$	CVC$_3$
9.0-19.9	42	2	0	17	0	3	0	3	4	34	4	13	29	0
20.0-29.9	26	0	2	8	3	0	1	2	1	23	2	7	19	0
30.0-39.9	14	0	1	3	3	2	1	2	2	11	1	1	13	0
40.0-49.9	2	0	1	0	0	0	1	1	0	2	0	2	0	0
Total	84	2	4	28	6	5	3	8	7	70	7	23	61	0

Table 3.2 Model selection result from the three distinct steps (univariate, bivariate and multivariate models) predicting the basal area increment of sugar maple trees. AICc is the Akaike Information Criteria, Δ_i is the delta AICc (difference in AICc with the best model), Wt_i is the AICc weight, R^2 is the conditional coefficient of correlation. LA: Leaf area, RH: Relative height, CDEN: Crown density, CDBK: Crown dieback, CVC: Crown vigour class, Bark: Bark aspect, CS: Conks and stromata, WS: Woodworms and sap wells, and CK: Stem and bark cracks. All models included an intercept among the fixed effects as well as a plot-level random intercept. Note that only the five best multivariate models are shown. Models with an interaction (*) also include the individual variables.

Sugar maple

Basal area increment (BAI)

Univariate models

Model	Variables	AICc	Δ_i	Wt_i	R^2
1	**DBH**	**772.18**	**0.00**	**1.00**	**0.45**
2	LA	826.12	53.94	0.00	0.40
3	RH	868.29	96.11	0.00	0.29
0	Intercept	959.67	187.49	0.00	-

Bivariate models

Model	Variables	AICc	Δ_i	Wt_i	R^2
4	**DBH*CDEN**	**731.18**	**0.00**	**1**	**0.53**
5	DBH*CDBK	755.16	23.98	0.00	0.49
6	DBH*CVC	786.52	36.34	0.00	0.47

Multivariate models

Model	Variables	AICc	Δ_i	Wt_i	R^2
7	**DBH*CDEN + Bark**	**729.11**	**0.00**	**0.22**	**0.55**
8	DBH*CDEN + Bark + CS	729.44	0.33	0.19	0.55
9	DBH*CDEN + Bark + Ck + CS	731.15	2.05	0.08	0.55
10	DBH*CDEN	731.18	2.07	0.06	0.53
11	DBH*CDEN + Bark + WS + Ck + CS	731.58	2.47	0.06	0.56

Figure 3.2 Mean observed A) basal area increment and B) growth efficiency as function of the DBH class and the crown density (CDEN) for sugar maple trees. Each point is the mean value by DBH class and the bars correspond to the standard errors.

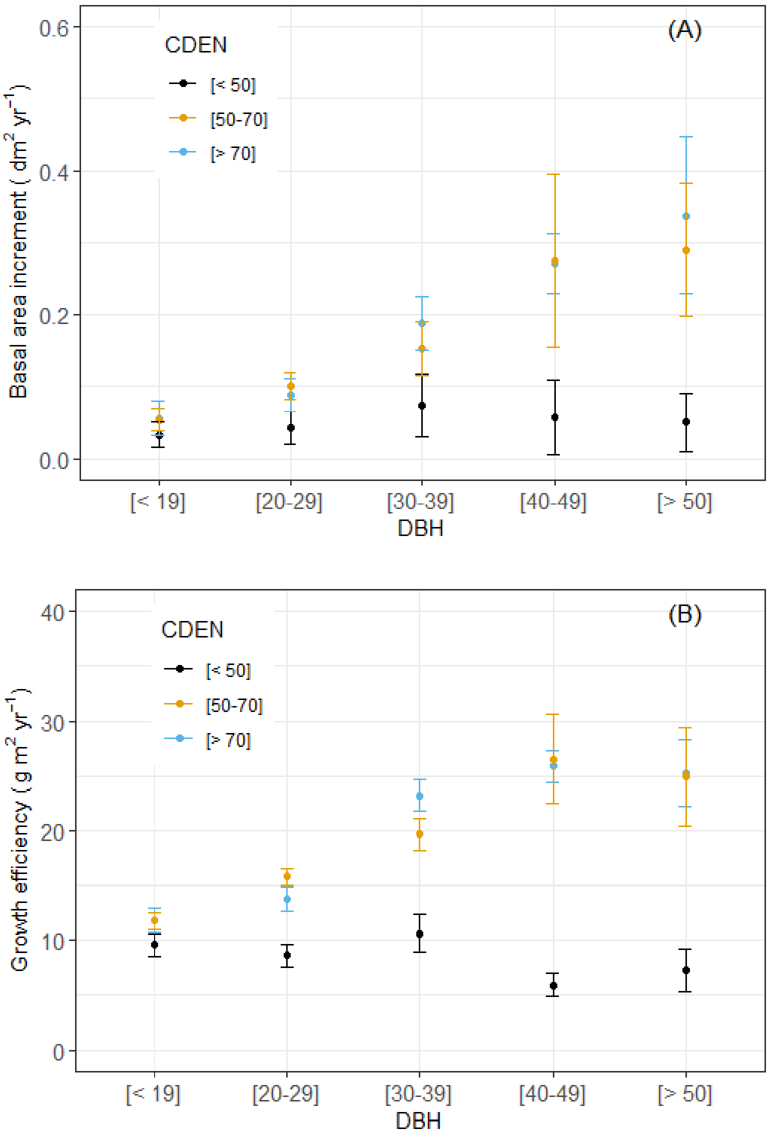

Table 3.3 Model selection result from the three distinct steps (univariate, bivariate and multivariate models) predicting the growth efficiency of sugar maple trees. AICc is the Akaike Information Criteria, Δi is the delta AICc (difference in AICc with the best model), Wti is the AICc weight, R^2 is the conditional coefficient of correlation. LA: Leaf area, RH: Relative height, CDEN: Crown density, CDBK: Crown dieback, CVC: Crown vigour class, Bark: Back character, WS: Woodworms and sap wells, BR: Stem base and root defects and, FP: Forks and pruning defects. All models included an intercept among the fixed effects as well as a plot-level random intercept. Note that only the five best multivariate models are shown. Models with an interaction (*) also include the individual variables.

Sugar maple					
		Growth efficiency (GE)			
Univariate models					
Model	Variables	AICc	Δ_i	Wt_i	R^2
1	**DBH**	**674.65**	**0.00**	**1.00**	**0.31**
2	RH	724.97	50.31	0.00	0.17
3	LA	750.81	76.15	0.00	0.12
0	Intercept	756.42	81.77	0.00	-
Bivariate models					
Model	Variables	AICc	Δ_i	Wt_i	R^2
4	**DBH*CDEN**	**655.64**	**0.00**	**0.95**	**0.36**
5	DBH*CDBK	661.36	5.72	0.05	0.34
6	DBH*CVC	669.92	14.28	0.00	0.34
Multivariate models					
Model	Variables	AICc	Δ_i	Wt_i	R^2
7	**DBH*CDEN**	**655.64**	**0.00**	**0.19**	**0.36**
8	DBH*CDEN + Bark	656.26	0.61	0.14	0.38
9	DBH*CDEN + WS	656.76	1.11	0.11	0.37
10	DBH*CDEN + BR	657.19	1.55	0.09	0.36
11	DBH*CDEN + FP	657.22	1.57	0.09	0.36

Table 3.4 Model-averaged parameter estimates and their 95 % confidence interval (CI) for sugar maple computed from the five best multivariate models. Parameter estimates in bold correspond to terms for which CI excluded zero (good predictor). Note that the intercept term code for Bark character is Bark1 (high vigour). Only the terms from the five best multivariate models are presented. DBH:CDEN is the interaction between the DBH and the crown density, CS: Conks and stromata, BR: Stem base and root defects, CK: Stem and bark cracks, WS: Woodworms and sap wells, FP: Forks and pruning defects and, $\text{Bark}_{1\text{-}3}$: Bark character from high vigour (1) to low vigour (3).

Sugar maple			
Models predicting BAI			
Term	Estimate	CI lower	CI upper
DBH:CDEN	**0.35**	**0.25**	**0.46**
Bark_2	-0.14	-0.42	0.13
Bark_3	0.02	-0.26	0.30
CK	-0.02	-0.15	0.11
CS	0.09	-0.19	0.38
WS	-0.04	-0.27	0.18
Model predicting GE			
DBH:CDEN	**0.19**	**0.09**	**1.18**
Bark_2	-0.02	-0.15	0.01
Bark_3	0.02	-0.16	0.22
BR	-0.01	-0.01	0.08
FP	-0.01	-0.06	0.07
WS	-0.02	-0.17	0.13

3.5.2. Yellow birch

As for sugar maple, the best univariate model to explain both BAI and GE of yellow birch trees included DBH (Table 3.5, model 1; Table 3.6, model 1). These models were significantly better than all other univariate models, with an AICc weight of 100 %. In the second step, the addition of crown density, without the interaction between DBH and crown density, resulted in the best bivariate model to explain the variation in BAI (Table 3.5, model 4). Despite not being part of the best bivariate model, the crown dieback and the crown vigour class also showed significant relationships ($P < 0.014$ and 0.04, respectively) with the BAI of yellow birch. The addition of the stem-related variables in the third modelling step did not decrease the AICc of the best bivariate model for BAI, and thus the best multivariate model included only DBH and crown density (Table 3.5, model 7). Multi-model inferences indicated that the unconditional confidence intervals of only DBH excluded zero (Table 3.7). Consequently, neither the stem-related variables nor the crown density can be considered as good predictors of yellow birch BAI. In the case of the GE models, the addition of crown-related variables did not decrease the AICc of the best univariate models (Table 3.6, model 4-6). Consequently, none of the crown-related variables were kept in the multivariate models explaining the variation of GE. The addition of the bark aspect, the presence of stem deformations and injuries, and conks and stromata decreased the AICc slightly and increased the R^2 of the best univariate model that included DBH (Table 3.6, models 7-10). However, multi-model inferences indicated again that the unconditional confidence intervals of only DBH excluded zero (Table 3.7). Overall, the best model explaining the variation in BAI and GE of yellow birch indicated that both variables increased with an increasing DBH (results not shown).

Table 3.5 Model selection result from the three distinct steps (univariate, bivariate and multivariate models) predicting the basal area increment of yellow birch trees. AICc is the Akaike Information Criteria, Δ_i is the delta AICc (difference in AICc with the best model), Wt_i is the AICc weight, R^2 is the conditional coefficient of correlation. LA: Leaf area, RH: Relative height, CDEN: Crown density, CDBK: Crown dieback, CVC: Crown vigour class, Bark: Back character, FP: Forks and pruning defects and, BR: Stem base and root defects. All models included an intercept among the fixed effects as well as a plot-level random intercept. Note that only the five best multivariate models are shown.

Yellow Birch					
		Basal area increment (BAI)			
Univariate models					
Model	Variables	AICc	Δ_i	Wt_i	R^2
1	**DBH**	**213.82**	**0**	**1.00**	**0.60**
2	LA	244.43	30.61	0.00	0.27
3	RH	256.50	42.68	0.00	0.18
0	Intercept	268.50	54.68	0.00	-
Bivariate models					
Model	Variables	AICc	Δ_i	Wt_i	R^2
4	**DBH + CDEN**	**212.25**	**0.00**	**0.44**	**0.60**
5	DBH+CVC	213.52	1.27	0.23	0.55
6	DBH + CDBK	213.54	1.30	0.23	0.56
Multivariate models					
Model	Variables	AICc	Δ_i	Wt_i	R^2
7	**DBH + CDEN**	**212.25**	**0.00**	**0.17**	**0.60**
8	DBH + CDEN + FP	212.27	0.03	0.17	0.60
9	DBH + CDEN + Bark	213.09	0.84	0.12	0.62
10	DBH + CDEN + BR	213.82	1.03	0.09	0.59
11	DBH	213.82	1.57	0.07	0.60

Table 3.6 Model selection result from the three distinct steps (univariate, bivariate and multivariate models) predicting the growth efficiency of yellow birch trees AIC is the Akaike Information Criteria, Δ_i is the delta AICc (difference in AICc with the best model), Wt_i is the AICc weight, R^2 is the conditional coefficient of correlation. LA: Leaf area, RH: Relative height, CDEN: Crown density, CDBK: Crown dieback, CVC: Crown vigour class, Bark: Back character, WS: Woodworms and sap wells, DI: Stem deformation and injuries, BR: Stem base and root defects stem base and root defects and, FP: Forks and pruning defects. All models included an intercept among the fixed effects as well as a plot-level random intercept. Note that only the five best multivariate models are shown.

Yellow Birch					
	Growth efficiency (GE)				
Univariate models					
Model	Variables	AICc	Δ_i	Wt_i	R^2
1	**DBH**	**152.11**	**0.00**	**1.00**	**0.34**
2	RH	158.47	6.36	0.00	0.28
0	Intercept	184.60	32.49	0.00	-
3	LA	185.95	33.84	0.00	-
Bivariate models					
Model	Variables	AICc	Δ_i	Wt_i	R^2
4	DBH + CVC	155.10	0.00	0.65	0.37
5	DBH + CDEN	157.65	2.10	0.23	0.34
6	DBH + CDBK	158.85	3.37	0.12	0.33
Multivariate models					
Model	Variables	AICc	Δ_i	Wt_i	R^2
7	**DBH + DI**	**149.91**	**0.00**	**0.24**	**0.38**
8	DBH + Bark + CS	150.51	0.61	0.17	0.41
9	DBH + Bark	150.80	0.89	0.15	0.39
10	DBH+CS	151.61	1.70	0.10	0.36
11	DBH	152.11	2.20	0.08	0.34

Table 3.7 Model-averaged parameter estimates and their 95 % confidence interval (CI) for yellow birch computed from the five best multivariate models. Parameter estimates in bold correspond to terms for which CI excluded zero (good predictor). Note that the intercept term code for Bark character is Bark1 (high vigour). Only the terms from the five best multivariate models are presented. CS: Conks and stromata, DI: Stem deformation and injuries, BR: Stem base and root defects, FP: Forks and pruning defects and, Bark1-3: Bark character from high vigour (1) to low vigour (3).

Yellow birch			
Models predicting BAI			
Term	Estimate	CI lower	CI upper
DBH	**1.1**	**0.79**	**1.42**
CDEN	0.1	-0.02	0.23
$Bark_2$	0.02	-0.26	0.31
$Bark_3$	-0.09	-0.63	0.44
BR	-0.04	-0.38	0.30
FP	-0.07	-0.47	0.32
Model predicting GE			
DBH	**1.09**	**0.77**	**1.41**
$Bark_2$	-0.05	-0.35	0.25
$Bark_3$	-0.26	-0.96	0.45
DI	-0.11	-0.53	0.32
CS	0.23	-0.53	1.00

3.6. Discussion

The general objective of this study was to establish relationships between two quantitative tree vigour indices and tree defects used in different tree vigour classification systems to evaluate their relevance for identifying the highly vigorous trees that are more likely to survive and grow well after partial harvesting. Statistical analyses were conducted to parsimoniously select defects that should be included in such systems to accurately evaluate tree vigour. For both species, the variable that was the most related to the vigour indices was tree DBH. In agreement, an increase of BAI with DBH has been observed in previous studies for sugar maple and yellow birch trees in northern hardwood stands (Jones & Thomas 2004; Jones & al. 2009). However, while the sugar maple BAI increased steadily from the lowest to the highest DBH class, the GE reached its maximum in the 40-49 DBH class after which it remained constant (see Figure 3.2). This observation could be the first sign of the decline in tree vigour that is related to increasing tree age and size (e.g. Niinemet et al. 2004; Binkley et al. 2004; Baret et al. 2018). Site-specific processes, in addition to physiological and morphological mechanisms such as a reduced transpiration rate per unit of leaf area (Baret et al. 2018) and a decrease in light capture efficiency (Niinemets et al. 2005) seems to be responsible for the widely observed age and size-related vigour decline. Interestingly, the monetary value per unit volume of sugar maple and yellow birch stems was observed to decrease from the same DBH threshold (Havreljuk et al. 2014). Therefore, silvicultural treatments promoting the growth of trees smaller than this threshold should improve both the stand growth efficiency and the production of valuable lumber pieces (Havreljuk et al. 2014).

Our results show that among all the studied defects, tree crown density, i.e. the amount of crown branches, foliage, and reproductive structures that intercept light (Schomaker 2007), is the best indicator of vigour, at least for sugar maple trees. This is in line with observations of higher 5-year survival of sugar maple trees with healthy crown conditions in managed northern hardwood forest (Guillemette et al. 2015; Morin et al. 2015). The significant interaction between crown density and DBH indicates that trees with the lowest crown densities did not follow the same pattern of increasing growth index values with DBH as trees with higher crown density, but instead tended to grow slowly regardless of the DBH classes. Although the same trends were observed with yellow birch trees, none of the crown variables were considered as good predictors according to multi-model inferences. The weaker relationships observed with yellow birch may be partly explained by a considerably reduced representation of yellow birch trees among the largest DBH classes, which reduced the variation of both crown conditions and GE values compared to sugar maple trees. Moreover, shade tolerant species such as sugar maple generally form denser crowns, with lower light transmittance and fewer leaf layers than lesser shade tolerant species (Canham et al. 1994; Reich et al. 2003; Valladares & Niinemets 2008). Sugar maple trees are also known to have lower leaf area per unit stem mass compared to other hardwoods (DeLucia et al. 1998), and a narrower crown than yellow birch (Messier & Nikinmaa 2000). Same trends were observed in our dataset, with larger leaf area and weaker crown density values in upper DBH classes for yellow birch trees. Consequently, while a weak crown density directly leads to a decline in vigour and growth for sugar maple trees, this relationship may be more elusive in species with a more complex crown architecture such as yellow birch. However, observation over a longer period and with a larger sample size is required to refine our understanding of the relationship between crown conditions and the vigour of yellow birch trees.

No stem-related variables were considered as good predictors of BAI or GE for both sugar maple and yellow birch trees. In line with the observations of Gauthier & Guillemette (2018), the bark aspect was the only stem-related variable significantly related to sugar maple BAI, but this was not the case for sugar maple GE and for both BAI and GE in yellow birch. The bark aspect was also a weak predictor of sugar maple BAI when crown density was already included in the model. Overall, these results support the relevance of the system developed by Schomaker (2007), which is based on the principle that the decline of tree vigour should result in crown degradation, no matter which inciting biotic or abiotic stressor can be identified as a causal factor. Consequently, taking account of stem-related defects to evaluate tree vigour appeared unnecessary when tree DBH and crown density are already included in the model. Tree vigour classification systems that use stem-related defects therefore appears unduly complex, a fact that is also supported by the widespread suggestion of simplifying them (Fortin et al. 2008; Hartmann et al. 2009; Guillemette et al. 2008; 2015; Cecil-Cockwell & Caspersen 2015; Moreau et al. 2018a). However, despite being weakly related to tree vigour, some stem-related defects have been proven to be useful to evaluate tree stem quality and estimate the potential monetary value of hardwoods (Havreljuk et al. 2014).

In light of these results, we recommend the use of DBH and crown density to assess the vigour of sugar maple trees and guide tree marking decisions. Obviously, crown density can only be measured during the leaf-on season, which in practice adds a constraint to the silvicultural planning. We argue that this change in practice is necessary to avoid that the trees left standing after a partial cut in northern hardwood stands are unproductive and prone to die shortly after the intervention (Moreau et al. 2019; 2020). The retention of vigorous trees after partial cuts should also help increase the probability of obtaining a positive tree growth response (Moreau et al. 2019; 2020), thereby increasing both stand productivity and value (Cecil-Cockwell & Caspersen 2015).

3.6.1. Limitations of the study

In this study, tree vigour indices that were based on recent growth indicated the extent to which individual defects were related to current tree vigor, but not over a long period of time such as a 25-year cutting cycle (Cecil-Cockwell & Caspersen 2015). To refine our understanding of the relationship between tree defects and vigour over a longer period, a temporal dimension must be added to the analysis using repeated measurements (Cecil-Cockwell & Caspersen 2015; Moreau et al. 2018a). When such longitudinal data will become available, it will then be possible to determine the rate of change of tree vigor based on the progression of existing defects and the addition of new defects (Cecil-Cockwell & Caspersen 2015). In addition, to help improve current tree vigour classification systems, empirical data should be collected on larger samples covering the entire range of major hardwood species in northeastern North America. Future long-term studies should also consider the risks of stem breakage, which could be related to stem defects that do not necessarily affect tree growth (Guillemette et al. 2017). Finally, the present study did not analyse stem form variables although some of them have been linked to the growth of hardwood species (Castle et al. 2018). It thus seems relevant that future work considers such stem form variables to potentially improve tree growth predictions.

3.7. Conclusion

This study demonstrates that the apparent stem defects used in several tree classification systems in North America are not significantly related to well-recognized quantitative vigour indices calculated for sugar maple and yellow birch trees. Based on this result, evaluating stem-related defects appears to be unnecessary if the aim is to evaluate the vigour of trees from these species. Conversely, our results indicate that crown density is a simpler, more comprehensive indicator of the tree vigour for sugar maple. Pending an extensive empirical validation of classification systems, we suggest it should be used to guide tree marking decisions prior to partial cutting interventions. Information from this study should be considered to refine tree vigour classification systems based on empirically validated results. Such systems are required to meet the challenge of increasing the vigour and growth of hardwoods stands managed under the silvicultural cutting systems reliant on partial cutting.

3.8. Acknowledgements

This research was funded by a Discovery Grant from the Natural Sciences and Engineering Research Council of Canada (NSERC), the Fonds de recherche du Québec – Nature et technologies (FRQNT), and Domtar Corporation. We are grateful to Eloïse Dupuis, Alexandre Morin-Bernard and Félix Poulin for their help with the fieldwork and to the staff from Domtar for their support on the project.

3.9. References

Baret, M. Pepin, S. & Pothier, D. (2018). Hydraulic limitations in dominant trees as a contributing mechanism to the age-related growth decline of boreal forest stands. *Forest Ecology and Management,* 427, 135-142.

Bigler, C., & Bugmann, H. (2004). Predicting the time of tree death using dendrochronological data. *Ecological Applications*, 14, 902–914.

Binkley, D. (2004). A hypothesis about the interaction of tree dominance and stand production through stand development. *Forest Ecology and Management*, 190, 265–271.

Boulet, B. (2007). Défauts et indices de la carie des arbres : Guide d'interprétation, 2^{e} éd. Les Publications du Québec, Québec, pp. 317

Canham C.D., Finzi A.C., Pacala S.W., & Burbank D.H. (1994). Causes and consequences of resource heterogeneity in forests—interspecific variation in light transmission by canopy trees. *Canadian Journal of Forest Research*, 24, 337–49

Castle, M., Weiskittel, A., Wagner, R., Ducey, M., Frank, J., & Pelletier, G. (2018). Evaluating the influence of stem form and damage on individual-tree diameter increment and survival in the Acadian Region: implications for predicting future value of northern commercial hardwood stands. *Canadian Journal of Forest Research*. 48, 1007-1019.

Cecil-Cockwell, M. J. L., & Caspersen, J. P. (2015). A simple system for classifying sugar maple vigour and quality. *Canadian Journal of Forest Research*, 45, 900-909

Christiansen, E. Waring, R.H. & Berryman, A.A. (1987). Resistance of conifers to bark beetle attack: Searching for general relationships. *Forest Ecology and Management*, 22, 89–106.

Coops, N. C., Waring, R. H., Wulder, M. A., & White, J. C. (2009). Prediction and assessment of bark beetle-induced mortality of lodgepole pine using estimates of stand vigor derived from remotely sensed data. *Remote Sensing of Environment*, 113(5), 1058-1066.

Delucia, E. H., Sipe, T. W., Herrick, J., & Maherali, H. (1998). Sapling biomass allocation and growth in the understory of a deciduous hardwood forest. *American Journal of Botany*, *85*(7), 955-963.

Duchesne, L., Ouimet, R., & Morneau, C. (2003). Assessment of sugar maple health based on basal area growth pattern. *Canadian Journal of Forest Research*, 33(11), 2074-2080.

Fortin, M., Bédard, S., DeBlois, J., & Meunier, S. (2008). Predicting individual tree mortality in northern hardwood stands under uneven-aged management in southern Québec, Canada. *Annals of Forest Science*, 65(2), 1.

Gauthier, M. M., & Guillemette, F. (2018). Bark type reflects growth potential of yellow birch and sugar maple at the northern limit of their range. *Plant ecology*, 219(4), 381-390.

Grondin, P., Jean, N., & Hotte, D. (2007). Intégration de la végétation et de ses variables explicatives à des fins de classification et de cartographie d'unités homogènes du Québec méridional, *Ministère des Ressources naturelles et de la Faune*, Direction de la recherche forestière. Mémoire de recherche No 150, pp. 62

Guillemette, F., Bédard, S., & Fortin, M. (2008). Evaluation of a tree classification system in relation to mortality risk in Québec northern hardwoods. *The Forestry Chronicle*, 84, 886–899.

Guillemette, F., Bédard, S., & Havreljuk, F. (2015). Probabilités de Mortalité des Feuillus Selon le Classement de la Priorité de Récolte; *Direction de la Recherche Forestière*: Québec, QC, Canada, pp. 11.

Guillemette, F., Gauthier, M. M., & Ouimet, R. (2017). Partitioning risks of tree mortality by modes of death in managed and unmanaged northern hardwoods and mixedwoods. *The Forestry Chronicle*, 93, 246-258.

Hartmann, H., Wirth, C., Messier, C., & Berninger, F. (2008). Effects of above-and belowground partial harvest disturbance on growth and water status of residual sugar maple. *Tree physiology,* 28(12), 1851-1862.

Havreljuk, F., Achim, A., & Pothier, D. (2013). Regional variation in the proportion of red heartwood in sugar maple and yellow birch. *Canadian journal of forest research*, 43, 278-287.

Havreljuk, F., Achim, A., Auty, D., Bédard, S., & Pothier, D. (2014). Integrating standing value estimations into tree marking guidelines to meet wood supply objectives. *Canadian journal of forest research*, 44(7), 750-759.

Jones, T.A., & Thomas, S.C. (2004). The time course of diameter increment responses to selection harvests in Acer saccharum. *Canadian journal of forest research*, 34, 1525–1533.

Jones, T. A., Domke, G. M., & Thomas, S. C. (2009). Canopy tree growth responses following selection harvest in seven species varying in shade tolerance. *Canadian journal of forest research*, 39(2), 430-440.

Lambert, M.C. Ung, C.H., & Raulier, F. (2005). Canadian national tree aboveground biomass equations. *Canadian Journal of Forest Research,* 35, 1996–2018.

Mazerolle, M.J. (2006). Improving data analysis in herpetology: using Akaike's Information Criterion (AIC) to assess the strength of biological hypotheses. *Amphibia-Reptilia,* 27, 169–180.

Mazerolle, M.J. (2017). AICcmodavg: Model selection and multimodel inference based on (Q)AIC(c). R package version 2.0-3.

Messier, C., & Nikinmaa, E. (2000). Effects of light availability and sapling size on the growth, biomass allocation, and crown morphology of understory sugar maple, yellow birch, and beech. *Ecoscience, 7*, 345-356.

Mitchell, R. G., Waring, R. H., & Pitman, G. B. (1983). Thinning lodgepole pine increases tree vigor and resistance to mountain pine beetle. *Forest Science*, 29(1), 204-211.

Moreau, E., Bédard, S., Moreau, G., & Pothier, D. (2018). Relationships between tree vigor indices and a tree classification system based upon apparent stem defects in northern hardwood stands. *Forests*, 9(10), 588.

Moreau, E., Bédard, S., Baral, S. K., & Pothier, D. (2018b). Evaluating electrical resistivity tomography and crown surface area to estimate leaf area of sugar maple and yellow birch. *Ecohydrology*, *11*(7), e2014.

Moreau, G., Achim, A., & Pothier, D. (2019). A dendrochronological reconstruction of sugar maple growth and mortality dynamics in partially cut northern hardwood forests. *Forest ecology and management*, 437, 17-26.

Moreau, G., Achim, A., & Pothier, D. (2020). Growth and survival dynamics of partially cut northern hardwood stands as affected by precut competition and spatial distribution of residual trees. *Forestry: An International Journal of Forest Research*, 93(1), 96-106.

Niinemets, Ü., Sparrow, A., & Cescatti, A. (2005). Light capture efficiency decreases with increasing tree age and size in the southern hemisphere gymnosperm Agathis australis. *Trees,* 19, 177–190.

Nyland, R.D. (1998). Selection system in northern hardwoods. *Journal of Forestry*, 96, 18-21.

Ontario Ministry of Natural Ressources. (2004). Ontario tree marking guide, Ver. 1.1. *Ontario Ministry of Natural Ressources*, 252 pp.

Pedersen, B. S. (1998). Modeling tree mortality in response to short-and long-term environmental stresses. *Ecological Modelling,* 105(2-3), 347-351.

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., Heisterkamp, S., Van Willigen, B., & Maintainer, R. (2017). Package ‘nlme’. *Linear and nonlinear mixed effects models*, version, 3.

Pothier, D., Fortin, M., Auty, D., Delisle-Boulianne, S., Gagné, L. V., & Achim, A. (2013). Improving tree selection for partial cutting through joint probability modelling of tree vigor and quality. *Canadian journal of forest research*, 43(3), 288-298.

Power, H., & Havreljuk, F. (2018). Predicting hardwood quality and its evolution over time in Quebec's forests. *Forestry: An International Journal of Forest Research*, 91(3), 259-270.

Raymond, P., Bédard, S., Roy, V., Larouche, C., & Tremblay, S. (2009). The Irregular Shelterwood System : Review, Classification, and Potential Application to Forests Affected by Partial Disturbances. *Journal of Forestry*, 107, 405–413.

Reich, P. B., Wright, I. J., Cavender-Bares, J., Craine, J. M., Oleksyn, J., Westoby, M., & Walters, M. B. (2003). The evolution of plant functional variation: traits, spectra, and strategies. *International Journal of Plant Sciences*, 164(S3), S143-S164.

Saucier, J.-P., Grondin, P., Robitaille, A., Gosselin, J., Morneau, C., Richard, P.-J.-H., Brisson, J., Sirois, L., Leduc, A., Morin, H., Thiffault, E., Gauthier, S., Lavoie, C. & Payette, S. (2009). Écologie forestière. Manuel de foresterie, 2e édition. *Ordre des ingénieurs forestiers du Québec*, Éditions Multimondes, Québec, pp.165-316.

Schomaker, M. (2007). *Crown-condition classification: a guide to data collection and analysis (Vol. 102)*. US Department of Agriculture, Forest Service, Southern Research Station.

Valladares, F., & Niinemets, Ü. (2008). Shade tolerance, a key plant feature of complex nature and consequences. *Annual Review of Ecology, Evolution, and Systematics*, 39, 237-257.

Waring, R. H., Thies, W. G., & Muscato, D. (1980). Stem growth per unit of leaf area: a measure of tree vigor. *Forest Science*, 26(1), 112-117.

Waring, R. H., Newman, K., & Bell, J. (1981). Efficiency of tree crowns and stemwood production at different canopy leaf densities. *Forestry: An International Journal of Forest Research*, 54(2), 129-137.

Waring, R. H., & Pitman, G. B. (1985). Modifying lodgepole pine stands to change susceptibility to mountain pine beetle attack. *Ecology*, 66(3), 889-897.

Waring, R.H., (1987). Characteristics of trees predisposed to die. *Bioscience* 37(8), 569–574.

Zuur, A. F., Ieno, E.N., & Elphick, C.S. (2010). A protocol for data exploration to avoid common statistical problems. *Methods in Ecology and Evolution*. 1, 3–14.

4. Chapitre 4

An accumulation of climatic stress events has led to years of reduced growth for sugar maple in southern Quebec, Canada

4.1. Abstract

Understanding the influence of climatic variation on forest dynamics is of great ecological and economic interest, and is essential to prescribe silvicultural interventions that will facilitate ecosystem acclimation to global change. However, the retrospective identification of climatic events responsible for the inter-annual variation of tree growth is challenging, notably because both their duration and their subsequent effects can be highly variable in time. In this study, we aimed to (1) quantify empirically the effect of climatic stress events on the short- and long-term growth dynamics of sugar maple trees; (2) compare the effects of different types of climatic events, i.e. drought and thaw-freeze; and (3) compare the effects of climatic stress events to those of traditional monthly-level climate metrics. To achieve this, we paired cross-dated tree-ring series to monthly- and daily-level climate metrics over more than 50 years in two distinct regions of southern Quebec. While the analysis from monthly-level metrics first suggested a weak and non-stationary relationship between climatic conditions and tree growth, the analysis from daily-level metrics showed that climatic stress events, and more particularly thaw-freeze events, were strongly related to the growth of sugar maple trees. Our results suggest that the synergic influence of cumulative climatic stress events, which was exacerbated by insect outbreaks during the early 1980s, induced an important shift in the growth dynamics of sugar maple and in its response to variation in climatic conditions. These results highlight the potential negative impact of global climate change on our capacity to predict stand productivity accurately, especially if climate-sensitive growth models are based on projections of future monthly metrics. Because adverse climatic events are expected to increase both in frequency and severity over the next decades, a general decrease in the growth rate of sugar maple is apprehended in southern Quebec.

4.2. Résumé

Cette étude visait à quantifier de manière empirique l’effet de deux types d’événements climatiques (sécheresse et gel-dégel) sur la dynamique de croissance de l’érable à sucre, et comparer l’effet de ces événements climatiques sévères à celui des tendances climatiques mensuelles. L’effet du climat sur la croissance a été analysé sur une période de 53 ans. Les analyses provenant des tendances climatiques mensuelles ont indiqué une relation faible et instable dans le temps avec la croissance. À l’inverse, les analyses provenant des données journalières ont montré que les stress climatiques ponctuels, et plus particulièrement les périodes de gel-dégel, étaient fortement liés à la croissance des arbres. Nos résultats indiquent que l’effet synergique d’une accumulation de plusieurs stress climatiques et d’épidémies d’insectes défoliateurs au début des années 1980 a induit un changement important dans la dynamique de croissance de l’érable à sucre et sa réponse aux conditions climatiques mensuelles.

4.3. Introduction

Forest ecosystem dynamics are affected by global climate change through the general increase in annual temperature, the frequency and severity of acute climatic events and changes in natural disturbance regimes (Bell et al. 2004; Iverson et al. 2008; Allen et al. 2010; Dai 2013). In eastern North America, a shift in composition toward slow-growing species that are more adapted to climate-induced stresses has already been observed (Zhang et al. 2018). Such shifts in forest composition and productivity will affect forest ecosystem dynamics and bring uncertainty about long-term forest growth (Zhang et al. 2018; SCAF 2018). A refined understanding of species-specific vulnerability to climatic stressors is thus required not only to better anticipate the effects of climate change on forest ecosystems but also to ultimately help devise and implement adaptive measures (Allen et al. 2015; D'Amato et al. 2013; Nolet & Kneeshaw 2018).

An important challenge related to the quantification of such vulnerability is that climatic stresses, which may vary in duration, can also induce “legacy” effects that may far outlast the event itself (Anderegg et al. 2015). For example, severe droughts are known to induce growth reductions that can last for several years (Anderegg et al. 2015; Vanoni et al. 2016; Nolet & Kneeshaw 2018).The time resolution that must be used to detect both the causal factors and the induced response is therefore highly variable. Also, such legacy effects can lead to interactions with additional stressors and produce compound events that may ultimately lead to a long-term growth decline of trees and induce changes in the ecosystem dynamics (Nolet & Kneeshaw 2018).

Sugar maple (*Acer saccharum* Marsh.) is a key species both ecologically and economically in the northern hardwoods forest of northeastern North America. This late-successional species dominates a vast bioclimatic zone and is used for maple syrup production as well as being appreciated by the furniture and flooring industries. These attributes make it a well-studied species, especially with the current concerns about its response to climatic stressors (Oswald et al. 2018). Although sugar maple is a slow-growing species, and is thus supposedly fairly resistant to climate-induced stresses, its vulnerability to climate change was evidenced by: (i) niche model predictions suggesting an important decrease of its future potential habitat under projected climate scenarios (Iverson et al. 2008); (ii) a significant growth decline observed across the range of the species over the last decades (e.g.

Duchesne et al. 2003; Nolet & Kneeshaw 2018; Bishop et al. 2015); and (iii) a higher vulnerability to climatic stressors than other companion species (Nolet & Kneeshaw 2018).

Despite the sensitivity of sugar maple to environmental conditions, results attempting to relate climatic variables to sugar maple growth dynamics seem somewhat contradictory (see Yin et al. 1993; Lane et al. 1993; Payette et al. 1996; Tardif et al. 2001; Gavin et al. 2008; Bishop et al. 2015). While some studies have observed moderate to strong relationships between sugar maple growth and climate variables (Lane et al. 1993; Yin et al. 1993; Tardif et al. 2001), others have observed weaker relationships, which were generally associated with a non-stationary sensitivity to climate conditions over time (Payette et al. 1996; Gavin et al. 2008; Bishop et al. 2015). This lack of consistency between results may partly be explained by the inclusion of only monthly-level climate metrics into modelling efforts, which may miss the effect of more acute events (Graumlich 1993). For example, novel metrics designed to capture the effects of climatic stress events, i.e. periods of unusual warmth in January and August, were significantly related to the crown conditions of sugar maple trees over a 25-year period (Oswald et al. 2018). Climatic stresses such as periods of drought and thaw-freeze events were also linked to decreases in the short- or long-term growth of this species (e.g. Graumlich 1993; Payette et al. 1996; Gavin et al. 2008; Nolet & Kneeshaw 2018). Despite such observations, the effects of climatic stress events have yet to be included in sugar maple growth models.

In this study, we paired cross-dated tree-ring series to daily climate metrics to quantify the effects of short-term climatic stresses on the growth dynamics of sugar maple trees from two distinct regions in southern Quebec. The growth response of individual trees to climatic stressors was investigated using a complementary set of four growth indices computed from tree-ring series covering a period of more than 50 years. More specifically, we aimed to: (1) quantify empirically the effect of climatic stress events on the short- and long-term growth dynamics of sugar maple trees; (2) compare the effects of different types of climatic stress events, i.e. drought and thaw-freeze; and (3) compare the effects of stress events to those of traditional monthly-level climate metrics.

4.4. Materials and methods

4.4.1. Sampling sites

Trees were sampled in two different areas on private woodlots owned by Domtar Corporation in southern Quebec, Canada. The first area (45° 90’ N; 70° 80’ W) was located in the Estrie administrative region, near the town of Saint-Malo, while the second area (45° 15’ N; 71° 55 ’W) was located in the Beauce administrative region, near Saint-Martin. These regions are both part of the eastern sugar maple-yellow birch bioclimatic subdomain, which is characterized by mean annual temperatures between 2.5 and 4 °C, mean annual precipitation between 915 and 1100 mm and a growing season of 145 to 165 days (Saucier et al. 2009). The topography of this bioclimatic subdomain is characterized by hills and slopes, and the main surface deposits are shallow or deep tills (Grondin et al. 2007). The sampling sites were located in naturally established uneven-aged northern hardwood stands dominated by sugar maple, followed by yellow birch (*Betula alleghaniensis* Britt.) and red maple (*Acer rubrum* L.), with a smaller presence of American beech (*Fagus grandifolia* Ehrh.), black cherry (*Prunus serotina* Ehrh.), basswood (*Tilia americana* L.), hophornbeam (*Ostrya virginiana* (Mill.) K. Koch), balsam fir (*Abies balsamea* (L.) Mill.), red spruce (*Picea rubens* Sargent) and eastern hemlock (*Tsuga canadensis* (L.) Carr.). A period of insect defoliation was reported in this area during the early 1980s, which temporary reduced the overall growth of sugar maple stands during the following decade (Payette et al., 1996 & personal communication, Domtar Corporation).

4.4.2. Data collection and tree-ring chronologies

The radial growth history was assessed from increment cores sampled on trees located in two sets of permanent sample plots (PSPs) that were established between 1998 and 2004 in our study regions (9 PSPs in Estrie, 5 PSPs in Beauce). Both sets of PSPs were established on nearby sites with mesic soil-moisture conditions, gentle slope and similar altitudes. During the summer of 2016, an increment core was extracted from all dominant/codominant live sugar maple trees within the 11.28 m-radius circular plots. Cores were taken at a height of 1 m above the ground surface in the direction of the plot center. A total of 154 sample cores were glued to wooden blocks before they were air dried and gradually sanded (Tardif et al. 2001). Only unbroken cores, with remaining bark at their end, without signs of decay and with complete delineation of latewood boundaries were retained for further analysis. Annual ring width was measured with a Velmex micrometer (±0.002 mm). To remove the age-related trend and isolate the climatic signal, each individual tree-ring series was standardized using a spline function with a 66 % frequency response (Cook & Peters 1981). One master standardized chronology per study region was constructed using these tree-ring series. Treating all plots from a region as one group allowed us to isolate a more comprehensive climatic signal in the region rather than a stand-specific signal

(Nolet & Kneeshaw 2018). Highly correlated (r > 0.3) tree-ring series were sequentially added to the master chronologies until they reached the recommended expressive population signal (EPS) of 0.85 (Wigley et al. 1984; Briffa & Jones 1990; Tardif et al. 2001). The resulting chronology in the Estrie region was composed of 21 trees with an EPS of 0.89 while that in Beauce was composed of 16 trees with an EPS of 0.87. The high EPS values in the two regions underline the high statistical robustness of the two chronologies and the adequate precision of the climatic reconstructions (Wigley et al. 1984).

4.4.3. Climatic data

Daily temperature and precipitation data were obtained from the climate stations nearest to both groups of sampling sites, with comparable altitude, a long time series of records and without a large amount of missing data (Payette et al. 1996; Lévesque et al. 2013). Missing data were estimated by linear regression using data from nearby stations (Lévesque et al. 2013). In Estrie, the nearest station was located in Saint-Malo (45° 12’ N; -71° 30’ W) at a distance of 8 km from the sampling sites. The climate stations of East Hereford (45° 08’ N; -71° 50’ W) and Coaticook (45° 15’ N; -71° 88’ W), located at 10 and 16 km from the sampling sites, respectively, were both used to estimate missing data. In the Beauce region, the nearest station without a large amount of missing data was located in Lac Mégantic (45° 36’ N; -71° 52’ W) at 25 km from the sampling sites. The climate station of St-Ludger (45° 75’ N; -70° 68’ W), located at 14 km from the sampling sites, was used to estimate missing data. When missing data occurred in all climate stations near a study region, values were estimated using the mean of that month (Tardif et al. 2001). The period covered by the climatic stations for both regions was 1963 to 2015.

4.4.4. Detection of climatic stress events

Climatic stress events were defined using an *a priori* approach based on previous results from the literature. Daily climate data were used to identify both thaw-freeze events and periods of drought. The severity of a thaw-freeze event was expressed using cumulated growth degree-days (GDD) during the thaw prior to a refreeze (Bourque et al. 2005). As defined by these authors, a biologically significant thaw started when the daily maximum temperatures reached 4 °C during the winter, a threshold representing the point at which biological activity begins (Braathe 1995; 1996). Cumulative GDD were then calculated based on the daily mean temperature values above the 4 °C threshold during the entire duration of the thaw event. The event deemed to have ended when the daily minimum temperature went below – 4 °C, a threshold corresponding to the air temperature below which the root-soil plate freezes in the absence of a snow cover (Bourque et al. 2005), and at which root and shoot metabolism is reduced (Zhu et al. 2000; 2001). For each individual year through the 1963-2015 period, the event with the maximum cumulative GDD was retained as a potential predictor of yearly growth variation.

Following a similar procedure, we defined a precipitation threshold for the identification of drought events. Our method considered the absence of precipitation, but also the fact that drought conditions are dependent on the evaporation demand, which in turn is affected by temperature. We thus based the identification of drought events on the supply and demand concept of water balance (Vicente-Serrano et al. 2010). This was achieved by using both the daily total precipitation and GDD records. First, as applied by Payette et al. (1996) in northern hardwood stands from the same bioclimatic zone, we used a daily precipitation threshold of 15 mm below which the growth of sugar maple trees is hindered if the condition is met for several consecutive days. Second, we took account of the evaporative demand by summing GDD from the initial day when the daily total precipitation was under 15 mm until the next day during which this threshold was exceeded. For each individual year through the 1963-2015 observation period, the event with the maximum value of this drought index was retained as a potential predictor of yearly growth variation.

4.4.5. Tree ring analysis

In addition to the ring width and the standardized growth chronologies described above, we computed two supplementary growth variables for further analysis. First, for each individual tree-ring series, we determined when an abrupt annual growth reduction occurred. Based on the method proposed by Das et al. (2007), an abrupt annual growth reduction was defined as a year-to-year negative percentage growth change (PGG) of more than 1 standard deviation from the mean of all the negative year-to-year PGG observed from all individual tree-ring series. In our study, this analysis showed that the mean of all negative year-to-year PGGs was 26 % with a standard deviation of 19 %. To remain conservative, we set a threshold of 50% PGG to mark years of abrupt annual growth reduction.

Second, we calculated a growth sensitivity index to assess year-to-year variability of each individual tree-ring series. The sensitivity index was expressed as the mean year-to-year variation over a 5-year window of observation. The sensitivity S_t at year t was defined as:

$$S_t = \left|\frac{(RW_t - RW_{t-1})}{(RW_t)}\right| \quad [1]$$

where RW_t is the radial growth measured at year t, and RW_{t-1} is the radial growth measured the previous year. The sensitivity index at year t was then computed using the average values of St over a five-year period from year *t-4* to year *t*. Such an index has previously been related to the sensitivity of trees to annual climatic variability (Fritts 1976), and has been recognized as a good predictor of imminent mortality in sugar maple (Moreau et al. 2019). It was thus used in this study as a proxy for the evolution of tree vigour during the observation period.

4.4.6. Statistical modelling process

4.4.6.1. Monthly climatic trends

As they represent summary metrics commonly used in dendroclimatic analyses (Oswald et al. 2018), the total monthly precipitation and mean temperatures were also used as potential predictors of mean annual growth in the two master standardized chronologies. A bootstrapped response function was calibrated for each month of the vegetation period of year t-1 (June to December) and year t (January to September) through the entire observation period. This approach was developed to test the significance of the regression coefficients while considering the autocorrelation between predictors (Fritts 1976; Tardif et al. 2001; Zhang & Biondi, 2013). We also investigated the temporal variability of growth-climate relationships using response functions with a 25-year moving window. These analyses were performed using the bootRes package in R (Zang & Biondi, 2013).

4.4.6.2. Climatic stress events

The growth response of individual trees to drought and thaw-freeze event during the 1963-2015 period was expressed using the individual standardized tree-ring series to eliminate the age-related trends. It was statistically modelled using a mixed-effects linear model with tree-level random effects. The fixed effects predictors were the yearly series of thaw-freeze and drought event indices. In a second model, we also modelled the effects of these predictors on annual standardized growth with a potential one-year lag. Models were developed using the lme function of the nlme package (Pinheiro et al. 2017) in R. The probability of a tree to experience an abrupt annual growth decline was modelled for all individual standardized tree-ring series using a mixed effects logistic regression with a tree-level random effect. The binomial distribution model included the relationship between the predictors (thaw-freeze and drought event indices) and a binary response indicating the occurrence or not of an abrupt annual growth decline. Again, we tested both the responses in the current year and with a possible one-year lag in separate models. The glmmTMB function of the glmmTMB package (Magnusson et al. 2017) was used for the mixed effects logistic regression. As for the construction of the master chronologies, individual standardised growth series from the two regions were modelled in two different groups. Model assumptions, i.e. the homogeneity of variance, normality of residuals, the presence of outliers and the over-dispersion, were validated with a graphical analysis of the residuals.

4.5. Results

4.5.1. Monthly climatic trends

In the Estrie region, none of the climatic variables had a significant effect on sugar maple growth, as represented by the bootstrapped response function coefficients computed with residual chronologies (Fig. 4.1A-B). In the Beauce region, growth was only significantly and positively related ($P < 0.05$) to the precipitation during August of the preceding year (Fig. 4.1C-D). In both regions, most of the tested predictor variables had non-stationary relationships with sugar maple growth during the observation period. While the response function coefficients of several variables were rather inconsistent from year to year, others changed steadily over time (Fig. 4.2). For example, in the Estrie region, temperature in April, September and precipitation in June changed from having negative to positive effects over the last decades (Fig. 4.2A). Similarly in the Beauce region, the effect of temperature in April steadily shifted through the observation from negative to positive, while that of May and June shifted from null to positive (Fig. 4.2B).

4.5.2. Severe climatic events

The most severe climatic events, defined as a shift of at least 1 standard deviation (sd) from the mean value of all annual maxima of cumulated GDD, are presented in Table 4.1. In the Estrie region, the most severe thaw-freeze events occurred in 1981 and 2010, while the most severe drought events were detected in 1973, 1978 and 1979. In the Beauce region, the most severe thaw-freeze events were recorded in 1981, 2003 and 2010, while the most severe drought events occurred in 1970, 1971 and 1980. Overall, the severity of the climatic events tended to be slightly higher in Estrie, particularly for drought events.

Several growth reductions were observed in the standardized master chronologies of both regions, particularly from the beginning of the 1980s. In the Estrie region, the 1983 drought and the 1986 and 2010 thaw-freeze events all corresponded with low values of standardized growth (Fig. 4.3A). The growth index value was also low in 1995, but this was unrelated to any of the climatic stress events we identified. Overall, the growth index from individual tree-ring series decreased significantly with increasing cumulated GDD during thaw-freeze (*p* < 0.0001, Fig. 4.4A) and drought (*p* = 0.032, Fig. 4.4C) events. However, growth was unrelated to climatic events that had occurred in the previous year. In the Beauce region, low values of the growth index were observed in 1981, 1984, 1986, 2003 and 2010, all of which except 1984 coincided with years of severe thaw-freeze events (Fig. 4.3B). The growth index tended to decrease significantly with increasing cumulated GDD during a thaw-freeze event (*p* < 0.0001, Fig. 4.4B) and cumulated GDD during a drought event (*p* = 0.0064, Fig. 4.4D). In this region, the growth index was also significantly related to GDD during a drought event that had occurred in the previous year (*p* = 0.0006).

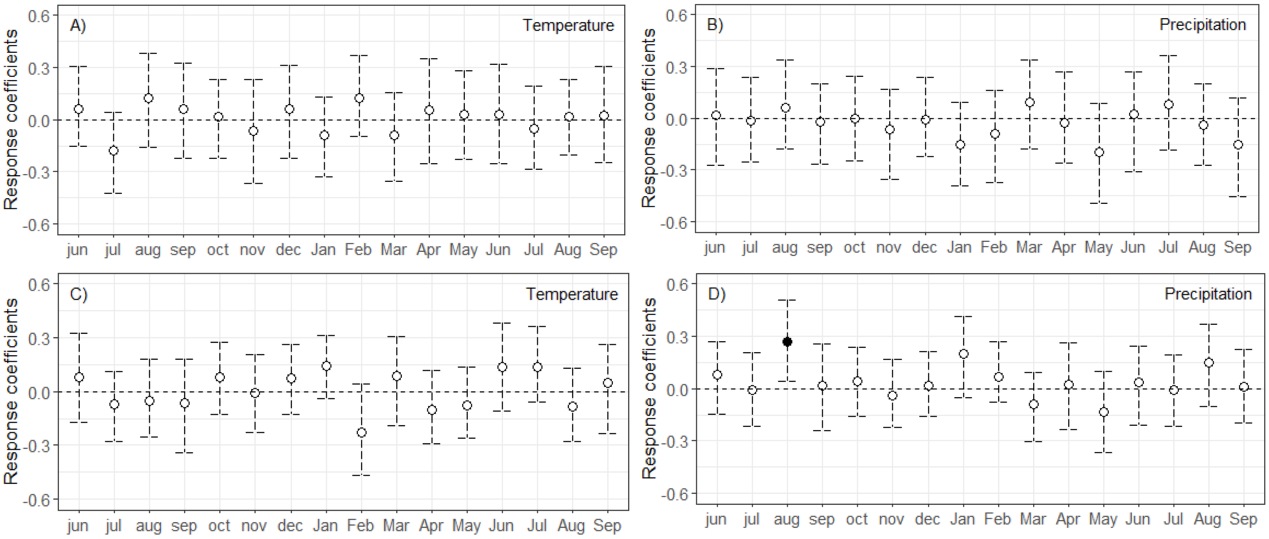

Figure 4.1 Bootstrapped response function coefficients computed between sugar maple residual chronologies and the monthly climatic variables over the 1963-2015 period for A) temperature and B) precipitation in Estrie and C) temperature and D) precipitation in Beauce. The lowercase letters on the x-axis indicate the months of the year prior to growth (year-1) while the uppercase letters indicate months of the years of growth. Statistically significant correlation coefficients (p < 0.05) are represented by solid circles.

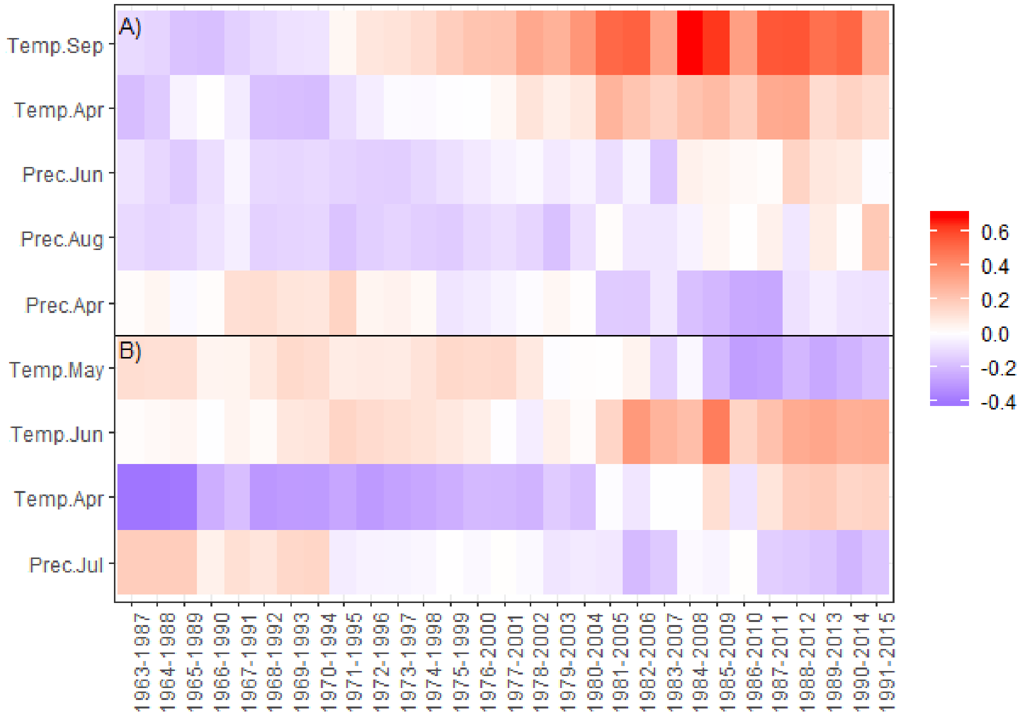

Figure 4.2 Non-stationary relationship between sugar maple growth and monthly climatic predictors in Estrie (A) and Beauce (B) regions. The colour scale represents the response function coefficients (dimensionless) that were calculated using a 25-year moving window (see Statistical and modelling process for more details).

For both regions, the 1960-1970 period was characterized by a progressive reduction in ring width (Fig. 4.3C-D). This was then followed by several years of slow growth during the 1980s, a pattern that occurred after a rapid succession of severe stress events in the 1970s and early 1980s. This period marked the onset of a period of high irregularity in ring width characterized by several narrow rings interspersed with pulses of increased radial growth. In the Estrie region, all trees experienced an abrupt growth decline during the 1983 drought event and the 1986-2010 thaw-freeze events. According to the logistic regression analyses, the probability of a tree to experience an abrupt growth decline increased sharply with an increase of cumulative GDD during a thaw-freeze event (Fig. 4.5A), while the effect was more moderate in the case of droughts (Fig. 4.5C). In the Beauce region, 94 % of the trees experienced at least one abrupt decline from 1980 to 1986, while 35 % of our sample trees also experienced a growth decline following the 2010 thaw-freeze event. For this region, only the cumulated GDD during a thaw-freeze event had a significant effect on the probability of a tree to experience an abrupt growth decline in the same year ($p < 0.0001$). In either region, the probability of an abrupt growth decline was unrelated to climatic events that had occurred during the previous year.

Table 4.1 Severe climatic events detected for the period 1963-2015 for the two study regions. GDD is the maximum cumulated growth degree-days during a thaw-freeze/drought event and days is the maximum cumulated days during a thaw-freeze/drought event. sd is the number of standard deviation shift from the mean GDD and days value. Years in bold indicated the most severe climatic events (a shift > 2 standard deviation from the mean GDD and days value). Note that the maximum cumulated days are presented only to help describe the climatic events.

Estrie								Beauce							
Winter thaw				Drought				Winter thaw				Drought			
Year	days	GDD	sd	Year	days	GDD	sd	Year	days	GDD	sd	Year	days	GDD	sd
1977	17	60	>1	1964	47	580	>1	**1981**	**23**	**123**	**>2**	1964	51	634	>1
1981	**24**	**148**	**>3**	1965	40	497	>1	1986	14	75	>1	1965	61	735	>1
1986	14	78	>1	**1973**	**57**	**885**	**>2**	1987	10	73	>1	**1970**	**60**	**830**	**>2**
1987	11	77	>1	1977	39	543	>1	**2003**	**33**	**146**	**>3**	**1971**	**61**	**819**	**>2**
2002	13	81	>1	**1978**	**73**	**1007**	**>2**	2008	16	79	>1	1975	38	661	>1
2010	**43**	**178**	**>4**	**1979**	**34**	**1145**	**>2**	**2010**	**45**	**161**	**>3**	**1980**	**68**	**844**	**>2**
2012	24	67	>1	1983	44	580	>1					1991	51	673	>1
				2005	41	571	>1					2000	46	596	>1
												2005	52	751	>1

In the Estrie region, the growth sensitivity index tented to increase progressively during the 1960-1980 period with a marked peak after the severe drought event that occurred in 1973 (Fig. 4.3E). Following the thaw-freeze event of 1981, the growth sensitivity index increased abruptly, peaked in 1987 and then decreased until 1994. This was followed by a gradual increase in growth sensitivity until 2015. In the Beauce region, the growth sensitivity index remained stable during the 1960-1980 period until it increased abruptly following the drought and thaw-freeze events of 1980 and 1981, peaked in 1985 and then decreased until 1995. After this period, growth sensitivity increased slowly until 2011. For both regions, values of the growth sensitivity index were generally higher from 1995 onward compared to the 1960-1980 period.

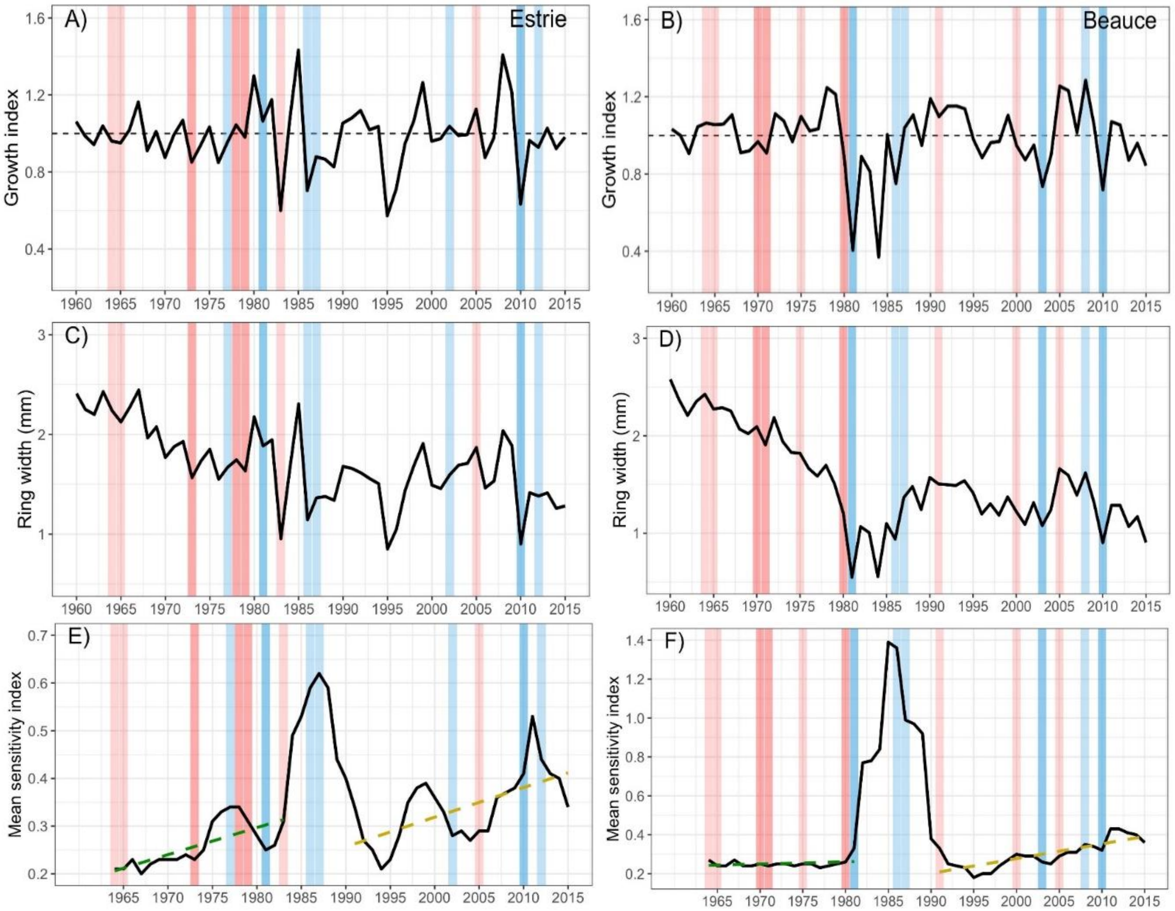

Figure 4.3 Average growth index chronologies (A) in Estrie (nbr = 21, EPS = 0.89), and (B) in Beauce (nbr = 16, EPS = 0.87). Average ring-width (mm) chronologies (C) in Estrie and (D) in Beauce. E) Growth sensitivity index calculated over a 5-year segment from all individual tree-ring series (E) in Estrie and (F) in Beauce. The linear relationship of the growth sensitivity index over time is illustrated by the green and yellow dashed line. In Estrie (E), the slope and intercept values of the green dashed line are 0.0057 and 0.20 respectively (the period 1963-1983), and the slope and intercept values of the yellow dashed line are 0.0062 and 0.26 (from 1990 onward). In Beauce (F), the slope and intercept values of the green dashed line are 0.0011 and 0.24 respectively (the period 1963-1980), and the slope and intercept values of the yellow dashed line are 0.0077 and 0.20 (from 1990 onward). Note that E) and F) do not have the same y-scale. Red and blue vertical lines illustrate severe drought and thaw-freeze events (sd>1), respectively, with darker lines representing the most severe events (sd > 2). The downward-pointing bracket indicates the insect defoliation period (1979-1982).

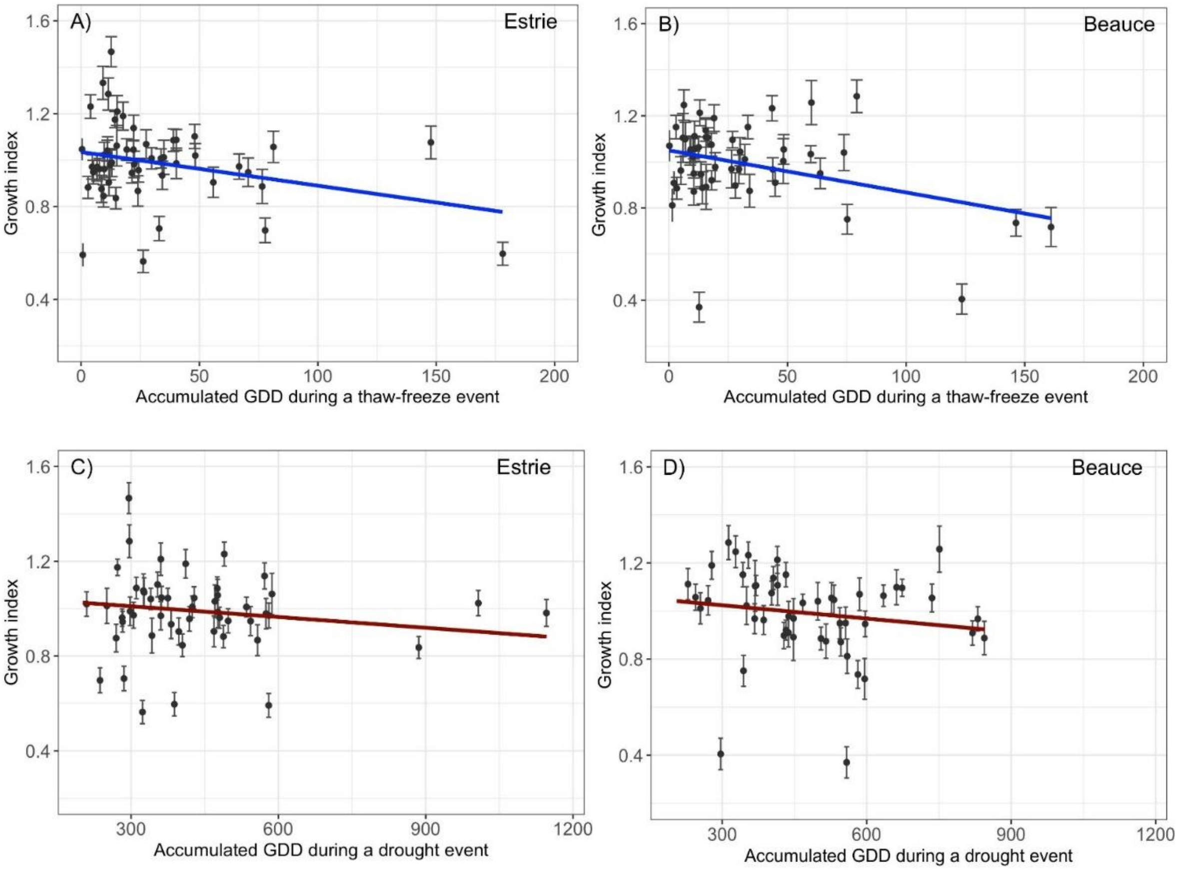

Figure 4.4 Mean observed growth index as a function of the accumulated GDD during thaw-freeze and drought event in Estrie (A; C) and Beauce (B; D), respectively. The blue and red line correspond to the growth index predictions computed with the mixed linear models, with slope and intercept values of -0.0014 and 1.035 for (A), -0.0018 and 1.050 for (B), -0.0002 and 1.056 for (C) and -0.0002 and 1.079 for (D), respectively.. Each point is the average annual growth index and bars correspond to the standard error.

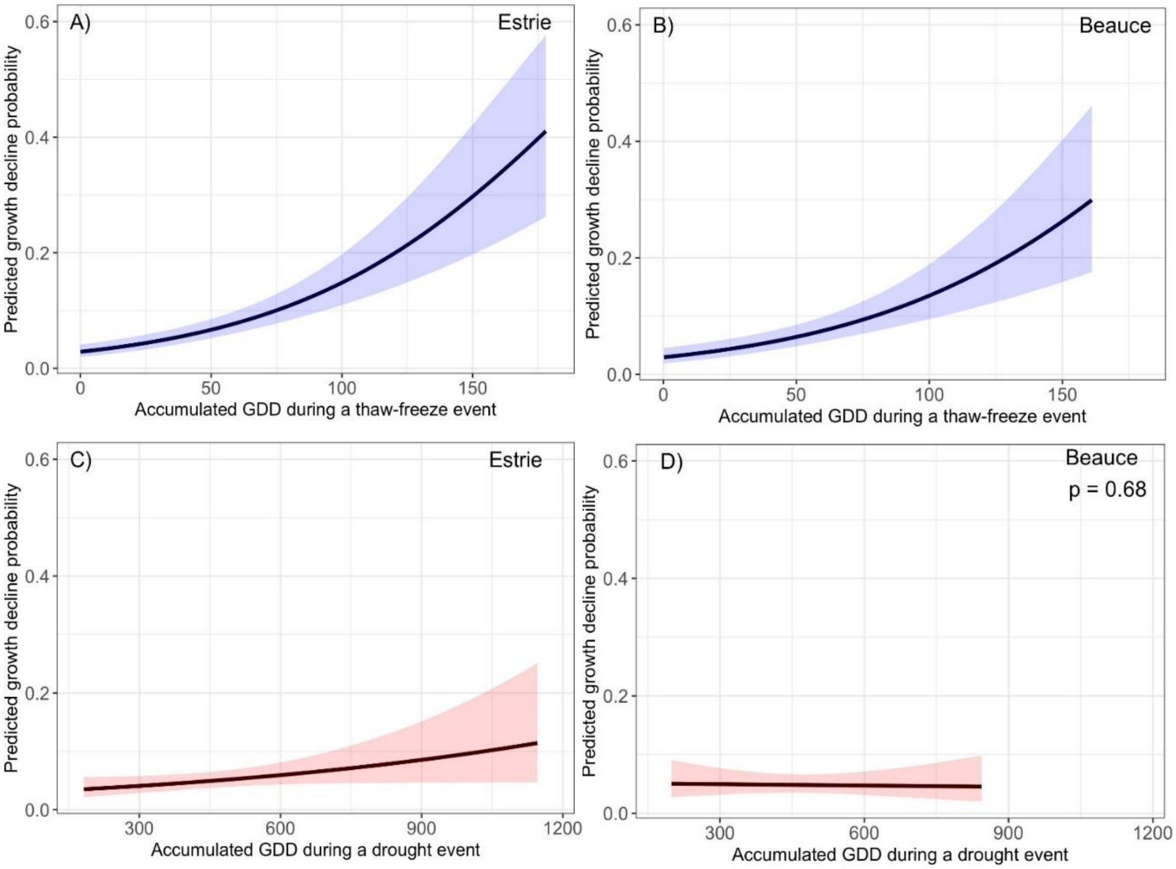

Figure 4.5. Mean predicted abrupt growth decline probability as affected by accumulated GDD during thaw-freeze and drought event in Estrie (A; C) and Beauce (B; D), respectively. Confidence intervals of growth decline predictions (shaded area) were calculated with α=0.05.

4.6. Discussion

4.6.1. Monthly climatic trends

Growth chronologies from this study had weak and non-stationary relationships with traditional monthly climatic metrics over the 1963-2015 period, similarly to what was previously observed in sugar maple forests from southern Quebec (Payette et al. 1996) and the northeastern United States (Gavin et al. 2008; Bishop et al. 2015). The non-stationary relationships observed in this study are in line with observations that the responses of sugar maple trees to climatic conditions are currently changing in North America (Tardif et al. 2001; Bishop et al. 2015; Nolet & Kneeshaw 2018). This may partly explain why the overall relationships between climatic conditions and sugar maple chronologies were weak in the present study. It also suggests that any comparisons of such relationships between different periods should be avoided (Tardif et al. 2001; Bishop et al. 2015). The quantified effects of monthly climatic variables on annual growth are currently used for long-term climatic reconstruction and for modelling the future productivity of sugar maple forests in a changing climate (Tardif et al. 2001; Iverson et al. 2008; Oswald et al. 2018). However, our results suggest that such metrics may not be appropriate for such purposes, especially in cases where yearly growth dynamics are of interest (Payette et al. 1996). Further studies are needed to identify more biologically meaningful metrics that do not break the climatic signal into arbitrary calendar-base units.

4.6.2. Climatic stress events

To our knowledge, this is the first study that could empirically quantify the impact of climatic stress events on the growth dynamics of sugar maple trees, a key species in in the northern hardwoods forests of North America. Our results, along with the expected increase in the severity and frequency of adverse climatic events in upcoming decades (Bell et al. 2004; Bourque et al. 2005; Iverson et al. 2008; Allan et al. 2010; Dai 2013; Comerford et al. 2013; SCAF 2018) bring a new perspective on the challenge of estimating the effects of the ongoing global climate change on tree growth. They suggest that more attention should be given to stress events that are, by nature, highly variable in duration and severity, which can make them hard to detect and quantify. For similar reasons, their future occurrence is also difficult to predict.

In our study, long-lasting thaw-freeze events were particularly damaging to sugar maple as they tended to induce abrupt growth declines in both study regions. Thaw-freeze events can affect trees through several physiological processes (Bourque et al. 2005). First, thaw-freeze events have been related to an increasing occurrence of xylem cavitation, which can reduce xylem conductivity, sap flow rate and total sap volume (Robitaille et al. 1995; Zhu et al. 2000; Zhu et al. 2001; Cox & Zhu 2003; Bourque et al. 2005). Second, in cases where the snow has melted during a long thaw, the return to freezing conditions can injure shallow roots through the freezing of cells and tissues. In turn, this can hinder root pressure development, limit the uptake of water and nutrients and disrupt of other root processes (Robitaille et al. 1995; Zhu et al. 2000; Tierney et al. 2001; Cox & Zhu 2003; Comerford et al. 2013). Third, if the bud burst is triggered by the thaw, the newly emerging shoots are prone to dieback induced by the freezing of the parenchyma cells (George & Burke 1986; Zhu et al. 2001). Damage to the root and shoot systems will cause a loss of carbon reserves, which in turn will force a reallocation of new resources to these tissues (Auclair et al. 1992). Given that stemwood production is a low priority in the resource allocation of trees (Waring 1987), radial growth is expected to remain low in years following a severe climatic event until trees recover. Prolonged thaw-freeze events were identified as a key element in triggering severe episode of forest dieback in North America (Auclair et al. 1992; 1996), and were related to abrupt growth decreases preceding tree death for several species in European temperate forests (Vanoni et al. 2016). While some plants have shown adaptative frost stress memory, which leads to a progressively increased tolerance to successive stress events (Walter et al. 2013), we did not find evidence to support this in our data. The reduced growth index values and the high proportion of abrupt growth declines observed in both regions during thaw-freeze events from 1981 to 2010 suggest that sugar maple has a weak adaptive capacity to the frost injuries induced by such events.

In line with previous observations (e.g. Payette et al. 1996; Nolet & Kneeshaw 2018), our results also underscore the important impact of drought on the growth dynamics of sugar maple trees. It is very likely that severe drought events during the late 1970s weakened sugar maple trees and made them more vulnerable to the effect of the acute thaw-freeze event that occurred in 1981. In addition to being negatively related to the annual growth index in both study regions, we also observed a significant one-year lagged response between the occurrence of drought and the annual growth index in the Beauce region. This delayed growth response was also revealed by the significant effect of the August precipitation from the preceding year in the bootstrapped response function. Our results are in accordance with Vanoni et al. (2016), who showed that while frost injuries generally affect tree growth during the same year as the event occurred, the effects of droughts can be delayed by 1 to 5 years. Again, such lagged effects are harder to detect and link directly to particular events, which may partly explain the weaker relationships observed in this study between sugar maple growth and droughts.

4.6.3. Impacts of cumulative stressors

The cumulative effect of adverse climatic events was not the only cause of the observed growth decline of sugar maple trees in this study. Indeed, forest tent caterpillar (*Malacosoma disstria*) defoliation occurred in our study areas from 1979 to 1982 (Payette et al. 1996 & personal communication, Domtar Corporation). Repeated defoliation over several years can cause severe radial growth reductions related to a decrease in carbon fixation and reserves (Hartman & Messier 2008). In addition to the repeated defoliations, severe drought and thaw-freeze events occurred consecutively between 1979 and 1981 in both regions. Our results suggest that the synergic influence of cumulative climatic events and insect outbreaks weakened sugar maple trees, which led to a growth pattern characterised by several abrupt growth declines and a marked increase in growth sensitivity that peaked 2-3 years later during the mid 1980s. Moreover, the cumulative effect of these stressors may have played a major role in the inconsistent relationships between growth and monthly climatic conditions, possibly by weakening the capacity of sugar maple trees to take advantage of favorable climatic conditions (Graumlich 1993; Tardif et al. 2001; Payette et al. 1996; Nolet & Kneeshaw 2018). Finally, foliar nutrient deficits of calcium, potassium and magnesium were also reported for sugar maple trees in our study area (Bal et al. 2015). Such nutrient deficits are known to predispose and contribute to sugar maple decline, thereby increasing its vulnerability to climatic and biotic stressors (Bal et al. 2015).

The period of severe growth decline during the 1980s corresponds to that already observed throughout the sugar maple range (Houle 1990; Payette et al. 1996; Hartmann & Messier 2008; Bishop et al. 2015; Nolet & Kneeshaw 2018). Such growth declines were observed in sugar maple trees from all ages and sizes (Bishop et al. 2015; Nolet & Kneeshaw 2018), indicating that the negative impact of cumulative stresses was not limited to older and larger trees. In many cases, this period of growth decline was related to sugar maple mortality from 2000 onwards (Moreau et al. 2019), which again underscores the importance of cumulative stresses and their detection to predict stand growth and vigour. Although a permanent growth recovery sometimes occurred following the growth decline of the 1980s (Payette et al. 1996; Hartmann & Messier 2008), the irregular growth patterns observed in this study during the 1990s and the 2000s rather suggest a negative legacy-effect of stressors from the 1980s (Anderegg et al. 2015). Similarly, Nolet & Kneeshaw (2018) observed a lack of growth recovery of sugar maple trees in western Quebec, which they attributed to irreversible damage related to massive vessel embolisms caused by severe droughts (Bréda et al. 2006). This situation could prove particularly problematic in older trees since sugar maple susceptibility to adverse climatic events may increase with age (Auclair et al. 1996).

4.6.4. Limitations of the study

In this study, we used a traditional dendroclimatological analysis that relied on standardized methods to construct stand-level chronologies. The strength of this approach is that using a small subset of highly correlated tree-ring series facilitates the detection of a strong and comprehensive climatic signal in the region of interest. Such an approach has been widely used in recent decades, and has proven to be very effective for deepening our understanding of the relationship between tree growth and climate. However, one important drawback is that the use of small subsets of dominant/codominant trees limits the inference we can make about the effects of adverse climatic events on the growth dynamics of the overall population of sugar maple trees (Canham et al. 2018). Consequently, further testing and validation of our results are needed with additional chronologies covering the entire native range of the species.

4.7. Management implications

Our results indicate that the effect of climate change on the radial stem growth of sugar maple is likely to be more influenced by the occurrence of acute climatic stresses than by the rise in average monthly temperature. Because drought and thaw-freeze events should become more frequent and severe in the future, we can anticipate a reduction in the growth of sugar maple. Considering the great ecological and economic importance of sugar maple in eastern North America, climate-smart silviculture practices should be promoted to stabilize ecosystem services (D’Amato et al. 2013). To help implement remedial measures, it will be important to better characterise the vulnerability of all major companion species to climatic stressors. For example, sugar maple trees have a higher proportion of fine roots in the shallow organic soil horizon compared to companion species such as American beech and yellow birch (Fahey & Hughes 1994). Sugar maple may therefore have a higher vulnerability to root damage due to the soil freezing (Comerford et al. 2013). Differences between the vulnerability of tree species can influence the long-term competition dynamics in the stand. From a silvicultural perspective, characterizing tree species vulnerability to climatic stressors should also be integrated among tree selection criteria before partial cutting (Moreau et al. 2020). Further research should also compare the resistance and resilience to climatic stressors between northern hardwood stands of different ages, densities, structures, species compositions and vigour. Such information is required to meet the challenge of implementing adaptative forest management strategies that will maintain healthy and productive forest ecosystems despite rapid changes in climatic conditions.

4.8. Acknowledgements

This research was funded by a Discovery Grant from the Natural Sciences and Engineering Research Council of Canada (NSERC), the Fonds de recherche du Québec – Nature et technologies (FRQNT), and Domtar Corporation. We are grateful to Michel Poudrier for his help with the data analysis and to Ann Delwaide for her help in the dendrochronological laboratory. We also thank Eloïse Dupuis, Alexandre Morin-Bernard and Félix Poulin for their help with the fieldwork and to the staff from Domtar for their support on the project.

4.9. References

Allen, C. D., Macalady, A. K., Chenchouni, H., Bachelet, D., McDowell, N., Vennetier, M., ... & Gonzalez, P. (2010). A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *Forest ecology and management*, 259(4), 660-684.

Allen, C. D., Breshears, D. D., & McDowell, N. G. (2015). On underestimation of global vulnerability to tree mortality and forest die-off from hotter drought in the Anthropocene. *Ecosphere*, 6(8), 1-55.

Anderegg, W. R., Schwalm, C., Biondi, F., Camarero, J. J., Koch, G., Litvak, M., ... & Wolf, A. (2015). Pervasive drought legacies in forest ecosystems and their implications for carbon cycle models. *Science*, 349(6247), 528-532.

Auclair, A. N. D., Worrest, R. C., Lachance, D. and Martin, H. C.: 1992, in Manion, E D. and Lachance, D. (eds.), Forest Decline Concepts, pp. 38-58. *American Phytopathological Society Press*, St. Paul, Minnesota. U.S.A., p. 249.

Auclair, A. N., Lill, J. T., & Revenga, C. (1996). The role of climate variability and global warming in the dieback of Northern Hardwoods. *Water, Air, and Soil Pollution*, 91(3-4), 163-186.

Bal, T. L., Storer, A. J., Jurgensen, M. F., Doskey, P. V., & Amacher, M. C. (2015). Nutrient stress predisposes and contributes to sugar maple dieback across its northern range: a review. *Forestry: An International Journal of Forest Research*, 88(1), 64-83.

Bell, J. L., Sloan, L. C., & Snyder, M. A. (2004). Regional changes in extreme climatic events: a future climate scenario. *Journal of Climate*, 17(1), 81-87.

Bishop, D. A., Beier, C. M., Pederson, N., Lawrence, G. B., Stella, J. C., & Sullivan, T. J. (2015). Regional growth decline of sugar maple (Acer saccharum) and its potential causes. *Ecosphere*, *6*(10), 1-14.

Bourque, C. P. A., Cox, R. M., Allen, D. J., Arp, P. A., & Meng, F. R. (2005). Spatial extent of winter thaw events in eastern North America: historical weather records in relation to yellow birch decline. *Global Change Biology*, 11(9), 1477-1492.

Braathe, P. (1995). Birch dieback-caused by prolonged early spring thaws and subsequent frost. *Norwegian Journal of Agricultural Sciences* 20, 1-59.

Braathe, P .(1996). Birch dieback caused by the effects of artificial spring frost on budburst and foliage. *Norwegian Journal of Agricultural Sciences,*10, 1-6.

Bréda, N., Huc, R., Granier, A., & Dreyer, E. (2006). Temperate forest trees and stands under severe drought: a review of ecophysiological responses, adaptation processes and long-term consequences. *Annals of Forest Science*, *63*(6), 625-644.

Briffa, K. R., & Jones, P. D. (1990). Basic chronology statistics and assessment. Page 137-152 *In* Methods of dendrochronology: applications in the environmental sciences. E.R. Cook and L.A. Kairiukstis, editors. Kluwer Academic, Norwell, Dordrecht.

Canham, C. D., Murphy, L., Riemann, R., McCullough, R., & Burrill, E. (2018). Local differentiation in tree growth responses to climate. Ecosphere, 9(8), e02368.

Comerford, D. P., Schaberg, P. G., Templer, P. H., Socci, A. M., Campbell, J. L., & Wallin, K. F. (2013). Influence of experimental snow removal on root and canopy physiology of sugar maple trees in a northern hardwood forest. *Oecologia*, 171(1), 261-269.

Cox, R. M., & Zhu, X. B. (2003). Effects of simulated thaw on xylem cavitation, residual embolism, spring dieback and shoot growth in yellow birch. *Tree Physiology*, 23(9), 615-624.

Cook, E. R., & Peters, K. (1981). The smoothing spline: a new approach to standardizing forest interior tree-ring width series for dendroclimatic studies.

D'Amato, A. W., Bradford, J. B., Fraver, S., & Palik, B. J. (2013). Effects of thinning on drought vulnerability and climate response in north temperate forest ecosystems. *Ecological Application*s, 23(8), 1735-1742.

Dai, A. (2013). Increasing drought under global warming in observations and models. *Nature climate change*, 3(1), 52-58.

Das, A. J., Battles, J. J., Stephenson, N. L., & Van Mantgem, P. J. (2007). The relationship between tree growth patterns and likelihood of mortality: a study of two tree species in the Sierra Nevada. *Canadian Journal of Forest Research*, *37*(3), 580-597.

Duchesne, L., Ouimet, R., & Morneau, C. (2003). Assessment of sugar maple health based on basal area growth pattern. *Canadian Journal of Forest Research*, 33(11), 2074-2080.

Fahey, T. J., & Hughes, J. W. (1994). Fine root dynamics in a northern hardwood forest ecosystem, Hubbard Brook Experimental Forest, NH. *Journal of ecology*, 533-548.

Fritts, H.C. (1976). Tree Rings and Climate. *Academic Press (London)*

Gavin, D. G., Beckage, B., & Osborne, B. (2008). Forest dynamics and the growth decline of red spruce and sugar maple on Bolton Mountain, Vermont: a comparison of modeling methods. *Canadian Journal of Forest Research*, 38(10), 2635-2649.

George, M. F., & Burke, M. J. (1986). Low temperature: physical aspects of freezing in woody plant xylem. In *Stress physiology and forest productivity* (pp. 133-150). Springer, Dordrecht.

Graumlich, L. J. (1993). Response of tree growth to climatic variation in the mixed conifer and deciduous forests of the upper Great Lakes region. *Canadian Journal of Forest Research*, 23(2), 133-143.

Grondin, P., Jean, N., Hotte, D. (2007). Intégration de la végétation et de ses variables explicatives à des fins de classification et de cartographie d'unité s homogènes du Québec meéridional, Ministère des Ressources naturelles et de la Faune, Direction de la recherche forestière. Mémoire de recherche No 150, 62 pp.

Hartmann, H., & Messier, C. (2008). The role of forest tent caterpillar defoliations and partial harvest in the decline and death of sugar maple. *Annals of botany*, 102(3), 377-387.

Houle, G. (1990). Growth patterns of sugar maple seedlings and mature trees in healthy and in declining hardwood stands. *Canadian Journal of Forest Research*, 20(7), 894-901.

Iverson, L. R., Prasad, A. M., Matthews, S. N., & Peters, M. (2008). Estimating potential habitat for 134 eastern US tree species under six climate scenarios. *Forest Ecology and Management*, 254(3), 390-406.

Lévesque, M., Saurer, M., Siegwolf, R., Eilmann, B., Brang, P., Bugmann, H., & Rigling, A. (2013). Drought response of five conifer species under contrasting water availability suggests high vulnerability of Norway spruce and European larch. *Global Change Biology*, 19(10), 3184-3199.

Lane, C. J., Reed, D. D., Mroz, G. D., & Liechty, H. O. (1993). Width of sugar maple (Acer saccharum) tree rings as affected by climate. *Canadian Journal of Forest Research*, 23(11), 2370-2375.

Magnusson, A., Skaug, H., Nielsen, A., Berg, C., Kristensen, K., Maechler, M., ... & Brooks, M. M. (2017). Package 'glmmTMB'. *R Package* Version 0.2. 0.

Moreau, G., Achim, A., & Pothier, D. (2019). A dendrochronological reconstruction of sugar maple growth and mortality dynamics in partially cut northern hardwood forests. *Forest ecology and management*, 437, 17-26.

Moreau, G., Achim, A., & Pothier, D. (2020). Relevance of stem and crown defects to estimate tree vigour in northern hardwood forests. *Forestry: An International Journal of Forest Research*.(In press)

Nolet, P., & Kneeshaw, D. (2018). Extreme events and subtle ecological effects: lessons from a long-term sugar maple–American beech comparison. *Ecosphere*, 9(7), e02336.

Oswald, E. M., Pontius, J., Rayback, S. A., Schaberg, P. G., Wilmot, S. H., & Dupigny-Giroux, L. A. (2018). The complex relationship between climate and sugar maple health: Climate change implications in Vermont for a key northern hardwood species. *Forest Ecology and Management*, 422, 303-312.

Payette, S., Fortin, M. J., & Morneau, C. (1996). The recent sugar maple decline in southern Quebec: probable causes deduced from tree rings. *Canadian Journal of Forest Research*, 26(6), 1069-1078.

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., Heisterkamp, S., Van Willigen, B., & Maintainer, R. (2017). Package 'nlme'. *Linear and nonlinear mixed effects models*, version, 3.

Robitaille, G., Boutin, R., & Lachance, D. (1995). Effects of soil freezing stress on sap flow and sugar content of mature sugar maples (Acer saccharum). *Canadian journal of forest research*, 25(4), 577-587.

Saucier, J.-P., Grondin, P., Robitaille, A., Gosselin, J., Morneau, C., Richard, P.-J.-H., Brisson, J., Sirois, L., Leduc, A., Morin, H., Thiffault, E., Gauthier, S., Lavoie, C. et Payette, S. 2009. Écologie forestière. Manuel de foresterie, 2e édition. Ordre des ingénieurs forestiers du Québec, Éditions Multimondes, Québec, pp.165-316.

Senate Committee on Agriculture and Forestry. (2018). Feast or Famine: Impacts of climate change and carbon pricing on agriculture, *agri-food and forestry*

Tardif, J., Brisson, J., & Bergeron, Y. (2001). Dendroclimatic analysis of Acer saccharum, Fagus grandifolia, and Tsuga canadensis from an old-growth forest, southwestern Quebec. Canadian Journal of Forest Research, 31(9), 1491-1501.

Tierney, G. L., Fahey, T. J., Groffman, P. M., Hardy, J. P., Fitzhugh, R. D., & Driscoll, C. T. (2001). Soil freezing alters fine root dynamics in a northern hardwood forest. *Biogeochemistry*, 56(2), 175-190.

Vanoni, M., Bugmann, H., Nötzli, M., & Bigler, C. (2016). Drought and frost contribute to abrupt growth decreases before tree mortality in nine temperate tree species. *Forest ecology and management*, 382, 51-63.

Vicente-Serrano, S. M., Beguería, S., & López-Moreno, J. I. (2010). A multiscalar drought index sensitive to global warming: the standardized precipitation evapotranspiration index. *Journal of climate*, 23(7), 1696-1718.

Waring, R. H. (1987). Characteristics of trees predisposed to die. Bioscience, 37(8), 569-574.

Wigley, T. M., Briffa, K. R., & Jones, P. D. (1984). On the average value of correlated time series, with applications in dendroclimatology and hydrometeorology. *Journal of climate and Applied Meteorology*, 23(2), 201-213.

Yin, X., Foster, N. W., Morrison, I. K., & Arp, P. A. (1994). Tree-ring-based growth analysis for a sugar maple stand: relations to local climate and transient soil properties. *Canadian journal of forest research*, 24(8), 1567-1574.

Zang, C., & Biondi, F. (2013). Dendroclimatic calibration in R: the bootRes package for response and correlation function analysis. *Dendrochronologia*, 31(1), 68-74.

Zhang, T., Niinemets, Ü., Sheffield, J., & Lichstein, J. W. (2018). Shifts in tree functional composition amplify the response of forest biomass to climate. *Nature*, 556(7699), 99-102.

Zhu, X. B., Cox, R. M., & Arp, P. A. (2000). Effects of xylem cavitation and freezing injury on dieback of yellow birch (Betula alleghaniensis) in relation to a simulated winter thaw. *Tree Physiology*, 20(8), 541-547.

Zhu, X. B., Cox, R. M., Meng, F. R., & Arp, P. A. (2001). Responses of xylem cavitation, freezing injury and shoot dieback to a simulated winter thaw in yellow birch seedlings growing in different nursery culture regimes. *Forest Ecology and Management*, 145(3), 243-253.

Conclusion

En Amérique du Nord, la coupe de jardinage a été implantée après plusieurs décennies d'exploitation forestière par la coupe à diamètre limite, une pratique reconnue pour avoir laissé de grandes superficies de peuplements feuillus dégradés et de faible vigueur (Nyland 1998; Guillemette et al. 2008). Or, le suivi des peuplements jardinés dans un contexte industriel a montré une productivité très variable et souvent plus faible que celle anticipée, questionnant ainsi sa capacité à améliorer la vigueur générale des peuplements feuillus et à fournir un rendement soutenu en bois de haute valeur aux secteurs de transformation primaires (Nyland 1998; Bédard & Brassard 2002; Pond et al. 2014). Pour atteindre ces deux objectifs, savoir évaluer la vigueur et le potentiel de croissance sur pied des arbres feuillus au moment de la récolte semble essentiel. Le premier volet de ce projet de recherche visait à mieux comprendre les facteurs qui prédisposent certains arbres à réagir positivement ou négativement à une coupe de jardinage mécanisée de manière à améliorer l'évaluation visuelle de leur potentiel de croissance dans les années suivant l'application du traitement.

Nos résultats ont d'abord montré un effet marginal du taux de dégagement induit par la coupe mécanisée sur la croissance et le taux de survie des arbres résiduels. Ce résultat s'explique en partie par une concentration de la récolte des arbres à l'intérieur et aux abords des sentiers de débardage, laissant ainsi de larges zones non traitées dans les peuplements résiduels. Pour augmenter l'effet positif du traitement, une récolte plus homogène au sein des peuplements semble nécessaire de manière à augmenter le pourcentage d'arbres résiduels libérés de leurs concurrents dans les zones où l'effet négatif du passage répété de la machinerie est moindre. Pour ce faire, l'utilisation de machines avec une portée maximale, l'implantation de sentiers secondaires avec un passage limité de la machinerie et l'augmentation du taux de prélèvement au sein des peuplements irréguliers sont des méthodes à explorer dans le futur.

L'effet marginal du traitement a été corroboré par nos analyses dendrochronologiques qui ont montré qu'uniquement 24 % des arbres résiduels ont connu une hausse de croissance significative après la coupe. Cette réaction de croissance est légèrement inférieure à celle induite par les perturbations naturelles au cours des décennies précédentes. Ces analyses ont aussi montré qu'aucun des arbres échantillonnés qui sont morts après l'application de la coupe de jardinage n'a connu une hausse de croissance marquée dans les années suivant la coupe. De plus, la majorité de ces arbres étaient en déclin depuis plusieurs décennies au moment de l'application du traitement. Ces résultats indiquent que le déclin de vigueur des arbres feuillus est un long processus qui est difficilement renversé par une réduction de la compétition au moment de la coupe. Or, en plus d'être improductifs pendant plusieurs décennies et de démontrer un faible potentiel de réaction de croissance, les arbres en perte de vigueur continuent d'utiliser les ressources du milieu, ce qui limite la croissance et la réaction de croissance des arbres sains dans les années suivant l'application du traitement. Ensembles, les résultats des deux premiers chapitres indiquent que la récolte des arbres en perte de vigueur au moment de la coupe aura plus d'impact pour augmenter la productivité des peuplements jardinés que la réaction de croissance des arbres résiduels. Afin d'approfondir notre compréhension des dynamiques de croissance au sein des peuplements feuillus, les recherches futures devraient viser à mieux définir les processus responsables du déclin du potentiel de réaction de croissance des arbres. Pour ce faire, l'étude des tendances de croissance à long terme à l'aide de méthodes dendrochronologiques semble avoir un bon potentiel.

Les résultats précédents ont montré l'importance d'identifier les arbres non vigoureux au moment de la récolte. Toutefois, les analyses du troisième chapitre ont montré que les multiples classes de défauts apparents du tronc et des racines qui sont présentement utilisés par les systèmes de classification de la vigueur en Amérique du Nord ne sont pas de bons indicateurs de la vigueur actuelle des arbres. En se basant sur ces résultats, l'évaluation de ces différentes classes de défaut ne semble pas nécessaire si l'on cherche à évaluer la vigueur et le potentiel de croissance des arbres sur pied. À l'inverse, une évaluation de la densité du houppier est un indicateur plus simple et plus efficace pour identifier les arbres vigoureux. Des relations similaires entre la vigueur de l'érable à sucre et les conditions du houppier ont été observées en Ontario (Tominaga et al. 2008), aux États-Unis (Morin et al. 2015), ainsi que chez plusieurs espèces feuillues des forêts tempérées européennes (e.g. Drobyshev et al. 2007; Seidling et al. 2012; Rybníček et al. 2015). Ces résultats sont en accord avec le principe selon lequel un déclin de la vigueur entraînera une dégradation des conditions du houppier, quels que soient les facteurs incitatifs (Schomaker 2007). Dans l'attente d'une validation complète et approfondie des systèmes de classification par l'addition de mesures répétées des défauts sur une plus longue période, nous suggérons l'utilisation de la densité du houppier pour guider les opérations de marquage dans les érablières. En plus de son utilisation pour les opérations de marquage au moment de la coupe, nos résultats montrent qu’une évaluation de la dégradation des conditions du houppier semble être un indicateur approprié pour suivre l’état global de la santé des forêts feuillues à l’aide de programmes d’inventaires à grande échelle (Drobyshev et al. 2007; Tominaga et al. 2008; Morin et al. 2015).

Étant donné qu’une croissance radiale rapide des arbres feuillus de dimensions marchandes semble limiter le développement de la coloration du cœur des arbres sur pied (Havreljuk et al. 2013), la récolte des arbres à faible croissance semble aussi favoriser la production de bois feuillus de haute valeur. Une fois les arbres non vigoureux identifiés par l’évaluation de la condition du houppier, l’identification des tiges ayant un faible potentiel de production de bois de haute valeur devrait être réalisée en utilisant des défauts de tronc tels que la présence de fentes, de sporophores, de cavités et de chancres (Havreljuk et al. 2014; Cecil-Cockwell & Caspersen 2015). De plus, notre étude a identifié un seuil de la taille des érables à sucre (40-49 cm au DHP) au-dessus duquel l’efficacité de croissance commence à décroitre. Or, ce seuil correspond aussi à la limite maximale de la valeur monétaire par mètre cube de bois rond pour l’érable à sucre et le bouleau jaune (Havreljuk et al. 2014 ; Saucier et al. 2014). Selon ces résultats, un aménagement orienté vers la production d’arbres de DHP inférieur à 50 cm serait bénéfique pour optimiser à la fois l’efficacité de croissance des peuplements feuillus, i.e. leur vigueur générale, et la production de bois de haute valeur (Havreljuk et al. 2014).

En plus du lien direct avec l’optimisation de la production de bois de haute valeur, l’augmentation de la vigueur générale de nos forêts feuillues semble impérative dans un contexte où l’on s’attend à une augmentation des stress climatiques en fréquence et en intensité au cours des prochaines années. Nos analyses des relations entre la croissance et les conditions climatiques ont montré un lien fort entre l’occurrence des stress climatiques et une diminution de la croissance de l’érable à sucre. Les épisodes de gel-dégel de forte intensité ont été particulièrement dommageables en provoquant des baisses abruptes de la croissance dans les deux régions étudiées. De plus, notre étude a montré l’impact majeur d’une accumulation de différents stress climatiques et biotiques dans un court laps de temps sur la dynamique de croissance et de mortalité des érablières. Évidemment, une augmentation de la fréquence et de l’intensité des stress climatiques dans les prochaines années augmentera du même coup la probabilité que de tels événements cumulatifs se produisent. Si un tel scénario se confirme, on peut s'attendre à une baisse de la productivité des peuplements d'érable à sucre dans le sud du Québec. Étant donné qu’en général, la croissance de l’érable à sucre est négativement corrélée à une hausse des températures annuelles (Canham et al. 2018), il est peu probable qu’un réchauffement progressif du climat tel qu’attendu dans les prochaines années puisse compenser cette baisse de productivité potentielle.

Contrairement à l’effet marqué des stress climatiques sur la dynamique de croissance de l’érable à sucre, nos résultats ont montré que le lien entre la croissance et les tendances climatiques mensuelles était très faible et instable dans le temps. Cette instabilité indique que la réponse de croissance de l’érable à sucre aux conditions climatiques est en train de changer en Amérique du Nord, ce qui empêche toutes comparaisons de ces relations entre différentes périodes (Tardif et al. 2001; Bishop et al. 2015; Nolet & Kneeshaw 2018). Ainsi, les tendances climatiques mensuelles ne semblent pas être les variables appropriées à utiliser pour modéliser la croissance de l’érable à sucre sous différents scénarios climatiques. Des recherches futures devraient viser à identifier des variables plus significatives sur le plan biologique et qui ne brisent pas le signal climatique arbitrairement selon notre calendrier. Pour ce faire, l’utilisation de variables climatiques à l’échelle de la journée semble être une approche prometteuse.

Afin d’intégrer l’effet potentiel des changements climatiques sur la productivité à long terme de nos peuplements forestiers, les recherches futures devraient viser à mieux caractériser la vulnérabilité des principales espèces feuillues aux événements ponctuels de stress climatique. Finalement, les recherches futures devraient également comparer la résistance et la résilience aux différents stress climatiques des peuplements feuillus de différents âges, densité, structure et composition. Ces informations sont cruciales afin de moduler les mesures d’aménagement actuelles en fonction des caractéristiques des peuplements, de manière à prescrire des interventions qui favoriseront le maintien des écosystèmes forestiers sains et productifs malgré les changements rapides des conditions climatiques.

Bibliographie

Allen, C. D., Macalady, A. K., Chenchouni, H., Bachelet, D., McDowell, N., Vennetier, M., ... & Gonzalez, P. (2010). A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *Forest ecology and management*, 259(4), 660-684.

Allen, C. D., Breshears, D. D., & McDowell, N. G. (2015). On underestimation of global vulnerability to tree mortality and forest die-off from hotter drought in the Anthropocene. *Ecosphere*, 6(8), 1-55.

Anderegg, W. R., Schwalm, C., Biondi, F., Camarero, J. J., Koch, G., Litvak, M., ... & Wolf, A. (2015). Pervasive drought legacies in forest ecosystems and their implications for carbon cycle models. *Science*, 349(6247), 528-532.

Arbogast, C. (1957). Marking guides for northern hardwoods under the selection system. USDA Forest Service, Paper No. 56, 20 pp.

Auclair, A. N. D., Worrest, R. C., Lachance, D. and Martin, H. C.: 1992, in Manion, E D. and Lachance, D. (eds.), Forest Decline Concepts, pp. 38-58. *American Phytopathological Society Press*, St. Paul, Minnesota. U.S.A., p. 249.

Auclair, A. N., Lill, J. T., & Revenga, C. (1996). The role of climate variability and global warming in the dieback of Northern Hardwoods. *Water, Air, and Soil Pollution*, 91(3-4), 163-186.

Bal, T. L., Storer, A. J., Jurgensen, M. F., Doskey, P. V., & Amacher, M. C. (2015). Nutrient stress predisposes and contributes to sugar maple dieback across its northern range: a review. *Forestry: An International Journal of Forest Research*, 88(1), 64-83.

Bailey, R. G. (1983). Delineation of ecosystem regions. *Environmental management*, 7(4), 365-373.

Baral, S. K., Danyagri, G., Girouard, M., Hébert, F., & Pelletier, G. (2016). Effects of suppression history on growth response and stem quality of extant northern hardwoods following partial harvests. *Forest Ecology and Management*, 372, 236–246.

Baret, M. Pepin, S. & Pothier, D. (2018). Hydraulic limitations in dominant trees as a contributing mechanism to the age-related growth decline of boreal forest stands. *Forest Ecology and Management,* 427, 135-142.

Bates, D., M. Maechler, B. Bolker, & S. Walker. (2015). lme4: linear mixed-effects models using Eigen and S4. R package version 1.1-8.

Bédard, S., & Brassard, F. (2002). Les effets réels des coupes de jardinage dans les forêts publiques du Québec en 1995 et 1996, *Ministère des Ressources naturelles du Québec*, Direction de la recherche forestière, Sainte-Foy, Québec, Canada, 15 p.

Bell, J. L., Sloan, L. C., & Snyder, M. A. (2004). Regional changes in extreme climatic events: a future climate scenario. *Journal of Climate*, 17(1), 81-87.

Bigler, C., & Bugmann, H. (2004). Predicting the time of tree death using dendrochronological data. *Ecological Applications*, 14, 902–914.

Binkley, D. (2004). A hypothesis about the interaction of tree dominance and stand production through stand development. *Forest Ecology and Management*, 190, 265–271.

Bishop, D. A., Beier, C. M., Pederson, N., Lawrence, G. B., Stella, J. C., & Sullivan, T. J. (2015). Regional growth decline of sugar maple (Acer saccharum) and its potential causes. *Ecosphere*, *6*(10), 1-14.

Black, B.A., & Abrams, M.D., (2003). Use of boundary-line growth patterns as a basis for dendroecological release criteria. *Ecological Applications*, 13, 1733–1749.

Black, B.A., & Abrams, M.D., (2004). Development and application of boundary-line release criteria. *Dendrochronologia*, 22, 31–42.

Black, B.A., Abrams, M.D., Rentch, J.S., & Gould, P.J. (2009). Properties of boundary-line release criteria in North American tree species. *Annals of Forest Science,* 66, 205-205.

Boivin-Dompierre, S., Achim, A., & Pothier, D. (2017). Functional response of coniferous trees and stands to commercial thinning in eastern Canada. *Forest Ecology and Management*, 384, 6–16.

Boulet, B. (2007). Défauts et indices de la carie des arbres: Guide d'interprétation, 2^{e} éd. Les Publications du Québec, Québec, pp. 317

Boulet, B., & Landry, G. (2015). La carie des arbres: Fondements, diagnostic et application, 3^{e} éd. Les publications du Québec, Québec, pp. 347

Bose, A. K., Weiskittel, A., Kuehne, C., Wagner, R. G., Turnblom, E., & Burkhart, H. E. (2018). Does commercial thinning improve stand-level growth of the three most commercially important softwood forest types in North America?. *Forest Ecology and Management*, 409, 683-693.

Bose, A. K., Weiskittel, A., Kuehne, C., Wagner, R. G., Turnblom, E., & Burkhart, H. E. (2018b). Tree-level growth and survival following commercial thinning of four major softwood species in North America. *Forest ecology and management*, 427, 355-364.

Bourque, C. P. A., Cox, R. M., Allen, D. J., Arp, P. A., & Meng, F. R. (2005). Spatial extent of winter thaw events in eastern North America: historical weather records in relation to yellow birch decline. *Global Change Biology*, 11(9), 1477-1492.

Braathe, P. (1995). Birch dieback-caused by prolonged early spring thaws and subsequent frost. *Norwegian Journal of Agricultural Sciences,* 20, 1-59.

Braathe, P .(1996). Birch dieback caused by the effects of artificial spring frost on budburst and foliage. *Norwegian Journal of Agricultural Sciences,* 10, 1-6.

Brais, S., & Camire, C. (1998). Soil compaction induced by careful logging in the claybelt region of northwestern Quebec (Canada). Canadian Journal of Soil Science, 78(1), 197-206.

Bréda, N., Huc, R., Granier, A., & Dreyer, E. (2006). Temperate forest trees and stands under severe drought: a review of ecophysiological responses, adaptation processes and long-term consequences. *Annals of Forest Science*, *63*(6), 625-644.

Briffa, K. R., & Jones, P. D. (1990). Basic chronology statistics and assessment. Page 137-152 *In* Methods of dendrochronology: applications in the environmental sciences. E.R. Cook and L.A. Kairiukstis, editors. Kluwer Academic, Norwell, Dordrecht.

Canham C.D., Finzi A.C., Pacala S.W., and Burbank D.H. (1994). Causes and consequences of resource heterogeneity in forests—interspecific variation in light transmission by canopy trees. *Canadian Journal of Forest Research*, 24, 337–49

Canham, C. D., Murphy, L., Riemann, R., McCullough, R., & Burrill, E. (2018). Local differentiation in tree growth responses to climate. Ecosphere, 9(8), e02368.

Cailleret, M., Bigler, C., Bugmann, H., Camarero, J. J., Cufar, K., Davi, H., ... & Suarez, M. L. (2016). Towards a common methodology for developing logistic tree mortality models based on ring-width data. *Ecological Applications*, *26*(6), 1827-1841.

Cailleret, M., Jansen, S., Robert, E. M., Desoto, L., Aakala, T., Antos, J. A., ... & Čada, V. (2017). A synthesis of radial growth patterns preceding tree mortality. *Global change biology*, *23*(4), 1675-1690.

Caspersen, J.P. (2006). Elevated mortality of residual trees following single-tree felling in northern hardwood forests. *Canadian Journal of Forest Research*, 36, 1255–1265.

Castle, M., Weiskittel, A., Wagner, R., Ducey, M., Frank, J., & Pelletier, G. (2018). Evaluating the influence of stem form and damage on individual-tree diameter increment and survival in the Acadian Region: implications for predicting future value of northern commercial hardwood stands. *Canadian Journal of Forest Research*. 48, 1007-1019.

Cecil-Cockwell, M. J. L., & Caspersen, J. P. (2015). A simple system for classifying sugar maple vigour and quality. *Canadian Journal of Forest Research*, 45, 900-909

Cherubini, P., Fontana, G., Rigling, D., Dobbertin, M., Brand, P., & Innes, J.L. (2002). Tree-life history prior to death: Two fungal root pathogens affect tree-ring growth differently. *Journal of Ecology*, 90, 839–850.

Christiansen, E. Waring, R.H. & Berryman, A.A. (1987). Resistance of conifers to bark beetle attack: Searching for general relationships. *Forest Ecology and Management*, 22, 89–106.

Comerford, D. P., Schaberg, P. G., Templer, P. H., Socci, A. M., Campbell, J. L., & Wallin, K. F. (2013). Influence of experimental snow removal on root and canopy physiology of sugar maple trees in a northern hardwood forest. *Oecologia*, 171(1), 261-269.

Cook, E. R., & Peters, K.(1981).The smoothing spline: a new approach to standardizing forest interior tree-ring width series for dendroclimatic studies. *Tree-ring bulletin*, 41,45

Coops, N. C., Waring, R. H., Wulder, M. A., & White, J. C. (2009). Prediction and assessment of bark beetle-induced mortality of lodgepole pine using estimates of stand vigor derived from remotely sensed data. *Remote Sensing of Environment*, 113(5), 1058-1066.

Cox D.R., & Oakes D. 1984 Analysis of survival data, Chapman and Hall, London - New York, 201 S. *Biometrical Journal*, 29. 114-114.

Cox, R. M., & Zhu, X. B. (2003). Effects of simulated thaw on xylem cavitation, residual embolism, spring dieback and shoot growth in yellow birch. *Tree Physiology*, 23(9), 615-624.

D'Amato, A. W., Bradford, J. B., Fraver, S., & Palik, B. J. (2013). Effects of thinning on drought vulnerability and climate response in north temperate forest ecosystems. *Ecological Application*s, 23(8), 1735-1742.

Dai, A. (2013). Increasing drought under global warming in observations and models. *Nature climate change*, 3(1), 52-58.

Das, A. J., Battles, J. J., Stephenson, N. L., & Van Mantgem, P. J. (2007). The relationship between tree growth patterns and likelihood of mortality: a study of two tree species in the Sierra Nevada. *Canadian Journal of Forest Research*, *37*(3), 580-597.

Davis, D.D., Torsello, M.L., & McClenahen, J.R. (1997). Influence of *Cryphonectria parasitica* basal cankers on radial growth of scarlet oak in Pennsylvania. *Plant Disease*, 81,369–373.

Delisle-Boulianne S, (2013). Mise au point d’un modèle de prélèvement par tiges individuelles pour simuler les coupes de jardinage en Outaouais. Université Laval, Québec, Canada. Mémoire de maîtrise. 27 pp.

Delisle-Boulianne, S., Fortin, M., Achim, A., & Pothier, D. (2014). Modelling stem selection in northern hardwood stands: assessing the effects of tree vigour and spatial correlations using a copula approach. *Forestry: An International Journal of Forest Research*, *87*(5), 607-617.

Delucia, E. H., Sipe, T. W., Herrick, J., & Maherali, H. (1998). Sapling biomass allocation and growth in the understory of a deciduous hardwood forest. *American Journal of Botany*, *85*(7), 955-963.

Després, T., Asselin, H., Doyon, F., Drobyshev, I., & Bergeron, Y. (2017). Gap dynamics of late successional sugar maple–yellow birch forests at their northern range limit. *Journal of Vegetation Science,* 28, 368–378.

Duchesne, L., Ouimet, R., & Morneau, C. (2003). Assessment of sugar maple health based on basal area growth pattern. *Canadian Journal of Forest Research*, 33(11), 2074-2080.

Drobyshev, I., Linderson, H., & Sonesson, K. (2007). Relationship between crown condition and tree diameter growth in southern Swedish oaks. *Environmental monitoring and assessment*, 128(1-3), 61-73.

Dyer, J.H., Gower S.T., Forrester, J.A., Lorimer, C.G., Mladenoff, D. J., & Burton, J.I. (2010). Effects of selective tree harvests on aboveground biomass and net primary productivity of a second-growth northern hardwood forest. *Canadian Journal of Forest Research*, 40, 2360–2369.

Fahey, T. J., & Hughes, J. W. (1994). Fine root dynamics in a northern hardwood forest ecosystem, Hubbard Brook Experimental Forest, NH. *Journal of ecology*, 533-548.

Fatichi, S., Leuzinger, S., & Körner, C. (2014). Moving beyond photosynthesis: From carbon source to sink-driven vegetation modeling. *New Phytologist*, 201,1086–1095.

Fisk, M.C. Fahey, T.J., Groffman, P.M., & Bohlen, P.J (2004). Earthworm invasion, fine-root distributions, and soil respiration in north temperate forests. *Ecosystems*, 7, 55–62.

Forget, E., Nolet, P., Doyon, F., Delagrande, S., Jardin, Y. (2007). Ten-year response of northern hardwood stands to commercial selection cutting in southern Quebec, Canada. *Forest Ecology and Management*, 242, 764–775.

Fortin, M., Bédard, S., DeBlois, J., & Meunier, S. (2008). Predicting individual tree mortality in northern hardwood stands under uneven-aged management in southern Québec, Canada. *Annals of Forest Science*, 65(2), 1.

Fortin, M. (2014). Using a segmented logistic model to predict trees to be harvested in forest growth forecasts, *Forest systems, 23, 139-152*

Fraver, S., & White, A.S. (2005). Identifying growth releases in dendrochronological studies of forest disturbance. *Canadian Journal of Forest Research*, 35, 1648–1656.

Fritts, H.C. (1976). Tree Rings and Climate. Academic Press, London, UK. 567 pp.

Gaudinski, J.B., Torn, M.S., Riley, W.J., Swanston, C., Trumbore, S.E., Joslin, J.D., Majdhi, H., Dawson, T.E., Hanson, P.J. (2009). Use of stored carbon reserves in growth of temperate tree roots and leaf buds: Analyses using radiocarbon measurements and modeling. *Global Change Biology*, 15, 992–1014.

Gauthier, M. M., & Guillemette, F. (2018). Bark type reflects growth potential of yellow birch and sugar maple at the northern limit of their range. *Plant ecology*, 219(4), 381-390.

Gavin, D. G., & Peart, D. R. (1993). Effects of beech bark disease on the growth of American beech (Fagus grandifolia). *Canadian Journal of Forest Research*, 23(8), 1566-1575.

Gavin, D. G., Beckage, B., & Osborne, B. (2008). Forest dynamics and the growth decline of red spruce and sugar maple on Bolton Mountain, Vermont: a comparison of modeling methods. *Canadian Journal of Forest Research*, 38(10), 2635-2649.

Genet, A., & Pothier, D. (2013). Modeling tree spatial distributions after partial harvesting in uneven-aged boreal forests using inhomogeneous point processes. *Forest Ecology and Management,* 305, 158–166.

George, M. F., & Burke, M. J. (1986). Low temperature: physical aspects of freezing in woody plant xylem. In *Stress physiology and forest productivity* (pp. 133-150). Springer, Dordrecht.

Graumlich, L. J. (1993). Response of tree growth to climatic variation in the mixed conifer and deciduous forests of the upper Great Lakes region. *Canadian Journal of Forest Research*, 23(2), 133-143.

Grigal, D. F. (2000). Effects of extensive forest management on soil productivity. *Forest Ecology and Management*, 138(1-3), 167-185.

Grondin, P., Jean, N., & Hotte, D. (2007). Intégration de la végétation et de ses variables explicatives à des fins de classification et de cartographie d'unités homogènes du Québec méridional, *Ministère des Ressources naturelles et de la Faune*, Direction de la recherche forestière. Mémoire de recherche No 150, pp. 62

Guariguata, M.R. (1998). Response of forest tree saplings to experimental mechanical damage in lowland Panama. *Forest Ecology and Management*, 102, 103–111.

Guillemette, F., Bédard, S., & Fortin, M. (2008). Evaluation of a tree classification system in relation to mortality risk in Québec northern hardwoods. *The Forestry Chronicle*, 84, 886–899.

Guillemette, F., Bédard, S., Havreljuk, F. (2015). Probabilités de Mortalité des Feuillus Selon le Classement de la Priorité de Récolte; *Direction de la Recherche Forestière*: Québec, QC, Canada, pp. 11.

Guillemette, F., Gauthier, M. M., & Ouimet, R. (2017). Partitioning risks of tree mortality by modes of death in managed and unmanaged northern hardwoods and mixedwoods. *The Forestry Chronicle*, 93, 246-258.

Hansen, E.M., Stone, J.K., Capitano, B.R., Rosso, P., Sutton, W., Winton, L., Kanaskie, A., & McWilliams, M.G. (2000). Incidence and impact of Swiss needle cast in forest plantations of Douglas-fir in coastal Oregon. *Plant Disease*, 84, 773-778.

Hartmann, H., Wirth, C., Messier, C., & Berninger, F. (2008). Effects of above-and belowground partial harvest disturbance on growth and water status of residual sugar maple. *Tree physiology,* 28(12), 1851-1862.

Hartmann, H., Beaudet, M., & Messier, C. (2008). Using longitudinal survival probabilities to test field vigour estimates in sugar maple (Acer saccharum Marsh.). *Forest Ecology and Management*, 256(10), 1771-1779.

Hartmann, H., & Messier, C. (2008). The role of forest tent caterpillar defoliations and partial harvest in the decline and death of sugar maple. *Annals of Botany*, 102, 377–387.

Hartmann, H., Beaudet, M., Mazerolle, M.J., & Messier, M. (2009). Sugar maple (Acer saccharum Marsh.) growth is influenced by close conspecifics and skid trail proximity following selection harvest. *Forest Ecology and Management,* 258, 823–831.

Havreljuk, F., Achim, A., & Pothier, D. (2013). Regional variation in the proportion of red heartwood in sugar maple and yellow birch. *Canadian journal of forest research*, 43, 278-287.

Havreljuk, F., Achim, A., Auty, D., Bédard, S., & Pothier, D. (2014). Integrating standing value estimations into tree marking guidelines to meet wood supply objectives. *Canadian journal of forest research*, 44(7), 750-759.

Hegyi, F.(1974). A simulation model for managing jack pine stands. In: Growth Models for Tree and Stand Simulation. *Royal College of Forestry,* Stockholm, Sweden, pp. 74–90.

Holmes, R.L., (1983). Computer assisted quality control in tree-ring dating and measurement. *Tree-Ring Bulletin*, 43, 69–78.

Houle, G. (1990). Growth patterns of sugar maple seedlings and mature trees in healthy and in declining hardwood stands. *Canadian Journal of Forest Research*, 20(7), 894-901.

Hothorn, H., Bretz, F., Westfall, P. (2019). multcomp. R package version 1.4-10

Huggett, B.A., Schaberg, P.G., Hawley, G.J., & Eager, C. (2007). Long-term calcium addition increases growth release, wound closure, and health of sugar maple (Acer saccharum) trees at the Hubbard Brook Experimental Forest. *Canadian journal of forest research,* 37, 1692-1700

Ickes, K., Dewalt, S.J., and Thomas, S.C. (2003). Resprouting of woody saplings following stem snap by wild pigs in a Malaysian rain forest. *Journal of Ecology*, 9, 222–233.

Iverson, L. R., Prasad, A. M., Matthews, S. N., & Peters, M. (2008). Estimating potential habitat for 134 eastern US tree species under six climate scenarios. *Forest Ecology and Management*, 254(3), 390-406.

Jones, T.A., & Thomas, S.C. (2004). The time course of diameter increment responses to selection harvests in Acer saccharum. *Canadian journal of forest research*, 34, 1525–1533.

Jones, T. A., Domke, G. M., & Thomas, S. C. (2009). Canopy tree growth responses following selection harvest in seven species varying in shade tolerance. *Canadian journal of forest research*, 39(2), 430-440.

Joseph, G., Kelsey, R.G., & Thies, W.G. (1998). Hydraulic conductivity in roots of ponderosa pine infected with black-stain (*Leptographium wageneri*) or annosus (*Heterobasidion annosum*) root disease. *Tree Physiology*, 18, 333–339.

Kaitera, J., Isaenva, L., & Jalkanem, R. (1995). Long-term damage on Scots pine caused by Gremmeniella abientina near a nickel smelter in the Kola peninsula. *European journal of forest pathology*, 25(6-7), 391-399.

Kern, C. C., Burton, J. I., Raymond, P., D'Amato, A. W., Keeton, W. S., Royo, A. A., ... & Willis, J. L. (2017). Challenges facing gap-based silviculture and possible solutions for mesic northern forests in North America. *Forestry: An International Journal of Forest Research*, 90(1), 4-17.

Kiernan, D.H., Bevilacqua, E., & Nyland, R.D. (2009). Individual-tree diameter growth model for sugar maple trees in uneven-aged northern hardwood stands under selection system. *Forest Ecology and Management*, 256,1579–1586.

Kuehne, C., Weiskittel, A.R., & Waskiewicz, J. (2019). Comparing performance of contrasting distance-independent and distance-dependent competition metrics in predicting individual tree diameter increment and survival within structurally-heterogeneous, mixed-species forests of Northeastern United States. *Forest Ecology and Management*, 433, 205–216.

Lambert, M.C. Ung, C.H., & Raulier, F. (2005). Canadian national tree aboveground biomass equations. *Canadian Journal of Forest Research,* 35, 1996–2018.

Lane, C. J., Reed, D. D., Mroz, G. D., & Liechty, H. O. (1993). Width of sugar maple (Acer saccharum) tree rings as affected by climate. *Canadian Journal of Forest Research*, 23(11), 2370-2375.

Latham, P. & Tappeiner, J., (2002). Response of old-growth conifers to reduction in stand density in western Oregon forests. *Tree Physiology*, 22, 137–146.

Leites, L.P., Robinson, A.P., Crookston, N.L. (2009). Accuracy and equivalence testing of crown ratio models and assessment of their impact on diameter growth and basal area increment predictions of two variants of the Forest Vegetation Simulator. C*anadian Journal of Forest Research*, 39, 655–665.

Lempereur, M., Martin-St-Paul, N.K., Damesin, C., Joffre, R., Ourcival, J.-M., Rocheteau & A., Rambal, S. (2015). Growth duration is a better predictor of stem increment than carbon supply in a Mediterranean oak forest: Implications for assessing forest productivity under climate change. *New Phytologist*, 207, 579–590.

Lévesque, M., Saurer, M., Siegwolf, R., Eilmann, B., Brang, P., Bugmann, H., & Rigling, A. (2013). Drought response of five conifer species under contrasting water availability suggests high vulnerability of Norway spruce and European larch. *Global Change Biology*, 19(10), 3184-3199.

Long, R.P., Horsley, S.B. & Hall, T.J. (2011). Long-term impact of liming on growth and vigor of northern hardwoods. *Canadian Journal of Forest Research*, 41,1295–1307.

Lorimer, C.G., & Frelich, L.E. (1989). A methodology for estimating canopy disturbance frequency and intensity in dense temperate forests. *Canadian Journal of Forest Research*, 19, 651–663.

Lorimer, C. G., & Frelich, L. E. (1994). Natural disturbance regimes in old-growth northern hardwoods: implications for restoration efforts. *Journal of Forestry*, 92(1), 33-38.

Magnusson, A., Skaug, H., Nielsen, A., Berg, C., Kristensen, K., Maechler, M., ... & Brooks, M. M. (2017). Package 'glmmTMB'. *R Package* Version 0.2. 0.

Majcen Z., Richard, Y., Ménard, M., Grenier, Y. (1990). Choix des tiges à marquer pour le jardinage d'érablières inéquiennes, Guide technique, *Ministère de l'Énergie et des Ressources du Québec*, Direction de la recherche forestière, Mémoire No. 96

Majcen, Z. (1996). Coupe de jardinage et coupe de succession dans cinq secteurs forestiers. Accroissement quinquennal en surface terrière et état de la régénération, *Ministère des Ressources naturelles et de la Faune du Québec*, Direction de la recherche forestière, Mémoire No. 70

Mallet, K.I., & Volney, W. J. A. (1999). The effect of *Armillaria* root disease on lodgepole pine tree growth. *Canadian Journal of Forest Research*, 29, 252–259.

Manion, P. D. (1981). Tree disease concepts. Prentice-Hall, Inc.

Martin, A. R., Caspersen, J. P., Fuller, M. M., Jones, T. A., & Thomas, S. C. (2014). Temporal dynamics and causes of postharvest mortality in a selection-managed tolerant hardwood forest. *Forest ecology and management*, 314, 183-192.

Mazerolle, M.J. (2006). Improving data analysis in herpetology: using Akaike's Information Criterion (AIC) to assess the strength of biological hypotheses. *Amphibia-Reptilia,* 27, 169–180.

Mazerolle, M.J. (2017). AICcmodavg: Model selection and multimodel inference based on (Q)AIC(c). R package version 2.0-3.

Messier, C., & Nikinmaa, E. (2000). Effects of light availability and sapling size on the growth, biomass allocation, and crown morphology of understory sugar maple, yellow birch, and beech. *Ecoscience, 7*, 345-356.

Miller, R.E., Colbert, S.R., & Morris, L.A. (2004). Effects of heavy equipment on physical properties of soils and on long-term productivity: a review of literature and current research. *National Council for Air and Stream Improvement Technical Bulletin No. 887*.

Mitchell, R. G., Waring, R. H., & Pitman, G. B. (1983). Thinning lodgepole pine increases tree vigor and resistance to mountain pine beetle. *Forest Science*, 29(1), 204-211.

Moore, J. D., & Ouimet, R. (2006). Ten-year effect of dolomitic lime on the nutrition, crown vigor, and growth of sugar maple. *canadian Journal of Forest research*, 36(7), 1834-1841.

Moore, J. & Ouimet, R. (2010). Effects of two Ca fertilizer types on sugar maple vitality. *canadian Journal of Forest research*, 40, 1985–1992

Moreau, E., Bédard, S., Moreau, G., & Pothier, D. (2018). Relationships between tree vigor indices and a tree classification system based upon apparent stem defects in northern hardwood stands. *Forests*, 9(10), 588; doi:10.3390/f9100588

Moreau, E., Bédard, S., Baral, S. K., & Pothier, D. (2018). Evaluating electrical resistivity tomography and crown surface area to estimate leaf area of sugar maple and yellow birch. *Ecohydrology*, *11*(7), e2014.

Moreau, G., Achim, A., & Pothier, D. (2019). A dendrochronological reconstruction of sugar maple growth and mortality dynamics in partially cut northern hardwood forests. *Forest ecology and management*, 437, 17-26.

Moreau, G., Achim, A., & Pothier, D. (2020). Growth and survival dynamics of partially cut northern hardwood stands as affected by precut competition and spatial distribution of residual trees. *Forestry: An International Journal of Forest Research*, 93(1), 96-106.

Moreau, G., Achim, A., & Pothier, D. (2020). Relevance of stem and crown defects to estimate tree vigour in northern hardwood forests. *Forestry: An International Journal of Forest Research* (In press)

Morin, R. S., Randolph, K. D. C., & Steinman, J. (2015). Mortality rates associated with crown health for eastern forest tree species. *Environmental Monitoring and Assessme*nt, 187, 1–11

MFFP. 2017. Ressources et industries forestières – Portrait statistique: Édition 2017. *Ministère des Ressources naturelles du Québec*, Direction du développement de l'industrie des produits du bois. Québec, Qué. 133 pp

Nagel, T. A., Svoboda, M., & Kobal, M. (2013). Disturbance, life history traits, and dynamics in an old-growth forest landscape of southeastern Europe. *Ecological Applications*, 24, 663–679.

Niinemets, Ü., Sparrow, A., & Cescatti, A. (2005). Light capture efficiency decreases with increasing tree age and size in the southern hemisphere gymnosperm Agathis australis. *Trees,* 19, 177–190.

Nolet, P., Hartmann, H., Bouffard, D., & Doyon, F. (2007). Predicted and observed sugar maple mortality in relation to site quality indicators. *Northern Journal of Applied Forestry*, 24(4), 258-264.

Nolet, P., & Kneeshaw, D. (2018). Extreme events and subtle ecological effects: lessons from a long-term sugar maple–American beech comparison. *Ecosphere*, 9(7), e02336.

Nowacki, G.J., & Abrams, M.D. (1997). Radial-growth averaging criteria for reconstructing disturbance histories from presettlement-origin oaks. *Ecological Monographs*, 67, 225–249.

Nyland, R.D. (1998). Selection system in northern hardwoods. *Journal of Forestry*, 96, 18-21.

Nyland, R. D. (2003). Even-to uneven-aged: the challenges of conversion. *Forest ecology and management*, 172(2-3), 291-300.

Ogle, K., Whitham, T.G., & Cobb, N.S. (2000). Tree-ring variation in Pinyon predicts likelihood of death following severe drought. *Ecology*, 81, 3237-3243.

Ontario Ministry of Natural Ressources. (2004). Ontario tree marking guide, Ver. 1.1. *Ontario Ministry of Natural Ressources*, 252 pp.

Oswald, E. M., Pontius, J., Rayback, S. A., Schaberg, P. G., Wilmot, S. H., & Dupigny-Giroux, L. A. (2018). The complex relationship between climate and sugar maple health: Climate change implications in Vermont for a key northern hardwood species. *Forest Ecology and Management*, 422, 303-312.

Payette, S., Fortin, M.J., & Morneau, C. (1996). The recent sugar maple decline in southern Quebec : probable causes deduced from tree rings. *Canadian Journal of Forest Research*, 26, 1069–1078.

Pedersen, B. S. (1998). Modeling tree mortality in response to short-and long-term environmental stresses. *Ecological Modelling,* 105(2-3), 347-351.

Pelletier, G. Landry, D. & Girouard, M. (2016). A Tree Classification System for New Brunswick. Version 2.0. *Northern Hardwoods Research Institute*. Edmundston, New Brunswick.

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., Heisterkamp, S., Van Willigen, B., & Maintainer, R. (2017). Package 'nlme'. *Linear and nonlinear mixed effects models*, version, 3.

Pond, N. C., Froese, R. E., & Nagel, L. M. (2014). Sustainability of the selection system in northern hardwood forests. *Forest Science*, 60(2), 374-381.

Pothier, D., Fortin, M., Auty, D., Delisle-Boulianne, S., Gagné, L. V., & Achim, A. (2013). Improving tree selection for partial cutting through joint probability modelling of tree vigor and quality. *Canadian journal of forest research*, 43(3), 288-298.

Pothier, D. (2019). Analysing the growth dynamics of mixed stands composed of balsam fir and broadleaved species of various shade tolerances. *Forest ecology and management*, 444, 21-29.

Power, H., & Havreljuk, F. (2018). Predicting hardwood quality and its evolution over time in Quebec's forests. *Forestry: An International Journal of Forest Research*, 91(3), 259-270.

R Development Core Team, 2018. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria, http://www.R-Landsc. Ecol. 21, 596–605.

Raymond, P., Bédard, S., Roy, V., Larouche, C., & Tremblay, S. (2009). The Irregular Shelterwood System : Review, Classification, and Potential Application to Forests Affected by Partial Disturbances. *Journal of Forestry*, 107, 405–413.

Reich, P. B., Wright, I. J., Cavender-Bares, J., Craine, J. M., Oleksyn, J., Westoby, M., & Walters, M. B. (2003). The evolution of plant functional variation: traits, spectra, and strategies. *International Journal of Plant Sciences*, 164(S3), S143-S164.

Robitaille, G., Boutin, R., & Lachance, D. (1995). Effects of soil freezing stress on sap flow and sugar content of mature sugar maples (Acer saccharum). *Canadian journal of forest research*, 25(4), 577-587.

Rybníček, M., Čermák, P., Žid, T., Kolář, T., Trnka, M., & Büntgen, U. (2015). Exploring growth variability and crown vitality of sessile Oak (Quercus petraea) in the Czech Republic. *Geochronometria*, 42(1), 17-27

Salas-Eljatib, C., Fuentes-Ramirez, A., Gregoire, T. G., Altamirano, A., & Yaitul, V. (2018). A study on the effects of unbalanced data when fitting logistic regression models in ecology. *Ecological Indicators*, 85, 502–508.

Saucier, J.-P., Grondin, P., Robitaille, A., Gosselin, J., Morneau, C., Richard, P.-J.-H., Brisson, J., Sirois, L., Leduc, A., Morin, H., Thiffault, E., Gauthier, S., Lavoie, C. & Payette, S. (2009). Écologie forestière. Manuel de foresterie, 2e édition. *Ordre des ingénieurs forestiers du Québec*, Éditions Multimondes, Québec, pp.165-316.

Schomaker, M. (2007). *Crown-condition classification: a guide to data collection and analysis (Vol. 102)*. US Department of Agriculture, Forest Service, Southern Research Station.

Seablom, T. J., & Reed, D. D. (2005). Assessment of factors contributing to residual tree damage from mechanized harvesting in northern hardwoods. *Northern Journal of Applied Forestry*, 22(2), 124-131.

Seidling, W., Ziche, D., & Beck, W. (2012). Climate responses and interrelations of stem increment and crown transparency in Norway spruce, Scots pine, and common beech. *Forest ecology and management*, 284, 196-204.

Senate Committee on Agriculture and Forestry. (2018). Feast or Famine: Impacts of climate change and carbon pricing on agriculture, agri-food and forestry. *Journals of the Senate.*

Seymour, R. S., White, A. S., & Philip, G. D. (2002). Natural disturbance regimes in northeastern North America—evaluating silvicultural systems using natural scales and frequencies. *Forest Ecology and Management*, 155(1-3), 357-367.

Shigo, A.L., (1985). Wounded forests, starving trees. *Journal of Forestry*. 83, 668–673.

Stan, A.B., & Daniels, L.D. (2010). Growth releases of three shade-tolerant species following canopy gap formation in old-growth forests. *Journal of Vegetation Science*, 21,74–87.

Suarez, M.L., Ghermandi, L., & Kitzberger, T. (2004). Factors predisposing episodic drought induced tree mortality in *Nothofagus* – site, climatic sensitivity and growth trends. *Journal of Ecology*, 92, 954–966.

Tardif, J., Brisson, J., & Bergeron, Y. (2001). Dendroclimatic analysis of Acer saccharum, Fagus grandifolia, and Tsuga canadensis from an old-growth forest, southwestern Quebec. Canadian Journal of Forest Research, 31(9), 1491-1501.

Therneau, T. M., & Lumley, T. (2014). Package 'survival'. Survival analysis Published on CRAN, 2, 3.

Thorpe, H. C., Thomas, S. C., & Caspersen, J. P. (2008). Tree mortality following partial harvests is determined by skidding proximity. *Ecological Applications*, 18(7), 1652-1663.

Tierney, G. L., Fahey, T. J., Groffman, P. M., Hardy, J. P., Fitzhugh, R. D., & Driscoll, C. T. (2001). Soil freezing alters fine root dynamics in a northern hardwood forest. *Biogeochemistry*, 56(2), 175-190.¸

Tominaga, K., Watmough, S. A., & Aherne, J. (2008). Predicting tree survival in Ontario sugar maple (Acer saccharum) forests based on crown condition. *Canadian journal of forest research*, 38(7), 1730-1741.

Trotsiuk, V., Hobi, M. L., & Commarmot, B. (2012). Age structure and disturbance dynamics of the relic virgin beech forest Uholka (Ukrainian Carpathians). *Forest Ecology and Management*, 265, 181-190.

Valladares, F., & Niinemets, Ü. (2008). Shade tolerance, a key plant feature of complex nature and consequences. *Annual Review of Ecology, Evolution, and Systematics*, 39, 237-257.

Vanoni, M., Bugmann, H., Nötzli, M., & Bigler, C., (2016). Drought and frost contribute to abrupt growth decreases before tree mortality in nine temperate tree species. *Forest Ecology and Management*, 382,51–63.

Vicente-Serrano, S. M., Beguería, S., & López-Moreno, J. I. (2010). A multiscalar drought index sensitive to global warming: the standardized precipitation evapotranspiration index. *Journal of climate*, 23(7), 1696-1718.

Waring, R. H., Thies, W. G., & Muscato, D. (1980). Stem growth per unit of leaf area: a measure of tree vigor. *Forest Science*, 26(1), 112-117.

Waring, R. H., Newman, K., & Bell, J. (1981). Efficiency of tree crowns and stemwood production at different canopy leaf densities. *Forestry: An International Journal of Forest Research*, 54(2), 129-137.

Waring, R. H., & Pitman, G. B. (1985). Modifying lodgepole pine stands to change susceptibility to mountain pine beetle attack. *Ecology*, 66(3), 889-897.

Waring, R.H., (1987). Characteristics of trees predisposed to die. *Bioscience* 37(8), 569–574.

Weber, P., Bugmann, H., Fonti, P., & Rigling, A. (2008). Using a retrospective dynamic competition index to reconstruct forest succession. *Forest Ecology and Management*, 254(1), 96-106.

Webster, C. R., & Jensen, N. R. (2007). A shift in the gap dynamics of *Betula alleghaniensis* in response to single-tree selection. *Canadian Journal of Forest Research*, 37(3), 682-689.

Wigley, T. M., Briffa, K. R., & Jones, P. D. (1984). On the average value of correlated time series, with applications in dendroclimatology and hydrometeorology. *Journal of climate and Applied Meteorology*, 23(2), 201-213.

Williamson, J. R., & Neilsen, W. A. (2000). The influence of forest site on rate and extent of soil compaction and profile disturbance of skid trails during ground-based harvesting. *Canadian Journal of Forest Research*, 30(8), 1196-1205.

Yin, X., Foster, N. W., Morrison, I. K., & Arp, P. A. (1994). Tree-ring-based growth analysis for a sugar maple stand: relations to local climate and transient soil properties. *Canadian journal of forest research*, 24(8), 1567-1574.

Zang, C., & Biondi, F. (2013). Dendroclimatic calibration in R: the bootRes package for response and correlation function analysis. *Dendrochronologia*, 31(1), 68-74.

Zhang, T., Niinemets, Ü., Sheffield, J., & Lichstein, J. W. (2018). Shifts in tree functional composition amplify the response of forest biomass to climate. *Nature*, 556(7699), 99-102.

Zhu, X. B., Cox, R. M., & Arp, P. A. (2000). Effects of xylem cavitation and freezing injury on dieback of yellow birch (Betula alleghaniensis) in relation to a simulated winter thaw. *Tree Physiology*, 20(8), 541-547.

Zhu, X. B., Cox, R. M., Meng, F. R., & Arp, P. A. (2001). Responses of xylem cavitation, freezing injury and shoot dieback to a simulated winter thaw in yellow birch seedlings growing in different nursery culture regimes. *Forest Ecology and Management*, 145(3), 243-253.

Zuur, A. F., Ieno, E.N., & Elphick, C.S. (2010). A protocol for data exploration to avoid common statistical problems. *Methods in Ecology and Evolution*. 1, 3–14.