UNIVERSITÉ DU QUÉBEC EN ABITIBI-TÉMISCAMINGUE

RÉGIME DES TROUÉES DANS LES ÉRABLIÈRES ANCIENNES DU TÉMISCAMINGUE

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AVANT-PROPOS

Cette thèse est rédigée sous forme d'articles. Ainsi, en plus d'une introduction et d'une conclusion générales, trois chapitres sont présentés sous la forme d'articles scientifiques. Les articles sont déjà publiés ou en préparation pour soumission à des revues avec comité de lecture. Pour cette raison, la forme peut changer de l'un à l'autre. Des répétitions entre les chapitres sont également inévitables.

Chapitre 2 – Després, T., Asselin, H., Doyon, F. & Bergeron, Y. 2014. Structural and spatial characteristics of old-growth temperate deciduous forests at their northern distribution limit. Forest Science 60: 871–880

Chapitre 3 – Després, T., Asselin, H., Doyon, F., Drobyshev I. & Bergeron, Y. (soumis). Gap disturbance regime at the northern limit of temperate deciduous forests. Journal of Vegetation Science.

Chapitre 4 – Després, T., Doyon, F., Cyr D., Asselin, H., & Bergeron, Y. (à soumettre). Can northern temperate deciduous forests be managed while maintaining their old-growth attributes?

Je suis le premier auteur de chacun des chapitres de cette thèse, ayant réalisé l'ensemble du travail depuis la collecte des données jusqu'à la rédaction. Mon directeur Hugo Asselin ainsi que mes codirecteurs Frédérik Doyon et Yves Bergeron ont suivi chaque étape de cette thèse et ont contribué à la rédaction des chapitres. Pour le chapitre 3, Igor Drobyshev a participé aux analyses dendrochronologiques et à la rédaction. Pour le chapitre 4, Dominic Cyr a partagé ses données et ses scripts et aidé à la modélisation et à la rédaction.

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RÉSUMÉ

L'aménagement forestier écosystémique est un concept visant à reproduire les patrons écologiques résultant de la dynamique forestière naturelle propre à une région. Les vieilles forêts constituent des témoins de la dynamique forestière à long terme et peuvent être utilisées comme référence pour l'aménagement écosystémique. L'objectif principal de cette thèse est de comprendre la dynamique des trouées de la forêt tempérée feuillue à sa limite nordique de répartition pour aider dans la mise en œuvre de l'aménagement écosystémique dans le sous-domaine bioclimatique de l'érablière à bouleau jaune de l'Ouest. En effet, le régime de trouées, qui est la perturbation principale en forêt tempérée feuillue, pourrait ne pas être le même au centre de l'aire de répartition qu'à sa limite nordique de répartition. Or, peu d'études sur le régime de trouées ont été menées à la limite nordique de la forêt feuillue tempérée.

La mise en place de l'aménagement écosystémique à la limite nordique de répartition de la forêt tempérée feuillue nécessite de connaître la structure naturelle de cette forêt. L'objectif était de décrire la structure de vieux peuplements à la limite nordique de répartition de la forêt tempérée feuillue. Pour cela, les structures de diamètre, d'âge et spatiales de 11 vieux peuplements ont été échantillonnées dans de grandes placettes-échantillons (0,25 ha). Les caractéristiques structurales des peuplements étudiés, à savoir leur structure diamétrale et leur structure d'âge, diffèrent de celles rapportées dans des études antérieures menées dans le centre de l'aire de répartition de la forêt tempérée feuillue. En effet, toutes les distributions diamétrales suivent une distribution de Weibull à deux ou trois paramètres, plutôt qu'une sigmoïde inversée. La distribution de Weibull suggère une mortalité constante, alors que la sigmoïde inversée suggère une forte mortalité pour les jeunes arbres, une mortalité modérée pour les arbres matures et une forte mortalité pour les arbres sénescents. Certaines structures d'âge montrent des pics de recrutement plutôt qu'un recrutement continu. La structure spatiale des arbres est généralement répartie aléatoirement, quelles que soient les variables étudiées (âge, diamètre, espèces, ou bois mort), comme ce qui a été montré dans d'autres études réalisées plus au sud, dans le centre de l'aire de répartition de la forêt tempérée feuillue. Ainsi, même si la structure spatiale est la même à la limite nordique de répartition que dans le centre de l'aire de répartition, la structure diamétrale et le recrutement diffèrent. Dans le contexte d'aménagement écosystémique, ces résultats suggèrent que le niveau des coupes doit varier par bloc et la sélection sylvicole devrait inclure occasionnellement de larges trouées créées par l'enlèvement de plusieurs arbres, en plus de trouées créées par l'enlèvement d'arbres uniques.

Le régime de trouées au centre de l'aire de répartition de la forêt tempérée feuillue est caractérisé par des trouées créées par la mort d'arbres uniques ou de petits groupes d'arbres. L'objectif était de déterminer si le régime de trouées de la forêt tempérée feuillue de l'est de l'Amérique du Nord à sa limite nordique de répartition est différent de celui du centre de son aire de répartition. Le taux de perturbation par les trouées dans l'érablière à bouleau jaune de l'Ouest, exprimé en pourcentage du territoire perturbé par année, est similaire aux taux de perturbation rapportés dans d'autres études réalisées dans le centre de l'aire de répartition. Cependant, les trouées sont plus abondantes et de plus petites tailles à la limite nordique de la forêt tempérée feuillue qu'au centre de l'aire de répartition du biome. Ainsi, l'aménagement écosystémique devrait être basé sur des coupes de sélection de plus petite taille qu'au centre de l'aire de répartition de la forêt tempérée feuillue.

Le régime de perturbations naturelles en forêt tempérée feuillue est caractérisé principalement par des petites trouées et, dans une moindre mesure, par des chablis partiels. L'objectif était de déterminer si les coupes partielles, lorsqu'ajoutées aux perturbations naturelles (trouées et chablis partiels) permettent le maintien de la composition spécifique et des attributs des forêts tempérées feuillues anciennes. La modélisation à l'échelle du paysage a permis de montrer qu'à partir de 0,60% de taux de coupe partielle annuels, la biomasse des arbres de plus de 200 ans et la nécromasse (bois mort) diminuent de façon significative. La composition spécifique ne change pas, quel que soit le scénario de coupe utilisé ou l'intensité des perturbations naturelles. Ainsi, afin d'éviter une érosion des attributs de vieilles forêts, il est recommandé de préserver les arbres de plus de 200 ans (ou de plus de 40 cm de diamètre) et de laisser du bois mort de différentes tailles sur les sites de coupe partielle afin de maintenir une variété d'habitats qui permettront la conservation de la biodiversité dans le cadre d'un aménagement écosystémique de la forêt.

Cette thèse a permis de mettre en évidence les spécificités de la forêt tempérée feuillue à sa limite nordique de répartition, notamment en termes de structure d'âge, de structure diamétrale et de régime des trouées (taille moyenne et fréquence). Ces informations seront utiles à la mise en place de l'aménagement écosystémique, notamment pour le maintien des vieux peuplements, du bois mort et pour que le taux total de perturbation ne dépasse pas un seuil critique.

Mots clés : Forêt tempérée feuillue nordique, régime de trouées, limite nordique, aménagement écosystémique, vieilles forêts, dendrochronologie, LANDIS-II, structure spatiale, érable à sucre, bouleau jaune

CHAPITRE I

INTRODUCTION GENERALE

L'aménagement forestier écosystémique est un concept basé sur la reproduction des patrons spatiotemporels engendrés par les perturbations naturelles (Perera et al. 2004; Gauthier et al. 2009; Grenon et al. 2010). La caractérisation de la variabilité historique des patrons spatiotemporels résultant de la dynamique des forêts naturelles est essentielle pour offrir des balises écologiques de référence à l'aménagement écosystémique (Landres et al. 1999; Cyr et al. 2009; Gauthier et al. 2009). Les premiers projets d'aménagement écosystémique ont commencé dans l'Ouest des États-Unis aux alentours de 1970 (Yaffee et al. 1996). Ce n'est que 20 ans plus tard, qu'en forêt boréale canadienne, plusieurs études ont permis de fournir les balises écologiques (p. ex. Payette 1992; Bergeron & Harvey 1997; Cyr et al. 2009) permettant l'émergence de projets-pilotes d'aménagement écosystémique (Gram et al. 2001; Haynes et al. 2006; Boulfroy & Lessard 2009). Or, les principales perturbations naturelles de la forêt boréale canadienne, à dominance résineuse, ne sont pas les mêmes que celles de la forêt tempérée feuillue : pour la forêt boréale canadienne, les perturbations occasionnées par le feu (Payette 1992; Bergeron et al. 2002) et les épidémies d'insectes (Jardon et al. 2003; Cooke & Lorenzetti 2006) dominent le régime de perturbations, tandis que pour la forêt tempérée feuillue, ce sont les trouées et les chablis qui dominent (Pickett & White 1985; Runkle 1985; Canham et al. 2001; McCarthy 2001; Seymour et al. 2002; Gravel et al. 2010). Un tel régime, caractérisé par le remplacement d'arbres individuels ou de petits groupes d'arbres (Woods 2004; Cowden et al. 2014), permet aux espèces tolérantes à l'ombre, souvent déjà présentes en sous-couvert, d'accéder au couvert tout en permettant aux espèces moins tolérantes de se maintenir dans le paysage suivant l'occurrence sporadique d'ouvertures de plus grandes tailles (Whitmore 1989; Peterson & Pickett 1991; Yamamoto 1992b). Cependant, les données disponibles en forêt tempérée feuillue pour caractériser cette dynamique de trouées sont fragmentaires au Canada, ce qui empêche la mise en œuvre de l'aménagement écosystémique, particulièrement à la limite nordique de répartition de la forêt tempérée feuillue, où une seule étude a été

publiée jusqu'à maintenant (Payette et al. 1990). Structure et composition des forêts
anciennes comme outil d’évaluation de la dynamique naturelle

L’étude des vieilles forêts et des forêts non perturbées par l’activité humaine permet de reconstituer le régime de perturbations naturelles à l’échelle du peuplement et du paysage. La structure diamétrale des arbres est couramment utilisée comme proxy de l’âge de la forêt. Tandis qu'il a longtemps été tenu pour acquis que la structure diamétrale des vieilles forêts feuillues suit une exponentielle négative (Tyrrell & Crow 1994; Goodburn & Lorimer 1999; Zhang et al. 2001; Westphal et al. 2006), des travaux récents ont montré que la distribution correspond davantage à une sigmoïde inverse (Piovesan et al. 2010; Alessandrini et al. 2011; Pond et al. 2014). La forme de la sigmoïde inverse est en partie attribuable au taux de mortalité des arbres qui est élevé pour les arbres jeunes, plus faible pour les arbres matures et redevient élevé lors de la période de sénescence des arbres (Goff & West 1975; Lorimer et al. 2001). Cependant, les vieilles forêts ne suivent pas toujours ces patrons (Burrascano et al. 2013). Par exemple, les perturbations intermédiaires peuvent interagir avec les perturbations à plus petite échelle comme les trouées (Woods 2004; Hanson & Lorimer 2007), modifiant la structure de taille et la structure d'âge des arbres (Canham et al. 1990; Beaudet & Messier 1998; Koukoulas & Blackburn 2005; Messier et al. 2009). Ainsi, comprendre les structures diamétrales et la répartition spatiale des arbres permet de mieux appréhender la dynamique forestière.

1.2 Régime naturel de perturbations en forêt tempérée feuillue

Plusieurs études portant sur le régime de perturbations naturelles ont été menées en forêt feuillue, notamment dans le Nord-Est des États-Unis (Runkle 1982; Seymour et al. 2002; D'Amato & Orwig 2008; Fraver et al. 2009) et au Québec (Payette et al.

1990; Drever et al. 2006; Drever et al. 2009). Trois différents types de perturbations ont été identifiés pour la forêt tempérée feuillue de l'est de l'Amérique du Nord : les feux (avec un cycle compris entre 770 et 1 000 ans) (Frelich & Lorimer 1991a; Doyon & Sougavinski 2002), les chablis (avec un cycle entre 1 700 et 7 000 ans) (Bégin 2011), ainsi que les trouées qui sont la principale perturbation naturelle de la forêt tempérée feuillue (avec un cycle compris entre 45 et 200 ans) (Payette et al. 1990; Doyon & Sougavinski 2002; Fraver et al. 2009). En comparaison, en forêt boréale, où le feu est la principale perturbation naturelle, le cycle varie entre 100 et 500 ans (Payette et al. 1989; Bergeron et al. 2002; Bergeron et al. 2006; Bergeron & Fenton 2012).

Les trouées sont un processus écologique important qui permet le maintien de la diversité forestière. Les trouées en forêt tempérée feuillue peuvent varier en taille de 10 m² à environ 1 ha (Lorimer 1989; Yamamoto 1992a; Tanaka & Nakashizuka 1997; Zeibig et al. 2005; Rugani et al. 2013). Fraver et al. (2009) ont calculé un taux annuel de renouvellement de la forêt tempérée feuillue dû aux perturbations naturelles de 0,96 % pour le Maine (États-Unis). Plus au sud, aux États-Unis, les taux de renouvellement varient de 0,5% à 1,07 % (Runkle 1982; Dahir & Lorimer 1996; D'Amato & Orwig 2008) (Figure 1.1). Pour le même type de forêt, mais dans une région plus nordique (Réserve écologique Tantaré au Québec), Payette et al. (1990) ont obtenu un taux annuel de renouvellement de 2,2 %. Cette valeur élevée pourrait s'expliquer par une différence dans la composition en espèces d'arbres, la structure de la forêt, la croissance des arbres, la longévité des arbres, la forme des cimes ou le climat. Cette variabilité spatiale du taux de renouvellement est importante, surtout si cette valeur doit servir de base à un aménagement écosystémique (Mladenoff & Pastor 1993). En effet, cela signifie que les aménagistes forestiers pourraient couper le double de ce qu'ils coupent plus au sud, dans l'aire centrale de répartition de la forêt tempérée feuillue.

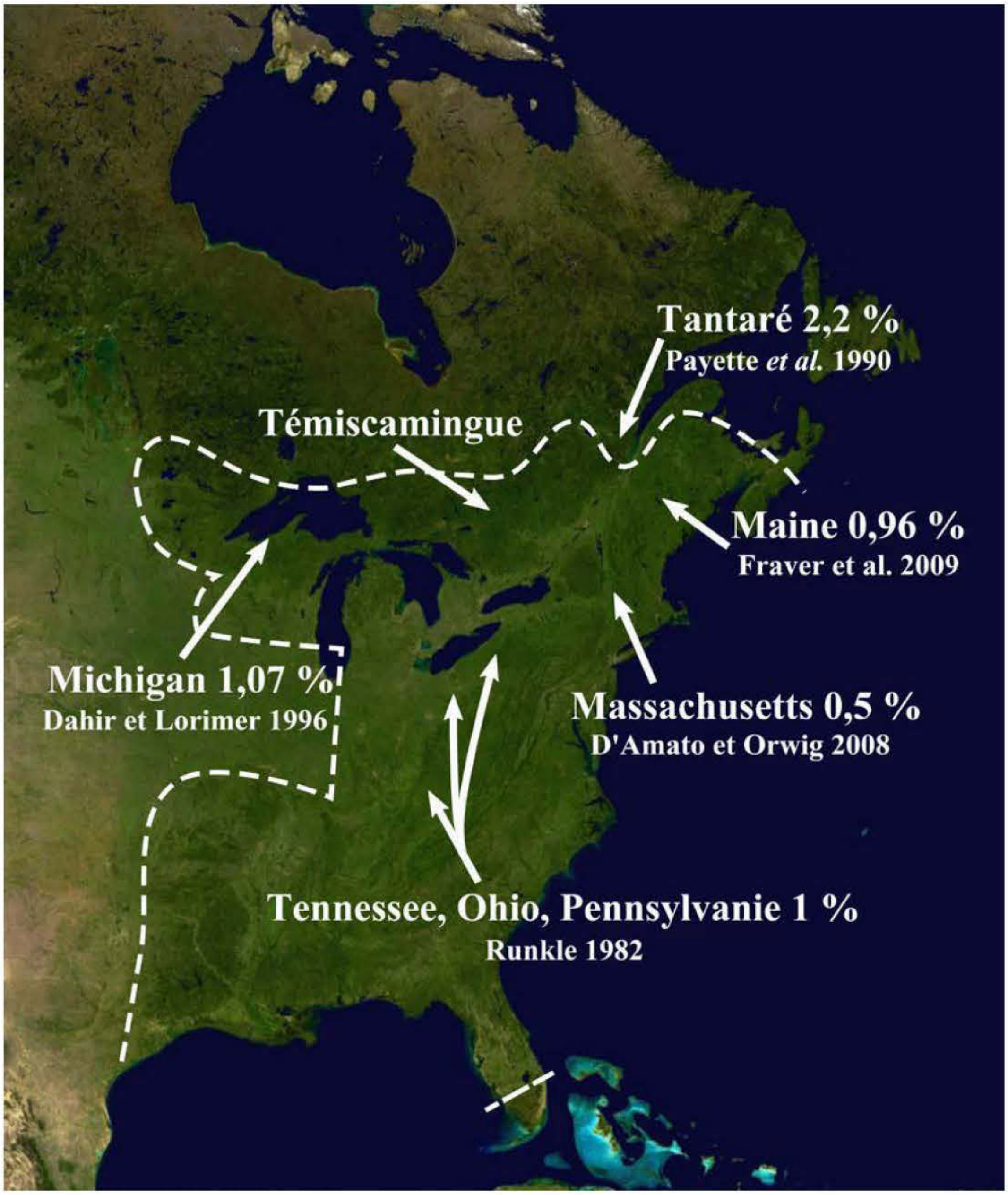

Figure 1.1 Taux de perturbation par les trouées mesurés dans différentes régions de la forêt tempérée feuillue de l'Est de l'Amérique du Nord. La ligne pointillée représente la limite de répartition de la forêt tempérée feuillue selon Currie & Bergen (2008).

1.3 Modélisation à l'échelle du paysage comme outil d'évaluation de la dynamique naturelle

L'aménagement forestier écosystémique a entre autres pour but de préserver les attributs des forêts anciennes en reproduisant les patrons spatiotemporels créés par les perturbations naturelles (Johnson et al. 1995; Gauthier et al. 2008). La modélisation est un outil permettant de simuler la dynamique forestière en fonction de différents paramètres, comme l'intensité des coupes ou des perturbations naturelles. Il existe un grand nombre de modèles qui décrivent la dynamique forestière et qui ont chacun des avantages et des inconvénients (Hong 2008; Taylor et al. 2009). Certains, tels JABOWA et FORET, simulent la dynamique forestière au sein de parcelles de petites tailles (moins de 1 ha, même si récemment ces modèles ont pu être utilisés à plus grande échelle) en utilisant les paramètres de croissance, mortalité, et l'interaction qu'il peut y avoir entre les arbres et leur environnement (Busing 1991; Bugmann 2001; Perry & Enright 2006; Taylor et al. 2009). De même, SORTIE-ND permet de modéliser explicitement dans l'espace la dynamique forestière à l'échelle de l'arbre en se basant sur la modélisation de la lumière au travers du couvert forestier (Canham et al. 1999). Cependant, SORTIE-ND ne permet pas de prendre en compte la dynamique à l'échelle du paysage et l'interaction entre les peuplements. Or, pour réaliser l'aménagement écosystémique, il est important de connaître la dynamique naturelle à l'échelle du peuplement, mais aussi à l'échelle du paysage.

Il existe plusieurs modèles qui ont été développés à l'échelle du paysage. Le modèle STORM, a permis de mieux connaître la structure des vieilles forêts (Frelich & Lorimer 1991b). STORM a permis de mettre en évidence la structure majoritairement inéquienne (multi-âge) des vieux peuplements alors que la proportion de forêts à l'état d'équilibre ne représente que 9,2% du paysage simulé. D'autres modèles à l'échelle du paysage, comme iLand (Seidl et al. 2014a; Seidl et al. 2014b) ou LANDIS-II, utilisent les données de systèmes d'information géographique combinées aux traits de vie des espèces pour modéliser à de grandes échelles spatiotemporelles le changement du couvert forestier (Mladenoff 2004; Perry & Enright 2006; Scheller & Mladenoff 2007; Hong 2008). De même, il est possible d'étudier l'effet de différents types d'aménagement forestier sur les caractéristiques de la forêt.

1.4 Objectifs

L'objectif général de cette thèse est de comprendre la dynamique de la perturbation naturelle principale de la forêt tempérée feuillue, à savoir les trouées, pour aider à la mise en œuvre de l'aménagement écosystémique dans le sous-domaine bioclimatique de l'érablière à bouleau jaune de l'Ouest dont la dynamique naturelle est peu connue. Pour cela, trois objectifs spécifiques ont été formulés :

1. **Caractériser les vieux peuplements du sous-domaine bioclimatique de l'érablière à bouleau jaune de l'Ouest.** La structure des vieux peuplements du sous-domaine bioclimatique de l'érablière à bouleau jaune de l'Ouest a été étudiée aux échelles inter- et intra-peuplements pour déterminer si certains attributs des vieilles forêts tempérées feuillues à leur limite nordique de répartition sont différents de ceux du centre de l'aire de répartition (chapitre 2). Les attributs étudiés sont la diversité spécifique, la structure (d'âge et diamétrale) et la répartition spatiale des cohortes d'âges et d'espèces.

2. **Reconstituer la dynamique des trouées dans l'érablière à bouleau jaune aux échelles du peuplement et du paysage.** En étudiant les vieilles forêts, il a été possible de connaître les perturbations passées grâce à la méthode de la dendrochronologie et ainsi de reconstituer la dynamique des trouées aux échelles du peuplement et du paysage sur une période de 60 ans (Lorimer et al. 1988;

Payette et al. 1990) (chapitre 3). Cela a permis de déterminer si le taux de renouvellement était le même sur l'ensemble du paysage.

3. **Mesurer l'impact de l'aménagement forestier dans l'érablière à bouleau jaune de l'Ouest sur la structure et les attributs de vieilles forêts tempérées feuillues.** La modélisation à l'échelle du paysage a permis de comparer le fonctionnement de la forêt sous différents régimes de perturbations (trouées seulement, trouées + chablis et trouées + chablis + coupes partielles) à l'échelle du paysage afin de voir si l'aménagement de la forêt tempérée feuillue nordique permettait de maintenir ses attributs de forêts anciennes (chapitre 4).

1.5 Zone d'étude

La forêt du sud de l'Abitibi-Témiscamingue (Québec, Canada) se trouve dans le sous-domaine bioclimatique de l'érablière à bouleau jaune de l'Ouest (MRNF 2010) (Figure 1.2). Ce sous-domaine bioclimatique, qui s'étend du 45^e au 48^e parallèle de latitude Nord, couvre une superficie de 65 600 km^2 (MRNF 2010). Les sols sont principalement des podzols de type humo-ferrique (Brown 1981). Sur ces sols poussent majoritairement l'érable à sucre (*Acer saccharum* Marsh.), le bouleau jaune (*Betula alleghaniensis* Britton), le sapin baumier (*Abies balsamea* (L.) Mill.), l'érable rouge (*Acer rubrum* L.), et l'épinette blanche (*Picea glauca* (Moench) Voss) (Brown 1981). Le climat est continental avec des hivers froids et des étés chauds. La température moyenne annuelle est de 4,2°C et la moyenne annuelle des précipitations est de 1044 mm dont environ 29% sous forme de neige (Environnement Canada 2011). Dans la forêt feuillue du Témiscamingue, les trouées constituent le régime de perturbation naturelle principal (Doyon & Sougavinski 2002). Le cycle de feu préindustriel est compris entre 188 et 493 ans dans cette région (Grenier et al. 2005; Drever et al. 2006). La dominance de l'érable à sucre au Témiscamingue serait récente et ferait suite aux derniers feux majeurs qui ont eu lieu dans la région il y a 160-220 ans (Pilon & Payette 2015). Les chablis sont moins fréquents dans la région du Témiscamingue, leur intervalle de retour étant compris entre 1 700 et 7 000 ans (Bégin 2011). Le régime de coupes partielles dans la forêt feuillue du Témiscamingue est composé majoritairement de coupes de jardinage et de coupes progressives irrégulières (ministère des Ressources naturelles 2013).

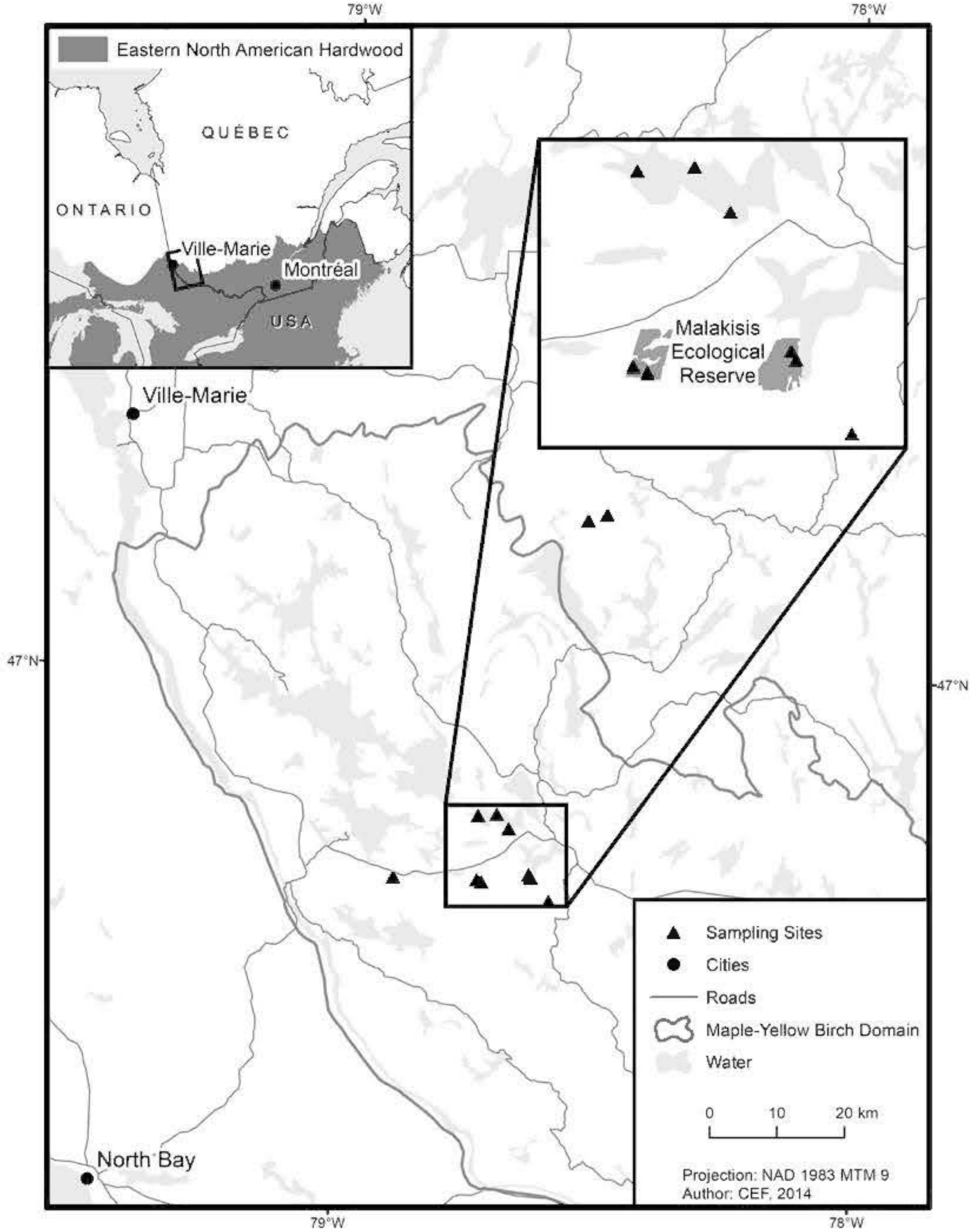

Figure 1.2 Localisation des placettes échantillons dans la région du Témiscamingue. L'insert en haut à droite représente un agrandissement de la zone autour de la réserve écologique du lac Malakisis (en gris foncé).

CHAPITRE II

STRUCTURAL AND SPATIAL CHARACTERISTICS OF OLD-GROWTH TEMPERATE DECIDUOUS FORESTS AT THEIR NORTHERN DISTRIBUTION LIMIT

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2.1 Abstract

Relic old-growth forests are unique witnesses of long-term forest dynamics that can be used as reference conditions for ecosystem-based forest management. In temperate deciduous forests, catastrophic stand-replacing disturbances are rare, and stand dynamics are controlled by endogenous tree-by-tree replacement. Processes might be different at the northern distribution limit of temperate deciduous forests, due to differences in climate and disturbance regimes. We studied tree species composition, diameter, age, and spatial structures of 11 old-growth temperate deciduous stands across an age gradient. Stand characteristics differed from expectation, based on previous studies that were conducted in the central region of temperate deciduous forests' range. Instead of increasing with age, tree species richness was higher in stands < 120-years-old due to the presence of relatively short-lived species like *Abies balsamea* and *Acer rubrum*. All diameter distributions followed a 2- or 3-parameter Weibull model, instead of a rotated sigmoid. Some age structures showed recruitment pulses, contrary to expectation of constant recruitment, and the spatial distribution of living trees was mostly random with regard to age and species at assessed distances (< 14 m). In the context of ecosystem-based forest management, our results suggest that harvest levels should vary across harvesting blocks and selection silviculture should occasionally include larger, multiple-tree gaps in addition to single-tree gaps.

2.2 Résumé

Les vestiges de vieille forêt constituent des témoins uniques de la dynamique forestière à long terme et peuvent être utilisés comme référence pour l'aménagement écosystémique. Dans les forêts tempérées feuillues, les perturbations totales sont rares, et la dynamique des peuplements est contrôlée par des perturbations endogènes de type remplacement arbre-par-arbre. Ces processus peuvent être différents à la limite nordique de la forêt tempérée feuillue, dû à des différences de climat ou de régime de perturbation. Nous avons étudié la composition spécifique, les structures de diamètre, d'âge et spatiale de 11 vieux peuplements tempérés feuillus le long d'un gradient d'âge. Les caractéristiques des peuplements diffèrent de ce qui est attendu, d'après des études antérieures qui ont été menées dans le centre de l'aire de répartition de la forêt tempérée feuillue. Plutôt que d'augmenter avec l'âge, la richesse spécifique est supérieure dans les peuplements < 120 ans à cause de la présence d'espèce peu longégives comme *Abies balsamea* et *Acer rubrum*. Toutes les structures diamétrales suivent une distribution de Weibull à deux ou trois paramètres, plutôt qu'une sigmoïde inversée. Des structures d'âge montrent des pics de recrutement, plutôt qu'un recrutement attendu continu, et la répartition spatiale des arbres vivants est principalement aléatoire par rapport à l'âge et aux espèces à une distance < 14 m. Dans le contexte d'aménagement écosystémique, nos résultats suggèrent que le niveau des coupes doit varier par bloc de coupe et la sélection sylvicole devrait inclure occasionnellement de larges trouées créées par plusieurs arbres en plus de trouées créées par un seul arbre.

2.3 Introduction

Relic old-growth forests are unique witnesses of long-term forest dynamics and can serve to establish ecological boundaries that support ecosystem-based forest management (Landres et al. 1999; Gauthier et al. 2009). This is particularly important in temperate deciduous forests, where catastrophic disturbances are rare, allowing endogenous tree-by-tree replacement to dominate stand dynamics (Payette et al. 1990; Fraver et al. 2009). Under such a regime, old-growth stands develop uneven-aged structures that usually result in a rotated sigmoid distribution at equilibrium (Goff and West 1975; Lorimer et al. 2001; Rubin et al. 2006). However, old-growth temperate forests are complex and their size or age distributions occasionally do not follow this distribution (Burrascano et al. 2013). Indeed, infrequent intermediate disturbances can interact with recurrent small-scale, low-intensity gap disturbances (Woods 2004; Hanson and Lorimer 2007). Such highly dynamic, small-scale shifting mosaic systems (Bormann and Likens 1979) result in varied local disturbance histories and residual structural patterns that generate heterogeneous growth conditions which have important consequences for tree size and age structures (Canham et al. 1990; Beaudet and Messier 1998; Beaudet et al. 2000; Koukoulas and Blackburn 2005; Messier et al. 2009). Fine-scale spatial heterogeneity and tree-level processes can have major effects on forest-level properties (Pacala and Deutschman 1995). Therefore, understanding the complex spatial organization of trees could significantly improve our understanding of forest dynamics by identifying levels and scales of influence of stand development processes (Pommerening 2002; Pommerening and Särkkä 2013).

Although the structure and spatial organization of old-growth temperate deciduous forests have been well documented in the central part of their distribution range (Busing and White 1997; Burrascano et al. 2013; Runkle 2013), only one study has been conducted at their northern distribution limit (Payette et al. 1990). The dynamics of old-growth temperate deciduous forests could vary across their distribution range due to differences in climate conditions, disturbance regimes and tree growth (Runkle 1982). For example, Payette et al. (1990) observed smaller gap sizes and faster canopy turnover at the northern distribution limit of temperate deciduous forests in Quebec (Canada). Such a pattern could be attributed to less suitable growth conditions that reduce longevity, limit crown development, and cause progressive limb shedding. Moreover, in the temperate deciduous forests of the northeastern United States, intermediate disturbances (Woods 2004) and large-scale catastrophic disturbances are more frequent under the influence of the North Atlantic hurricane zone (Frelich and Graumlich 1994). In addition to cooler climatic conditions, a different disturbance regime could subsequently lead to a different forest structure or spatial organization at the northern range limit of temperate deciduous forests.

Our objective was to describe tree species composition, age, size, and spatial structures of old-growth temperate deciduous forests at their northern distribution limit. Characterizing the structure of old-growth forests provides important information for forest managers (D'Amato and Orwig 2008; Silver et al. 2013). Recognizing and describing distinctive patterns in old-growth temperate deciduous forests at their northern distribution limit, when these are compared to more central locations within their range would help forest managers adapt ecosystem-based practices accordingly. Following studies that were conducted in the central region of the temperate deciduous forests, we hypothesized that (1) old-growth stands would be increasingly heterospecific with age, as new tree species are recruited through the stochastic process of gap dynamics (Hubbell 2001); (2) age structure would be monotonic as a result of continuous recruitment (Fraver et al. 2009); (3) diameter distribution would first follow a negative exponential or Weibull function indicating continuous recruitment (Rubin et al. 2006), before switching to a rotated sigmoid in the oldest stands, thereby indicating a low mortality rate for mature trees (Lorimer et al. 2001; Westphal et al. 2006); and (4) tree age and diameter would be randomly distributed regardless of stand age as a result of stochastic gap dynamics (Payette et al. 1990).

2.4 Material and methods

2.4.1 Study area

The study sites were located within or slightly north of the sugar maple – yellow birch bioclimatic domain in western Quebec, Canada (46°70' – 47°22' N, 78°49' – 78°89' W) (Figure 1). This region covers 65,500 km2 and is characterized by humo-ferric podzols (Brown 1981). The most abundant forest community in the area is sugar maple (*Acer saccharum* Marsh.) – yellow birch (*Betula alleghaniensis* Britton), with fewer occurrences of yellow birch – balsam fir (*Abies balsamea* (L.) Mill.), yellow birch – hemlock (*Tsuga canadensis* (L.) Carr.), and balsam fir – eastern white cedar (*Thuja occidentalis* L.) communities (Brown 1981). Climate is continental with cold winters and warm summers. Mean annual temperature is 4.4°C and total annual precipitation is 963 mm with an average of 23% falling as snow (Robitaille and Saucier 1998).

Frequent canopy openings created by the death of one or a few trees constitute the principal natural disturbance in the study area (Doyon and Sougavinski 2002). The fire cycle was estimated to be between 188 and 493 years, with the last major fire in the region occurring in 1923 AD (Grenier et al. 2005). Less than 5,000 ha of forests have burned since 1950 (Grenier et al. 2005; Drever et al. 2006; Roy et al. 2010). Catastrophic windthrows are less frequent than fire; their cycle were estimated to be between 1,700 and 7,000 years (Roy et al. 2010; Bégin 2011). However, a catastrophic windthrow had affected more than 25,000 ha of the study area in 2006 AD, with 30% to 100% of the forest canopy cover affected (Roy et al. 2010).

2.4.2 Field sampling

We sampled 11 old-growth forest stands, all of which were separated by at least 500 m (Figure 2.1). Old-growth stands are rare in the study area, where industrial forest management has been active for more than 70 years. Thus, sampled stands were located in protected areas (4 in the Lake-Malakisis Ecological Reserve, 4 in Exceptional Forest Ecosystems), or on islands (3) (Figure 2.1). Island and mainland sites had similar disturbance rates (0.9 ± 0.22 % per year and 1.1 ± 0.33 % per year, respectively) (Després et al., unpublished data). Stand selection was based on three criteria: (i) no trace of harvesting (i.e., every log could be associated with its stump); (ii) presence of dead trees at different decomposition stages; and (iii) trees of different sizes.

In each stand, a 2,500 m2 circular sample plot was randomly located, while making sure that a 100 m buffer zone was maintained between plots and roads, lakes, or other non-forested areas. All sampled stands were at least 5 ha in size. In each plot, we recorded the species of each individual, together with its diameter at breast height (dbh, 1.3 m), height (social rank using Kraft classes; Schütz 1990), and crown area (approximated using the longest vertical projection of the branches and crown form; full circle, half circle, or quarter). The spatial location of every dead snag or living tree (dbh $\geq$ 9.1 cm) was registered using an ultrasonic range finder (Vertex IV Hypsometer, Haglöf Inc., Madison, MS, USA). For dead snags without a dbh, stump diameter was measured at 30 cm. We cored every living tree as close as possible to its base (usually within 20-30 cm above the ground surface), trying to reach the pith (3 trials). We dried and sanded all cores.

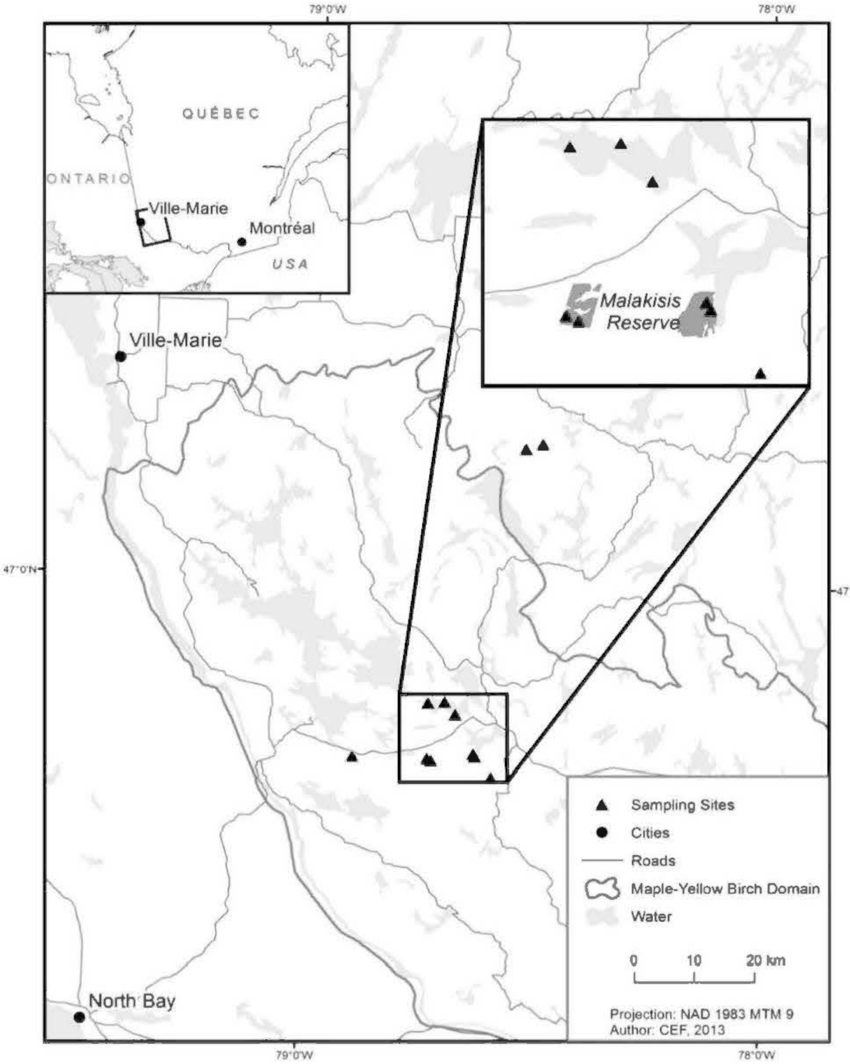

Figure 2.1 Location of the sampling plots in the Temiscamingue region. The inset in the upper right corner is an enlargement of the zone surrounding the Lake-Malakisis Ecological Reserve (shown in dark grey).

2.4.3 Dendrochronological analysis

The cores were cross-dated using pointer years (Yamaguchi 1991). Cross-dating was statistically verified using COFECHA (Holmes 1983) (Table 2.1). A number of the resulting chronologies exhibited low average correlations when examined with COFECHA, but this was to be expected due to the large variation in local light conditions affecting growth of shade-tolerant species. A pith locator was used to estimate pith position when the pith was not included in the core (Applequist 1958). We estimated the precision of the pith locator to be around 10 to 20 years because of tree-to-tree variability in growth patterns. Due to the poor age estimates with the pith locator, we considered all ages as being minimum estimates. Trees with heart rot could not be aged and, thus, were excluded from stand age calculation.

To assess the effect of stand age on forest community patterns, we used the 90th percentile for the age distribution of trees which had been successfully aged. This age indicator was used to rank forest communities according to minimum time since the last stand-replacing disturbance. This approach is similar to that proposed by Keeton et al. (2007, 2011), who used the oldest cohort of trees as an index of stand age.

Table 2.1 Total number of trees (one core per tree) used for dendrochronological analysis for each species combining individuals from all 11 plots. The time span covered and the interseries correlation are also provided.

	No. of trees	Time span	Interseries correlation
Sugar maple	570	1742-2011	0.172
Yellow birch	108	1751-2011	0.203
Balsam fir	60	1896-2011	0.384
Red maple	28	1913-2011	0.408
White spruce	15	1900-2011	0.489

2.4.4 Stand structure

We calculated an importance value (Curtis and McIntosh 1951) as the average of relative density and relative dominance (basal area) to characterize species the composition in each plot. We fitted the observed dbh distributions to theoretical negative exponential, logistic, and 2- and 3-parameter Weibull distributions (Goodburn and Lorimer 1999; Zhang et al. 2001) and used Kolmogorov-Smirnov tests to assess distribution fits. The logistic function was used to describe a rotated sigmoid distribution. Statistical analyses were performed in R (R Core Team 2014), using the fitdistrplus package to calculate the theoretical dbh distributions (Delignette-Muller et al. 2013). The Akaike information criterion corrected for small sample size (AICc) was used to select the best-fitting model. Tree recruitment patterns were visually explored using age distributions.

2.4.5 Spatial structure

Gap dynamics is a stochastic process that should lead to spatial randomness (Petritan et al. 2013). To test the hypothesis of spatial randomness of age, dbh and species, we recorded the spatial coordinates of trees within each plot, and performed a spatial point pattern analysis on continuous (dbh, age) and discrete (species, dead trees) variables, also known as "marks" (Stoyan and Stoyan 1994; Illian et al. 2008). We used the translation correction to account for edge effects (Illian et al. 2008; Grabarnik et al. 2011). All plots were under similar climatic and topographic conditions and, thus, were considered homogeneous (i.e., stationary) and isotropic. We further assumed that plot location had no effect on point patterns. For quantitative marks (age and dbh), we used the mark-weighted L-function L_mm (r), which is the square-root transformation of the mark-weighted K-function K_mm (r) (Penttinen et al. 1992; Illian et al. 2008; Grabarnik et al. 2011) used to stabilize the variance (Illian et al. 2008; Grabarnik et al. 2011). The mark-weighted L-function tests for mark independence, which corresponds to random labeling, and indicates stimulation or inhibition between marks. Stimulation indicates that neighboring trees have a larger dbh (or are older) than the mean stand dbh (or age), whereas inhibition indicates that neighboring trees have a smaller dbh (or are younger) than the mean stand dbh (or age) (see Illian et al. 2008 for details).

For qualitative marks (species, dead trees), we used the L-function L(r) to test for attraction or repulsion. For the species variable, the L-function was only calculated for plots with at least 30 individuals of the same species (Aakala et al. 2012). We tested the complete spatial randomness (CSR) hypothesis of marked Poisson point processes by using Monte-Carlo goodness-of-fit simulations and deviation tests (Loosmore and Ford 2006; Grabarnik et al. 2011). We computed 999 simulations to approximate $\alpha = 0.05$ (Grabarnik et al. 2011).

Because sample size was low within each individual plot, we used replicated point pattern analysis using all plots combined to validate the results that were obtained from single plots (Illian et al. 2008). Aggregated summary characteristics were calculated by simple averaging, as all plots were of the same dimensions (Illian et al. 2008). We calculated 999 Monte-Carlo simulations and deviation tests of these aggregated estimators, as previously described (Loosmore and Ford 2006; Grabarnik et al. 2011). Spatial statistical analyses were performed within R (R Core Team 2014), using the spatstat package (Baddeley and Turner 2005).

2.5 Results

2.5.1 Species composition

Stand age, as described by the 90th percentile of the aged trees, varied from 99 to 195 years, but trees that were older than 200 years were present in all but two plots. The number of living trees and tree density varied among plots (Table 2.2).

		Living trees			Dead trees		
Sample plots	Age (yr)	Living trees (n)	Density (stems/ha)	Basal area (m^2/ha)	Dead trees (n)	Density (stems/ha)	Basal area (m^2/ha)
SP5	99	93	372	18.9	53	212	8.7
SP11	111	102	408	24.6	45	180	7.7
SP10	117	95	380	24.3	32	128	18.7
SP3	119	87	348	22.9	24	96	3.8
SP9	129	77	308	27.7	35	140	7.0
SP6	134	132	528	22.4	72	288	11.8
SP8	147	93	372	18.6	24	96	9.2
SP7	151	66	264	22.4	22	88	8.2
SP2	167	94	376	22.1	18	72	17.5
SP1	184	89	356	20.4	28	112	12.0
SP4	195	82	328	24.0	41	164	6.9

Table 2.2 Number of trees, density (stems/ha), and basal area (m^2/ha) for living and dead trees in each plot. Sample plots (SP) are sorted by minimum age using the 90th percentile of the ages of dated trees.

Basal area of living trees varied to a lesser degree and ranged between 18.6 and 27.7 m^2/ha across all plots (Table 2.2). Mean (± SD) crown area was 87.5 ± 69.7 m2 for dominant sugar maple and 100.0 ± 71.3 m2 for dominant yellow birch, corresponding to crown diameters of 10.6 and 11.3 m, respectively. Sugar maple and yellow birch had high importance values in all plots; three plots were dominated by yellow birch and the other eight were dominated by sugar maple (Table 2.3). Yellow birch importance values tended to decrease with stand age, while the opposite trend was observed for sugar maple. For stands that were dominated by yellow birch (plots 4, 5 and 6), tree species composition was similar regardless of stand age, while for those stands that were dominated by sugar maple (in addition to yellow birch), balsam fir and red maple (*Acer rubrum* L.) were present in stands that were younger than 120 years, while white spruce (*Picea glauca* (Moench) Voss), eastern white cedar, and eastern hemlock were present in 120- to 160 year-old stands. Eastern hop-hornbeam (*Ostrya virginiana* (Mill.) K. Koch) and red oak (*Quercus rubra* L.) were present in stands

Table 2.3 Importance value of each species by sample plot (SP) for all living trees. Plots are sorted by minimum age. Acsa: *Acer saccharum* Marsh.; Beal: *Betula alleghaniensis* Britton; Abba: *Abies balsamea* (L.) Mill.; Tsca: *Tsuga canadensis* (L.) Carr.; Acru: *Acer rubrum* L.; Pigl: *Picea glauca* (Moench) Voss; Thoc: *Thuja occidentalis* L.; Bepa: *Betula papyrifera* Marsh.; Osvi: *Ostrya virginiana* (Mill.) K. Koch; Quru: *Quercus rubra* L.; Pogr: *Populus grandidentata* Michx.; Pist: *Pinus strobus* L.

Sample plot	Acsa	Beal	Abba	Tsca	Acru	Pigl	Thoc	Bepa	Osvi	Quru	Pogr	Pist
SP5	15.44	39.68	25.98		17.58						1.33	
SP11	77.08	18.27	1.13		1.25	1.71						0.56
SP10	70.93	25.61	1.44		0.59	1.43						
SP3	54.60	29.59	7.46	0.73	1.16	5.26	1.20					
SP9	75.86	8.74		7.69			7.72					
SP6	8.13	63.49	16.51	2.91	0.45	1.42	0.92	6.17				
SP8	62.92	33.44				1.31				2.32		
SP7	77.22	7.77		15.01								
SP2	94.88	3.55							1.57			
SP1	90.22	5.28							2.95	1.54		
SP4	36.72	46.21	10.63	2.14	2.16	2.14						

that were older than 160 years (Table 2.2). For stands that were dominated by sugar maple, tree species diversity decreased with age (t = –2.50, df = 6, p = 0.047).

2.5.2 Stand structure

Nine of the 11 stands had their dbh distribution follow a negative exponential, and all followed a 2- or 3-parameter Weibull function (Table 2.4). In comparison, only 5 of the 11 plots were well fitted by a logistic function (Table 2.4). A goodness-of-fit test showed that the 3-parameter Weibull function was always the best theoretical function for describing the dbh structure, exept for SP9 which was better fitted by a 2-parameter Weibull function (Table 2.5). Tree recruitment was continuous through time, occurring almost every decade in all stands (Figure 2.2).

Table 2.4 Comparison of dbh distributions with theoretical distributions (negative exponential, logistic, 2- and 3-parameters Weibull) for each sample plot. Only living individuals with dbh $\geq$ 9.1 cm were included in the analysis. D = value of the Kolmogorov-Smirnov statistic. Plots are sorted by minimum age. Asterisks indicate when the observed data were considered to be statistically different from the theoretical distribution.

	Negative exponential		Logistic		2-p Weibull		3-p Weibull	
Sample plot	*D*	*p*	*D*	*p*	*D*	*p*	*D*	*p*
SP5	0.15	0.024*	0.25	<0.001*	0.09	0.445	0.09	0.375
SP11	0.10	0.256	0.13	0.064	0.09	0.391	0.07	0.678
SP10	0.07	0.769	0.17	0.010*	0.07	0.807	0.06	0.846
SP3	0.11	0.269	0.13	0.090	0.07	0.795	0.08	0.557
SP9	0.10	0.422	0.11	0.344	0.08	0.727	0.08	0.724
SP6	0.10	0.150	0.11	0.077	0.07	0.483	0.08	0.420
SP8	0.19	0.002*	0.23	<0.001*	0.13	0.090	0.14	0.064
SP7	0.08	0.773	0.16	0.069	0.09	0.721	0.07	0.904
SP2	0.12	0.119	0.17	0.008*	0.09	0.485	0.08	0.615
SP1	0.1	0.386	0.19	0.004*	0.06	0.948	0.06	0.946
SP4	0.07	0.777	0.18	0.012*	0.06	0.904	0.07	0.774

Most stands showed recruitment pulses that were centered around 1920-1930 AD and 1870-1880 AD, but a few stands (plots 7 and 10) showed a more constant pattern of recruitment (Figure 2.2).

Table 2.5 AICc values for logistic, exponential, 2-parameter Weibull and 3-parameter Weibull distributions for each sample plot. The lowest AICc values indicate the best fits. Asterisks indicate the lowest AICc value for each sample plot.

	AICc			
Sample plot	Logistic	Exponential	2-p Weibull	3-p Weibull
SP5	1180.24	1068.43	1062.73	997.56*
SP11	1286.49	1237.11	1236.93	1235.98*
SP10	1217.61	1147.79	1149.83	1130.87*
SP3	1103.02	1062.62	1060.50	1060.12*
SP9	1004.37	982.31	977.77*	979.30
SP6	1573.68	1544.23	1527.93	1527.44*
SP8	1183.39	1080.64	1079.51	1036.08*
SP7	872.69	827.27	829.37	821.50*
SP2	1201.61	1130.10	1132.10	1116.18*
SP1	1134.43	1061.59	1063.53	1048.14*
SP4	1068.97	1007.40	1009.45	991.00*

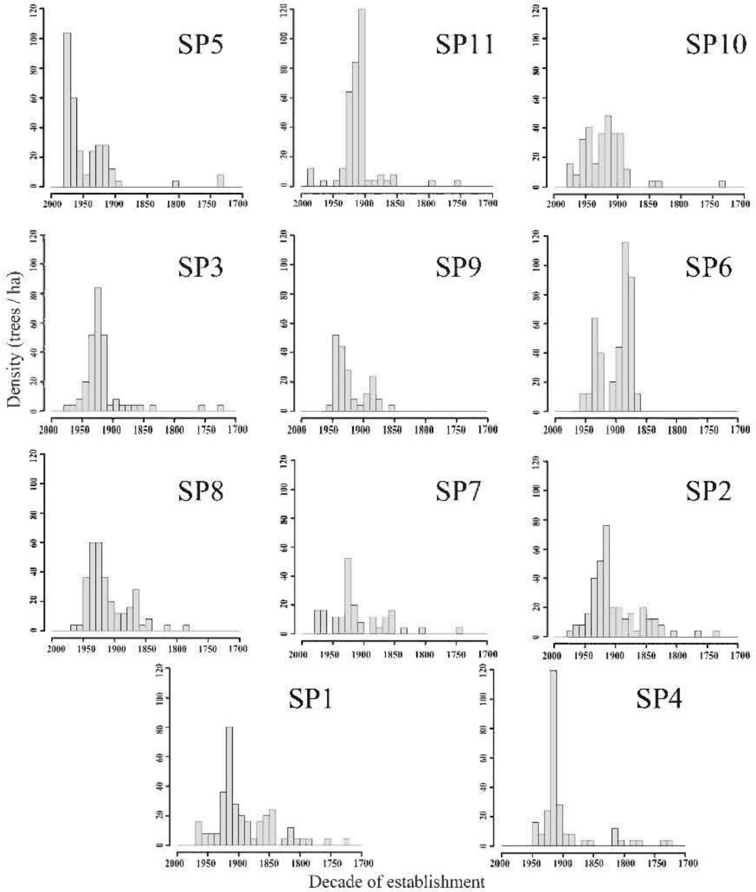

Figure 2.2 Tree (dbh ≥ 9.1 cm) age structure for each sampling plot. Plots are sorted by minimum age from upper left to lower right.

2.5.3 Spatial structure

The mark-weighted L-function for tree age showed random labeling for 10 of the 11 plots (Table 2.6). A significant spatial structure was only detected for plot 7 (inhibition, indicating a uniform distribution, Figure 2.3A). The replicated point pattern analysis for age confirmed independence, which corresponded to random labeling (Table 2.6). The spatial structure of dbh did not follow random labeling in three plots where inhibition patterns were found (plots 1, 5 and 7, Figure 2.3B, C and

D), and two other plots were close to the significance level (plots 3 and 9) (Table 2.6). The replicated point pattern analysis confirmed inhibition at ~ 6-13 m (Figure 2.3E). The distribution of tree species showed complete spatial randomness (CSR) and those results were confirmed by the replicated point pattern analysis (Table 2.6).

Table 2.6 Deviation from mark independence corresponding to random labeling of age and dbh, and complete spatial randomness (CSR) of species for living trees in old-growth temperate deciduous forests of western Quebec. Sample plots are sorted by age (90th percentile). For quantitative marks (age and dbh), the mark weighted L-function $L_{mm}(r)$ was used. For discrete marks (species) the L-function $L(r)$ was computed. Acsa: sugar maple; Beal: yellow birch; Abba: balsam fir. u = value of the Diggle-Cressie-Loosmore-Ford test of CSR statistic.

	Age	dbh	Species		
	$L_{mm}(r)$	$L_{mm}(r)$	$L_{Acsa}(r)$	$L_{Beal}(r)$	$L_{Abba}(r)$
Sample plot	u	u	u	u	u
SP5	77.96	177.79*			8.38
SP11	2.17	20.00	0.22		
SP10	23.17	5.50	1.26		
SP3	12.83	106.71$^+$	7.40$^+$		
SP9	7.29	60.84$^+$	0.63		
SP6	1.96	18.35		1.55	6.87
SP8	5.95	38.30	4.17$^+$		
SP7	130.72*	123.53*	5.35		
SP2	10.77	7.31	2.50		
SP1	6.82	89.58*	2.06		
SP4	37.43	53.94	1.84		
Replicated	1.32	35.45**	17.89	-	17.89

Note: $^+ p < 0.1$; $*p < 0.05$; $** p < 0.01$

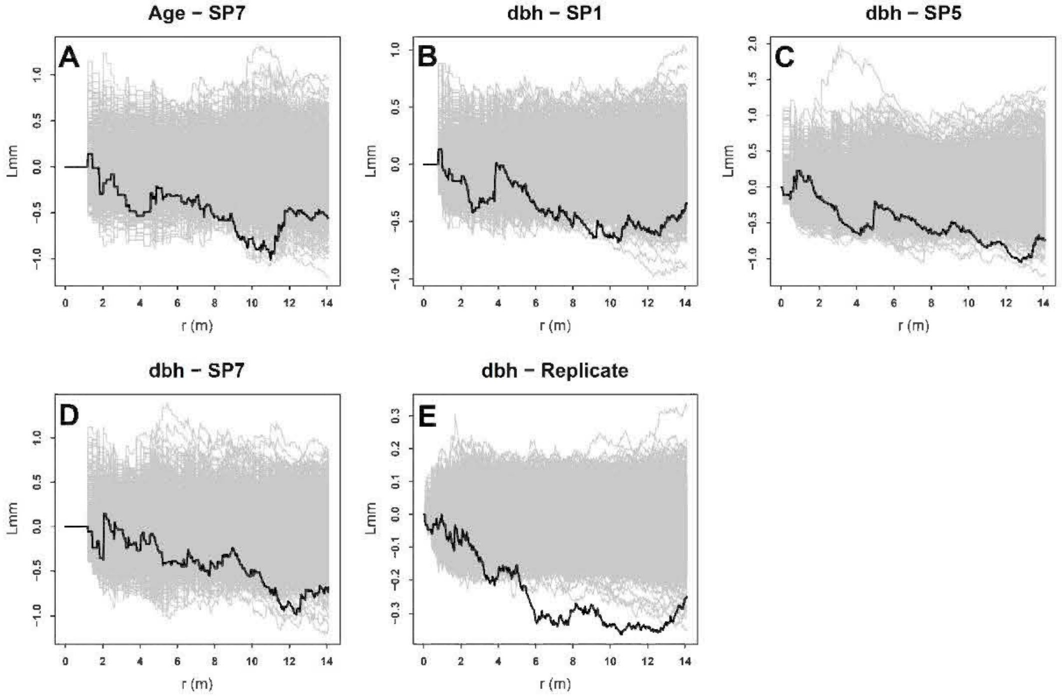

Figure 2.3 Mark-weighted L-function for age (SP 7, A) and dbh (SP 1, 5, 7 and replicate, B, C, D and E respectively) as a function of radius (in meters). The black line corresponds to the observed L_{mm} value and each grey line to one of the 999 Monte-Carlo simulations of the envelope test. Negative L_{mm} values outside the envelope represent inhibition, whereas positive L_{mm} values outside the envelope represent aggregation. L_{mm} values within the envelope limits represent random labelling. Note that these figures are not statistically reliable as it is impossible to control for type I error of the envelope test. They should only be used as a guide to interpret the results of the deviation test.

2.5.4 Spatial structure of dead trees

The number and density of dead trees, and snag basal area varied from one plot to another (Table 2.2). The mean (± SD) fraction of dead trees as a percentage of total trees (living + dead) was 27.2 ± 6.6 %. In stands that were dominated by sugar maple, there were fewer dead trees in older plots compared to younger plots (Table 2.7). The spatial structure of dead trees followed CSR in all plots (Table 2.7). The replicated point pattern analysis confirmed CSR (Table 2.7).

Table 2.7 Deviation from complete spatial randomness (CSR) for the spatial structure of dead trees in old-growth temperate deciduous forests of western Quebec, from L-function $L(r)$. Sample plots are sorted by age (90th percentile). $\%_{\text{dead trees}}$ = percentage of dead trees (in density), u = value of the Diggle-Cressie-Loosmore-Ford test of CSR.

Sample plot	$\%_{\text{dead trees}}$	u	p
SP5	36.3	2.25	0.47
SP11	30.6	2.46	0.59
SP10	25.2	2.17	0.86
SP3	21.6	10.88	0.46
SP9	31.5	2.12	0.84
SP6	35.3	0.37	0.93
SP8	20.5	19.00	0.22
SP7	25.0	3.35	0.94
SP2	16.1	19.66	0.44
SP1	24.4	14.64	0.18
SP4	33.3	4.10	0.42
Replicated	28.1	11.08	0.93

2.6 Discussion

2.6.1 Stand composition

Along the minimum age span of the 11 plots (~ 100 to 200 years), we detected a change in species composition, particularly in stands that were dominated by sugar maple (Table 2.3). Based on Hubbell (2001), we hypothesized that in a quasi-equilibrium state equivalent to the old-growth temperate deciduous forests that we sampled, stochastic recruitment processes would cause new tree species to arrive with time. However, tree species richness decreased instead of increasing, contrary to our hypothesis. Higher species richness in younger stands was associated mainly with the presence of short-lived species such as balsam fir and red maple. Our study only focused on tree species, and we could not verify for possible temporal changes in species richness for other taxa (shrubs, herbs, and mosses, among others).

2.6.2 Stand structure

Old-growth temperate deciduous forests are often assumed to be characterized by a rotated sigmoid (logistic) dbh distribution at equilibrium (Goodburn and Lorimer 1999; Lorimer et al. 2001), with a U-shaped pattern representing high mortality of small suppressed trees, low mortality of vigorous canopy trees, and high mortality of large senescent trees (Runkle 2000; Rubin et al. 2006). However, in our study area, size distributions of all stands were well fitted to the negative exponential distribution or to a 2- or 3-parameter Weibull function, but not to a logistic distribution (Figure 2.4). The Weibull function is a generalized function that could represent a negative exponential distribution (Westphal et al. 2006). The goodness-of-fit test showed that the 3-parameter Weibull was the best theoretical function for describing the dbh structure (except for SP9 which was better fitted by a 2-parameter Weibull function), contrary to our hypothesis that the oldest stands would follow a rotated sigmoid distribution. This unexpected result could be explained by the location of the study sites at the northern range limit of temperate deciduous forests, which are characterized by cooler climatic conditions and a faster stand replacement period that is due to smaller and more frequent gaps (Payette et al. 1990).

A high proportion of dead trees was found in all plots, compared to mature temperate deciduous stands (Burrascano et al. 2013). In stands that were dominated by sugar maple, the proportion of dead trees decreased with stand age. Perhaps the mortality rate was lower in the older stands because they were at or near equilibrium (Tyrrell and Crow 1994). This response needs to be investigated further, considering the importance of dead wood and snags in old-growth temperate deciduous forests (Hodge and Peterken 1998; Burrascano et al. 2008; Wirth et al. 2009).

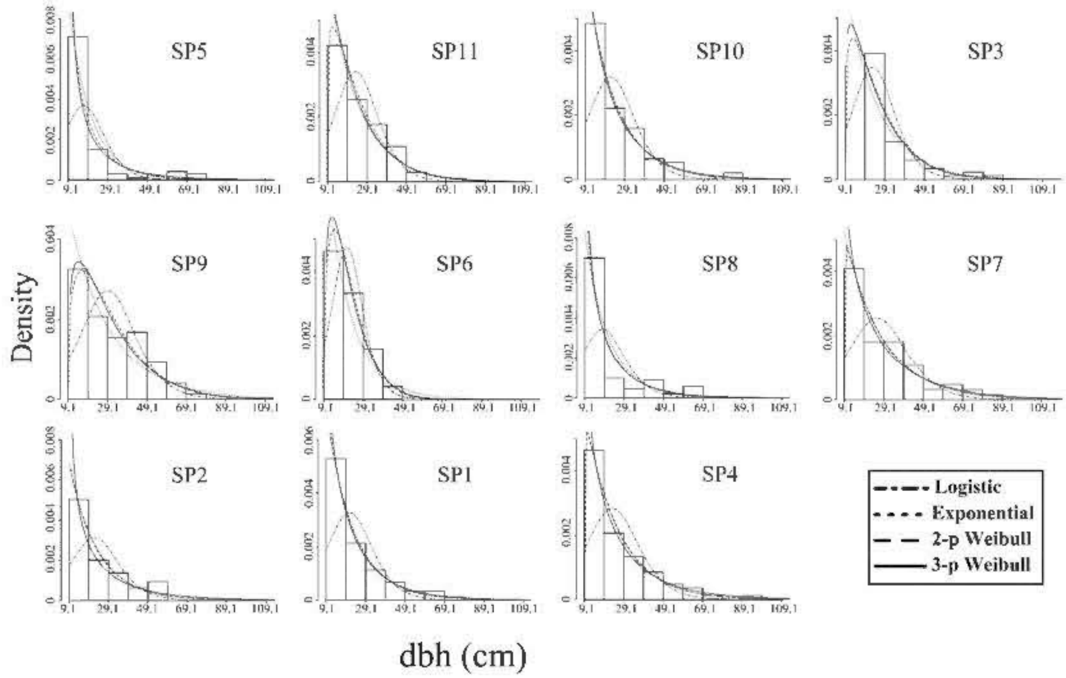

Figure 2.4 Theoretical distributions (logistic, exponential, and 2- and 3-parameter Weibull) fitted to dbh density distributions for each sample plot. Plots are sorted by minimum age from upper left to lower right.

2.6.3 The Weibull size distribution as a strange attractor

The study stands usually showed continuous recruitment, which is consistent with both our hypothesis and gap phase dynamics (Fraver et al. 2009). However, recruitment was generally not constant, and pulses were recorded around 1870-1880 AD in 4 of the 11 stands, and around 1920-1930 AD in 8 of the 11 stands (Figure 2.2). Recruitment pulses could result from intermediate disturbances such as windstorms, or from the harvesting of large white pines (*Pinus strobus* L.) at the end of the 19th and at the beginning of the 20th century (Vincent 1995; Roy et al. 2010). Indeed, the pulse recorded at the end of the 19th century could correspond to the establishment of the first sawmill in the study area in 1874 AD (Vincent 1995). The pulse at the beginning of the 20th century could correspond to a series of natural intermediate disturbances, including spruce budworm (*Choristoneura fumiferana* Clem.) outbreak in 1910 AD and fires between 1921 and 1923 AD, as well as the intensification of white pine harvesting (Grenier et al. 2005; Drever et al. 2006).

Although recruitment patterns (continuous vs. pulse) differed among plots, dbh structures all converged towards a 2- or 3-parameter Weibull distribution. Indeed, the signal of intermediate disturbances that was seen in the age structures (recruitment pulses) was lost in the dbh distributions. It often has been suggested that a negative exponential or a Weibull size distribution involves constant recruitment and mortality (e.g., Niklas et al. 2003; Rubin et al. 2006). Obviously, forests rarely follow these premises for a long time. Our results suggest that intermediate disturbances can modify the rate of recruitment, and that growth and mortality vary with size classes, as has been reported elsewhere (Bédard and Majcen 2003; Fortin et al. 2008).

As an alternative mechanism for explaining the convergence in dbh structure for forests with different recruitment histories, we suggest that the temporally variable and spatially heterogeneous light environment that was generated by gap dynamics in old-growth temperate deciduous forests offers a wide range of growth conditions. This allows trees of the same age to grow into different size classes while aging, with many growing slowly under low light conditions and a few growing quickly under prolonged favorable light conditions. This growth difference generates a Weibull dbh distribution. For example, in our study area, a sugar maple with a 30 cm dbh could equally be 70-years-old or 180-years-old (data not shown). Under such dynamics, forests can experience different disturbance histories, but they all converge towards the same structural archetype, which acts like a strange attractor (Roberts 1996). Such chaotic determinism has been understood to commonly emerge in natural forest systems that are subject to gap dynamics (Crawley and Ross 1990; Wu and Loucks 1995; Stone and Ezrati 1996).

2.6.4 Tree spatial structure

Neither the mark-weighted L-function for age nor the L-function for species demonstrated any specific spatial pattern (Table 2.6). The spatial distribution of dead trees was also random within all plots (Table 2.7). This lack of spatial structure in tree spatial patterns supports our hypothesis that gaps in temperate deciduous forests are small and occur randomly (Frelich and Graumlich 1994; Chokkalingam and White 2001; Curzon and Keeton 2010). However, the mark-weighted L-function for dbh did not show random labeling (Table 2.6); rather, it indicated inhibition at ~ 6 to 13 m distances. This range includes the mean crown size of dominant sugar maple and yellow birch trees (crown diameters of 10 and 11 m, respectively). Thus, small suppressed trees are over-represented at the boundary of two dominant crowns, which is likely due to higher light availability (Messier et al. 2009). Random gap occurrence creates a heterogeneous light environment under the forest canopy that varies with time. The footprint that is created by randomness persists with age, but not with diameter, providing further evidence of the "strange attractor" process that was described in the previous section.

2.7 Conclusion

In this study, we found that the structural characteristics of old-growth temperate deciduous forests were different in several ways at the northern limit of their range compared to more central locations. First, species richness did not increase with age (Hubbell 2001), although species composition did vary. This supports the current practice of tree-marking in the study area, where short-lived companion species to sugar maple (e.g., balsam fir, red maple) are planned to be harvested first. Second, the age structure of some stands did show constant recruitment as expected (Fraver et al. 2009), but other stands showed recruitment pulses, possibly indicative of intermediate disturbances. This would suggest that selection silviculture should occasionally include larger, multiple-tree gaps in addition to single-tree gaps (Hanson and Lorimer 2007). Third, no shift in diameter distributions from a Weibull to a rotated sigmoid was observed (Lorimer et al. 2001; Westphal et al. 2006). Hence, selection cutting across the range of diameter classes does not seem to be a problem in our study area, in contrast to other regions where it would fail to recreate the rotated sigmoid distribution (Goodburn and Lorimer 1999). Fourth, spatial randomness was observed for age, species and dead trees, which supports varying harvest levels across harvesting blocks (Keeton 2006; North and Keeton 2008). Further research is needed to attain a better understanding of old-growth temperate deciduous forests at their northern distribution limit, most notably with respect to the estimation of disturbance rates.

2.8 Acknowledgments

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2.9 References

Aakala, T., S. Fraver, B.J. Palik, and A.W. D'Amato. 2012. Spatially random mortality in old-growth red pine forests of northern Minnesota. *Can. J. For. Res.* 42(5):899-907.

Applequist, M.B. 1958. A simple pith locator for use with off-center increment cores. *J. For.* 56(2):141.

Baddeley, A., and R. Turner. 2005. Spatstat: an R package for analyzing spatial point patterns. *J. Stat. Softw.* 12(6):1-42.

Beaudet, M., and C. Messier. 1998. Growth and morphological responses of yellow birch, sugar maple, and beech seedlings growing under a natural light gradient. *Can. J. For. Res.* 28(7):1007-1015.

Beaudet, M., C. Messier, D.W. Hilbert, E. Lo, Z.M. Wang, and M.J. Lechowicz. 2000. Leaf- and plant-level carbon gain in yellow birch, sugar maple, and beech seedlings from contrasting forest light environments. *Can. J. For. Res.* 30(3):390-404.

Bédard, S., and Z. Majcen. 2003. Growth following single-tree selection cutting in Québec northern hardwoods. *Forest. Chron.* 79(5):898-905.

Bégin, E. 2011. Caractérisation des régimes de perturbations par le chablis et des vents extrèmes dans l'érablière à bouleau jaune du Québec. Unpublished M.Sc. thesis, UQAM, Montréal, Qc. 110 p.

Bormann, F.H., and G.E. Likens. 1979. Pattern and process in a forested ecosystem. Springer-Verlag. 253 p.

Brown, J.L. 1981. Les forêts du Témiscamingue, Québec: écologie et photo-interprétation. Laboratoire d'écologie forestière, Université Laval. 447 p.

Burrascano, S., W.S. Keeton, F.M. Sabatini, and C. Blasi. 2013. Commonality and variability in the structural attributes of moist temperate old-growth forests: A global review. *For. Ecol. Manag.* 291:458-479.

Burrascano, S., F. Lombardi, and M. Marchetti. 2008. Old-growth forest structure and deadwood: Are they indicators of plant species composition? A case study from central Italy. *Plant Biosyst* 142(2):313-323.

Busing, R.T., and P.S. White. 1997. Species diversity and small-scale disturbance in an old-growth temperate forest: A consideration of gap partitioning concepts. *Oikos* 78(3):562-568.

Canham, C.D., J.S. Denslow, W.J. Platt, J.R. Runkle, T.A. Spies, and P.S. White. 1990. Light regimes beneath closed canopies and tree-fall gaps in temperate and tropical forests. *Can. J. For. Res.* 20(5):620-631.

Chokkalingam, U., and A. White. 2001. Structure and spatial patterns of trees in old-growth northern hardwood and mixed forests of northern Maine. *Plant Ecol.* 156(2):139-160.

Crawley, M.J., and G.J.S. Ross. 1990. The population dynamics of plants [and discussion]. *Philosophical Transactions: Biological Sciences* 330(1257):125-140.

Curtis, J.T., and R.P. McIntosh. 1951. An upland forest continuum in the prairie-forest border region of Wisconsin. *Ecology* 32(3):476-496.

Curzon, M.T., and W.S. Keeton. 2010. Spatial characteristics of canopy disturbances in riparian old-growth hemlock – northern hardwood forests, Adirondack Mountains, New York, USA. *Can. J. For. Res.* 40(1):13-25.

D'Amato, A.W., and D.A. Orwig. 2008. Stand and landscape-level disturbance dynamics in old-growth forests in western Massachusetts. *Ecol. Monogr.* 78(4):507-522.

Delignette-Muller, M.L., R. Pouillot, J.-B. Denis, and C. Dutang. 2013. fitdistrplus: help to fit of a parametric distribution to non-censored or censored data. R package version 1.0-1

Doyon, F., and S. Sougavinski. 2002. Caractérisation du régime de perturbations naturelles de la forêt feuillue du Nord-Est de l'Amérique du Nord. Institut québécois d'aménagement de la forêt feuillue. 123 p.

Drever, C.R., C. Messier, Y. Bergeron, and F. Doyon. 2006. Fire and canopy species composition in the Great Lakes–St. Lawrence forest of Témiscamingue, Québec. *For. Ecol. Manag.* 231(1-3):27-37.

Fortin, M., S. Bédard, J. DeBlois, and S. Meunier. 2008. Predicting individual tree mortality in northern hardwood stands under uneven-aged management in southern Québec, Canada. *Ann. For. Sci.* 65(2).

Fraver, S., A.S. White, and R.S. Seymour. 2009. Natural disturbance in an old-growth landscape of northern Maine, USA. *J. Ecol.* 97(2):289-298.

Frelich, L.E., and L.J. Graumlich. 1994. Age-class distribution and spatial patterns in an old-growth hemlock–hardwood forest. *Can. J. For. Res.* 24(9):1939-1947.

Gauthier, S., M.-A. Vaillancourt, A. Leduc, L. De Grandpré, D. Kneeshaw, H. Morin, P. Drapeau, and Y. Bergeron. 2009. Ecosystem management in the boreal forest. Presses de l'Université du Québec, Québec, Canada. 539 p.

Goff, F.G., and D. West. 1975. Canopy-understory interaction effects on forest population structure. *For. Sci* 21(2):98-108.

Goodburn, J.M., and C.G. Lorimer. 1999. Population structure in old-growth and managed northern hardwoods: an examination of the balanced diameter distribution concept. *For. Ecol. Manag.* 118(1-3):11-29.

Grabarnik, P., M. Myllymäki, and D. Stoyan. 2011. Correct testing of mark independence for marked point patterns. *Ecol. Model.* 222(23-24):3888-3894.

Grenier, D.J., Y. Bergeron, D. Kneeshaw, and S. Gauthier. 2005. Fire frequency for the transitional mixedwood forest of Timiskaming, Quebec, Canada. *Can. J. For. Res.* 35(3):656-666.

Hanson, J.J., and C.G. Lorimer. 2007. Forest structure and light regimes following moderate wind storms: Implications for multi-cohort management. *Ecol. Appl.* 17(5):1325-1340.

Hodge, S.J., and G.F. Peterken. 1998. Deadwood in British forests: priorities and a strategy. *Forestry* 71(2):99-112.

Holmes, R.L. 1983. Computer-assisted quality control in tree-ring dating and measurement. *Tree-Ring Bulletin* 1983(43):51-67.

Hubbell, S.P. 2001. The unified neutral theory of biodiversity and biogeography. Princeton University Press. 375 p.

Illian, J., P.A. Penttinen, H. Stoyan, and D. Stoyan. 2008. Statistical analysis and modelling of spatial point patterns. Wiley, England. 560 p.

Keeton, W.S. 2006. Managing for late-successional/old-growth characteristics in northern hardwood-conifer forests. *For. Ecol. Manag.* 235(1-3):129-142.

Keeton, W.S., C.E. Kraft, and D.R. Warren. 2007. Mature and old-growth riparian forests: Structure, dynamics, and effects on adirondack stream habitats. *Ecol. Appl.* 17(3):852-868.

Keeton, W.S., A.A. Whitman, G.C. McGee, and C.L. Goodale. 2011. Late-successional biomass development in northern hardwood-conifer forests of the northeastern United States. *For. Sci* 57(6):489-505.

Koukoulas, S., and G.A. Blackburn. 2005. Spatial relationships between tree species and gap characteristics in broad-leaved deciduous woodland. *J. Veg. Sci.* 16(5):587-596.

Landres, P.B., P. Morgan, and F.J. Swanson. 1999. Overview of the use of natural variability concepts in managing ecological systems. *Ecol. Appl.* 9(4):1179-1188.

Loosmore, N.B., and E.D. Ford. 2006. Statistical inference using the G or K point pattern spatial statistics. *Ecology* 87(8):1925-1931.

Lorimer, C.G., S.E. Dahir, and E.V. Nordheim. 2001. Tree mortality rates and longevity in mature and old-growth hemlock-hardwood forests. *J. Ecol.* 89(6):960-971.

Messier, C., J. Posada, I. Aubin, and M. Beaudet. 2009. Functional relationships between old-growth forest canopies, understorey light and vegetation dynamics. P. 115-139 in *Old-growth forests*, Wirth, C., G. Gleixner, and M. Heimann (eds.). Springer, Berlin Heidelberg.

Niklas, K.J., J.J. Midgley, and R.H. Rand. 2003. Tree size frequency distributions, plant density, age and community disturbance. *Ecol. Lett.* 6(5):405-411.

North, M.P., and W.S. Keeton. 2008. Emulating natural disturbance regimes: An emerging approach for sustainable forest management. P. 341-372 in *Patterns and processes in forest landscapes*, Lafortezza, R., G. Sanesi, J. Chen, and T.R. Crow (eds.). Springer Netherlands.

Pacala, S.W., and D.H. Deutschman. 1995. Details that matter: The spatial distribution of individual trees maintains forest ecosystem function. *Oikos* 74(3):357-365.

Payette, S., L. Filion, and A. Delwaide. 1990. Disturbance regime of a cold temperate forest as deduced from tree-ring patterns: the Tantaré Ecological Reserve, Quebec. *Can. J. For. Res.* 20(8):1228-1241.

Penttinen, A., D. Stoyan, and H.M. Henttonen. 1992. Marked point processes in forest statistics. *For. Sci* 38(4):806-824.

Petritan, A.M., R.S. Nuske, I.C. Petritan, and N.C. Tudose. 2013. Gap disturbance patterns in an old-growth sessile oak (*Quercus petraea* L.)–European beech (*Fagus sylvatica* L.) forest remnant in the Carpathian Mountains, Romania. *For. Ecol. Manag.* 308(0):67-75.

Pommerening, A. 2002. Approaches to quantifying forest structures. *Forestry* 75(3):305-324.

Pommerening, A., and A. Särkkä. 2013. What mark variograms tell about spatial plant interactions. *Ecol. Model.* 251:64-72.

R Core Team. 2014. R: A language and environment for statistical computing. R Foundation for Statistical Computing. Vienna, Austria. http://www.R-project.org/

Roberts, D.W. 1996. Modelling forest dynamics with vital attributes and fuzzy systems theory. *Ecol. Model.* 90(2):161-173.

Robitaille, A., and J.P. Saucier. 1998. Paysages régionaux du Québec méridional. Les publications du Québec, Québec. 213 p.

Roy, M.-E., F. Doyon, P. Nolet, and Bouffard D. 2010. Historique des perturbations et réponse de la végétation forestière dans l'érablière à bouleau jaune de l'ouest au Témiscamingue au cours du 20ième siècle. P. 57. Institut québécois d'aménagement de la forêt feuillue, Ripon, Québec.

Rubin, B.D., P.D. Manion, and D. Faber-Langendoen. 2006. Diameter distributions and structural sustainability in forests. *For. Ecol. Manag.* 222(1-3):427-438.

Runkle, J.R. 1982. Patterns of disturbance in some old-growth mesic forests of Eastern North America. *Ecology* 63(5):1533-1546.

Runkle, J.R. 2000. Canopy tree turnover in old-growth mesic forests of eastern North America. *Ecology* 81(2):554-567.

Runkle, J.R. 2013. Thirty two years of change in an old-growth Ohio beech-maple forest. *Ecology* 94(5):1165-1175

Schütz, J.P. 1990. Sylviculture 1: principes d'éducation des forêts. Presses polytechniques et universitaires romandes, Lausanne. 243 p.

Silver, E.J., A.W. D'Amato, S. Fraver, B.J. Palik, and J.B. Bradford. 2013. Structure and development of old-growth, unmanaged second-growth, and extended rotation *Pinus resinosa* forests in Minnesota, USA. *For. Ecol. Manag.* 291:110-118.

Stone, L., and S. Ezrati. 1996. Chaos, cycles and spatiotemporal dynamics in plant ecolgy. *J. Ecol.* 84(2):279.

Stoyan, D., and H. Stoyan. 1994. Fractals, random shapes, and point fields: methods of geometrical statistics. Wiley, Chichester, UK. 399 p.

Tyrrell, L.E., and T.R. Crow. 1994. Structural characteristics of old-growth hemlock-hardwood forests in relation to age. *Ecology* 75(2):370-386.

Vincent, O.F. 1995. Histoire de l'Abitibi-Témiscamingue. Institut québécois de recherche sur la culture, Québec. 765 p.

Westphal, C., N. Tremer, G.v. Oheimb, J. Hansen, K.v. Gadow, and W. Härdtle. 2006. Is the reverse J-shaped diameter distribution universally applicable in European virgin beech forests? *For. Ecol. Manag.* 223(1-3):75-83.

Wirth, C., G. Gleixner, and M. Heimann. 2009. Old-growth forests: Function, fate and value. Springer, Verlag, Berlin, Heidelberg. 538 p.

Woods, K.D. 2004. Intermediate disturbance in a late-successional hemlock-northern hardwood forest. *J. Ecol.* 92(3):464-476.

Wu, J., and O.L. Loucks. 1995. From balance of nature to hierarchical patch dynamics: A paradigm shift in ecology. *The Quarterly Review of Biology* 70(4):439-466.

Yamaguchi, D.K. 1991. A simple method for cross-dating increment cores from living trees. *Can. J. For. Res.* 21(3):414-416.

Zhang, L., J.H. Gove, C. Liu, and W.B. Leak. 2001. A finite mixture of two Weibull distributions for modeling the diameter distributions of rotated-sigmoid, uneven-aged stands. *Can. J. For. Res.* 31(9):1654-1659.

CHAPITRE III

GAP DISTURBANCE REGIME OF OLD-GROWTH TEMPERATE DECIDUOUS FORESTS AT THEIR NORTHERN RANGE LIMIT

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3.1 Abstract

Questions: Natural disturbance dynamics near species' distribution limits can differ from those at the range center. This has implications for ecosystem-based forest management, which seeks to emulate the spatio-temporal patterns created by natural disturbances. This study aimed to determine if the gap disturbance regime of the eastern North American temperate deciduous forest at its northern distribution limit is different than in the center of its range. A secondary question was to evaluate if there is a relationship between species composition and gap disturbance rate at the stand scale.

Location: Old-growth forests dominated by sugar maple (*Acer saccharum* Marsh.) or yellow birch (*Betula alleghaniensis* Britton), at the northern limit of temperate deciduous forests in western Quebec, Canada (between 46°70’ – 47°22’ N and 78°49’ – 78°89’ W).

Methods: To reconstruct past gap disturbances, we identified growth releases using the boundary line method applied to tree-ring chronologies obtained from 0.25 ha plots sampled within 11 stands. We reconstructed past canopy gaps using release events, calculated historical gap disturbance rates, and used redundancy analysis to evaluate the relationship between gap disturbance rate and species composition at the plot scale.

Results: The mean gap disturbance rate across the 11 sampled stands was 0.96 ± 0.51% per year. Mean gap size was 39 ± 44 m^2 and almost 85% of the gaps were smaller than 50 m^2. Stands with smaller gaps and lower gap disturbance rates had high importance values for balsam fir (*Abies balsamea* (L.) Mill) and/or yellow birch.

Conclusions: The gap disturbance rate (percent area disturbed by gaps per year) found at the northern limit of the temperate deciduous forest was similar to that reported in studies from the central part of its range. However, gaps were more numerous and smaller.

3.2 Résumé

Questions: La dynamique des perturbations naturelles proches de la limite de répartition des espèces peut être différente par rapport à celle de son centre de répartition. Ceci à des implications pour l'aménagement forestier écosystémique, qui a pour but de reproduire le patron spatio-temporel créé par les perturbations naturelles. Cette étude a pour objectif de déterminer si le régime de trouée de la forêt tempérée feuillue de l'est de l'Amérique du Nord à sa limite nordique de répartition est différent de celui du centre de son aire de répartition. Un second objectif était d'évaluer s'il y a une relation entre la composition spécifique et le taux de perturbation des trouées à l'échelle du peuplement.

Localisation: Vieilles forêts dominées par l'érable à sucre (*Acer saccharum* Marsh.) et le bouleau jaune (*Betula alleghaniensis* Britton), à la limite nordique de la forêt tempérée feuillue de l'ouest du Québec, Canada (entre 46°70' – 47°22' N et 78°49' – 78°89' O).

Méthodes: Pour reconstituer les trouées, nous avons identifié les reprises de croissances en utilisant la méthode du « boundary line » appliquée aux chronologies de cernes de croissance des arbres de 11 peuplements de 0,25 ha chacun. Nous avons reconstitué les trouées passées en utilisant les reprises de croissance, calculé le taux historique des perturbations par les trouées et effectué une analyse multivarié pour évaluer la relation entre le taux de perturbation des trouées et la composition spécifique à l'échelle de la placette.

Résultats: Le taux moyen de perturbation sur l'ensemble des 11 peuplements échantillonnés est de 0,96 ± 0.51% par an. La taille moyenne des trouées est de 39 ± 44 m² et presque 85% des trouées sont plus petites que 50 m². Les peuplements avec des trouées plus petites et un taux de perturbation des trouées plus faible ont une plus grande valeur d'importance pour le sapin baumier (*Abies balsamea* (L.) Mill) et/ou le bouleau jaune.

Conclusions: Le taux de perturbation des trouées (pourcentage de superficie perturbé par les trouées par an) à la limite nord de la forêt tempérée feuillue est similaire à ceux rapportés dans des études réalisées au centre de l'aire de répartition. Cependant, les trouées sont plus nombreuses et plus petites.

3.3 Introduction

The natural disturbance regime of broadleaf temperate deciduous forests is characterized by canopy gaps created by the death of one or a few trees, resulting from senescence or low-severity disturbances (Lorimer & Frelich 1989; Fraver et al. 2009). Gap size can vary from less than 10 m² to more than 1 ha (Yamamoto 1992a; Tanaka & Nakashizuka 1997; Drobyshev 2001; Zeibig et al. 2005; Rugani et al. 2013; Hobi et al. 2015). Gap size distribution is usually skewed towards smaller sizes, with most of the gaps smaller than 100 m² (e.g., Zeibig et al. 2005; Petritan et al. 2013). The annual gap disturbance rate (i.e., percent area disturbed by gaps per year) has been estimated to vary from 0.5% to 1% in old-growth temperate deciduous forests at the center of their distribution range in eastern USA (Runkle 1982; Dahir & Lorimer 1996; D'Amato & Orwig 2008; Fraver et al. 2009). Data are scarcer at the northern range limit of temperate deciduous forests and the only study published so far reported an annual gap disturbance rate of 2.2% in southern Quebec (Payette et al. 1990). However, this study was conducted on a hilltop where site conditions are different from those encountered in lowland mesic sites.

Different natural disturbance dynamics at species' distribution limits compared to their central ranges have implications for ecosystem-based forest management, which seeks to emulate the spatio-temporal patterns created by natural disturbances. We hypothesized that a different disturbance rate at the northern limit of the eastern North American temperate deciduous forest could result from differences in tree size distribution, tree residence time in the canopy, tree growth, or tree recruitment dynamics. More specifically, we hypothesized that (1) gap disturbance rates (percent area disturbed by gaps per year) would be higher at the northern limit than in the central range, due to shorter tree lifespan under less favorable climatic conditions (Payette et al. 1990; Purves 2009). We further hypothesized (2) that mean gap size would be smaller at the northern limit of temperate deciduous forests than in the central range because tree crowns are smaller in the north (Payette et al. 1990; Petritan et al. 2013; Rugani et al. 2013). Finally, we hypothesized (3a) that at the stand scale, a higher proportion of conifers would lead to a lower disturbance rate, due to their smaller crowns and lower average height, as compared to deciduous trees (Kneeshaw & Prévost 2007). However, conifers have a shorter residence time in the canopy than deciduous trees, and thus we posited the alternative hypothesis (3b) that a higher proportion of conifers could increase the disturbance rate (Kneeshaw & Prévost 2007). We tested the hypotheses by reconstructing the gap disturbance regimes of 11 old-growth stands located at the northern distribution limit of the eastern North American temperate deciduous forest using dendrochronological analysis and tree mapping to estimate gap size distributions and annual disturbance rates as suggested by Rankin & Tramer (2002). We discuss our results by comparing the values we obtained with those reported in studies conducted in more centrally-located parts of the temperate deciduous forest biome in eastern North America.

3.4 Material and methods

3.4.1 Study area

The study sites are located at the northernmost margin of the sugar maple (*Acer saccharum* Marsh.) – yellow birch (*Betula alleghaniensis* Britton) bioclimatic domain of western Quebec, Canada, in the Temiscamingue region (between 46°70' – 47°22' N and 78°49' – 78°89' W), a forest type typical of the broadleaf temperate deciduous forests of north-eastern North America (Westveld 1956) (Fig. 3.1). The mean annual temperature is 4.4 °C and total annual precipitation is 963 mm with an average of 23% falling as snow (Robitaille & Saucier 1998). Soils are humo-ferric podzols (Brown 1981).

Frequent canopy openings created by the death of one or a few trees constitute the main natural disturbance in the study area (Roy et al. 2010), creating a random pattern of tree age, diameter and species (Després et al. 2014). Wildfires are rare in the study area and the fire cycle was estimated at several hundred years for the post-settlement period (Drever et al. 2006). Catastrophic blowdowns are also infrequent, with a cycle estimated to be between 1700 and 7000 years (Roy et al. 2010; Bégin 2011).

3.4.2 Field sampling

Old-growth stands are rare in the study area, where industrial forest management has been active for more than 70 years. Thus, sampled stands were located in protected areas (four stands in the Lake-Malakisis Ecological Reserve and four stands in Exceptional Forest Ecosystems (Villeneuve 1994; Villeneuve & Brisson 2003)), or on islands (three stands). All sampled stands were at least 5 ha in size. We sampled 11 old-growth stands in the summer of 2011, all of which were separated by at least 500 m (Fig. 3.1). As the study aimed at reconstructing the gap regime, stand selection was based on three criteria: (i) no trace of harvesting (i.e., every stem on the ground could be associated with its stump), (ii) presence of dead trees at different size and decomposition stages (from recently dead to completely rotten) (Tyrrell & Crow 1994), and (iii) varied tree size classes reflecting an uneven-aged structure with a range of diameters from advance regeneration (< 10 cm DBH (diameter at breast height)), to large trees (> 30 cm DBH). This last criterion has been used previously to identify old-growth temperate deciduous forests across Quebec (Villeneuve & Brisson 2003). The sampled stands were mainly composed of sugar maple and yellow birch. Balsam fir (*Abies balsamea* (L.) Mill.), red maple (*Acer rubrum* L.), white spruce (*Picea glauca* (Moench) Voss) and eastern hemlock (*Tsuga canadensis* (L.)

Carr.) also occurred but were less common across all sampling plots, whereas eastern white cedar (*Thuja occidentalis* L.), large-toothed aspen (*Populus grandidentata* Michx.), and eastern hop-hornbeam (*Ostrya virginiana* (Mill.) K. Koch) were present in one or two stands (App. A). In each selected old-growth stand, we randomly

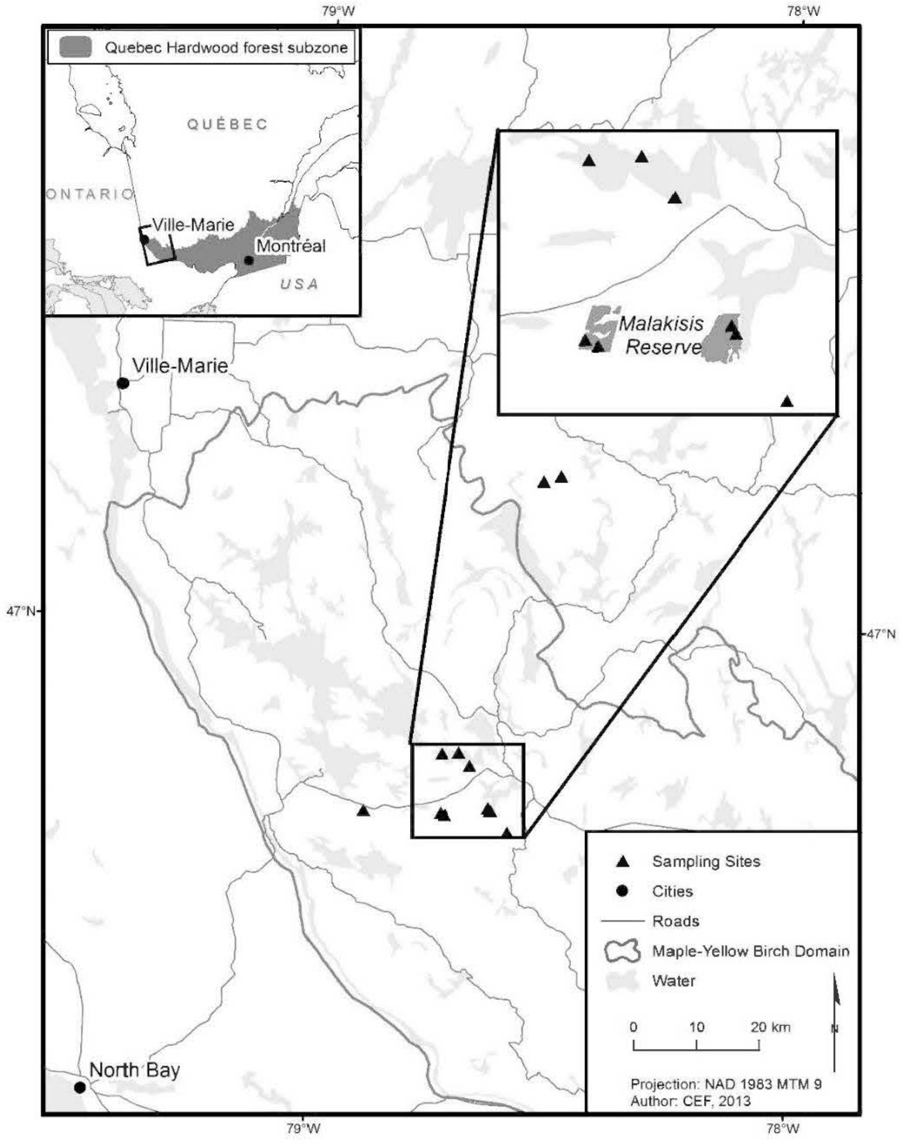

Figure 3.1 Location of the sample plots in western Quebec, close to the northern limit of temperate deciduous forests. The inset in the upper right corner is an enlargement of the zone surrounding the Lake Malakisis Ecological Reserve (shown in dark grey).

located a 2500 m^2 (0.25 ha) circular sampling plot, making sure that a 100 m buffer zone was maintained between plots and roads, water bodies and other non-forested areas.

In each plot, we mapped and measured the DBH of all dead and living trees $\geq$9.1 cm DBH. We also measured the maximum radius of the crown of each living tree. We cored every living tree as close as possible to its base (usually within 20-30 cm above the ground surface), trying to reach the pith and making up to three trials. We dried, sanded and scanned all cores using Expression 10 000 XL scanner (Epson Inc.) and measured tree rings to the nearest 0.01 mm using CooRecorder (version 7.6, Cybis Elektronic & Data AB, Saltsjöbaden, Sweden). We cross-dated the cores using pointer years (Stokes & Smiley 1968) and we used COFECHA to verify cross-dating accuracy (Holmes 1983). Shade-tolerant species are difficult to cross-date due to missing rings (Lorimer et al. 1999) and a large effect of local light conditions as they grow under cover, hence cross-dating to yearly resolution was only possible for the last 80 years.

To assess the effect of stand age on forest community patterns, we ranked stands according to the 90th percentile of the age distribution of successfully-aged trees. This approach is similar to that proposed by Keeton et al. (2007, 2011) for sites where the last stand-replacing disturbance is likely to be more ancient than the oldest tree of the stand.

3.4.3 Estimation of gap disturbance regime parameters

We reconstructed gap formation by combining tree-ring data and tree locations (as was done previously by Payette et al. (1990), Rankin & Tramer (2002), Fraver &

White (2005) and Khakimulina et al. (2015) using different methods). We used the well-documented boundary line criterion for growth releases detection (Black & Abrams 2003, 2004). We assumed that growth releases detected in the tree-ring series were related to the death of a neighboring tree or group of trees (Lorimer & Frelich 1989). To perform the boundary line method, we needed to first compute the percentage growth change for each ring using the method developed by Henry & Swan (1974) and popularized by Nowacki & Abrams (1997):

$$\textit{Percentage growth change} = \frac{M_2 - M_1}{M_1} \times 100 \qquad [1]$$

where M1 and M2 represent mean ring width over the preceding and following 10 years, respectively (Leak 1987; Nowacki & Abrams 1997). Using equation [1] implied that the first and last 10 years of the chronologies could not be analyzed.

We used the method described by Black & Abrams (2003) to compute growth releases. Growth releases were assumed to indicate gap creation when the percentage growth change was beyond a given threshold. To obtain this threshold, we plotted the relationship between percentage growth change and prior growth (i.e., average radial growth of the 10 previous years). Then, for every 0.5 mm increment of prior growth, the 10 highest percentage growth changes were averaged. Those averages were fitted with different functions (exponential, logarithmic, linear or power functions). The function with the highest R^2 was retained as the 100% threshold of the boundary line. For further analyses, only peaks of growth change $\geq$ 10% between two consecutive year were selected to avoid identifying consecutive years as release years (Black & Abrams 2003). Growth changes above 50% of the boundary line were interpreted as major releases, whereas growth changes between 20% and 49.9% of the boundary line were regarded as moderate releases.

We used data from our study plots to compute sugar maple and yellow birch boundary lines. However, for balsam fir, red maple and white spruce, the number of individuals in our sampling plots was too low to compute boundary lines. Thus, we enlarged our dataset by adding trees from other old-growth sites: 168 red maples from sites on till deposits located less than 50 km from the study area (Zhang et al. 2014), and 598 balsam fir and 123 white spruce trees from sites 270 km north of the study area on mesic clay deposits (Bergeron 2000). For balsam fir and white spruce, surface deposits are different from those of the study area, and this could have caused different growth responses to release. However, no other data was available to compute boundary lines.

We drew maps of tree locations using the spatstat R package (Baddeley & Turner 2005) and used the information in combination with growth release data to reconstruct gap formation between 1942 and 2001. The year 2001 was the last possible year to detect growth change according to equation [1]. We delineated gaps in four steps: (1) We mapped every living tree for three 20-year periods: 1942-1961, 1962-1981, 1982-2001. (2) We assumed that major growth releases indicated gap formation and subsequent filling at the focal tree location, whereas moderate releases indicated formation and subsequent filling of a nearby gap through lateral branch expansion (Runkle 2013; Blackburn et al. 2014). Hence, when mapping gaps, trees showing major growth releases were included inside gaps, whereas trees with moderate or without releases were used to delineate the margins of the extended gaps (App. S2). We measured the areas of extended gaps i.e. the area of the canopy gap together with the adjacent area extending to the bases of surrounding canopy trees (sensu Runkle 1981). Such a gap definition is assumed to better take into account the area affected by increased light intensity as a result of canopy disturbance (Runkle 1981). (3) For isolated trees showing a moderate or major release, a circle of 2.93 m radius was used to approximate minimum gap size (equal to 27 m^2). This radius corresponded to the mean distance between the stems of two neighboring trees for all trees measured within all sampling plots. This was justified by the fact that extended gaps were delimited by the stems of surrounding trees. For isolated trees located less than 5.8 m (equal to the diameter of isolated tree gap) from the edge of the plot (56, trees representing 14% of all gaps), we considered those gaps as incomplete and determined their size to be half the value used for isolated trees within the plot (i.e., 14 m^2 instead of 27 m2) (App. B). (4) When two trees with a moderate release were separated by less than 8 m (i.e., the diameter of a circle with an area equal to two times the area used as gap size for isolated trees (54 m^2)), the gap was delimited as a single circle with a diameter equal to the distance between the trees (App. B). For three adjoining trees with a distance of less than 10 m between the two farther trees (i.e., the diameter of a circle with an area equal to three times the area used as gap size for isolated trees (78 m^2)), the gap was delimited as a single circle with a diameter equal to the distance between the two farther trees (App. B).

Applying the above-mentioned rules sometimes resulted in two delineated gap polygons sharing a common segment (i.e., the two polygons were contiguous), leaving us with the options of keeping the two gap polygons separated or grouping them. Considering that this choice could have an effect on gap size distribution, we defined gaps using two different procedures when more than one gap delineation was possible: (1) gap number maximization (GNM), where contiguous gaps were considered separately; and (2) gap size maximization (GSM), where contiguous gaps were grouped. For both procedures, we computed the gap size distribution for each sampling plot and for three consecutive 20-year periods. We then computed annual disturbance rates (i.e., percent area disturbed (in m^2) per year) for each sampling plot and for each 20-year period by summing all gap sizes before dividing by the sampling plot area (0.25 ha) and by 20 years.

We used bootstrap Kolmogorov-Smirnov tests conducted with the Matching R package (Sekhon 2011) to compare gap size distributions between gap delineation procedures and among different time periods. We adjusted the $\alpha = 0.05$ threshold value to account for multiple (6) comparisons (Bonferonni adjustment: $\alpha = 0.00833$). We performed an ANOVA to compare disturbance rates between time periods.

We compared tree release records from the sampled stands (percent trees showing releases per unit time) to historical records of natural disturbances (i.e., blowdowns, wildfires, insect outbreaks, etc.). However, growth release peaks detected with the boundary line method can occur several years after disturbance (Copenheaver et al. 2014).

We used the vegan R package (version 2.0-10) to conduct a redundancy analysis (RDA) to explore the link between annual gap disturbance rate (dependent variable) and tree composition, stand age, and mean gap size (independent variables computed for each of the 11 plots for all three time periods combined). We used the importance value as the community data matrix. Importance values were calculated as the average of relative density (% number of trees) and relative dominance (% basal area) (Curtis & McIntosh 1951), to characterize species composition in each plot. We performed a Hellinger transformation on the importance value to reduce the weight of rare species (Legendre & Gallagher 2001; Borcard et al. 2011). Preliminary analysis showed no evidence that the relationship between species' importance values and the constraining matrix of environmental variables was not linear, thus justifying the use of RDA. We used permutations to test the significance of the RDA canonical axes (Borcard et al. 2011).

3.5 Results

3.5.1 Disturbance rate

The mean annual disturbance rate (percent area disturbed per year) for the entire studied period (1942-2001) and for all plots combined was 0.96 ± 0.51 % (minimum = 0.59%, maximum = 1.56%) (Table 3.1). Considering all plots and time periods separately, 67% of the annual disturbance rates were between 0.5 and 1.0% and only 15 % were higher than 1.5% (Table 3.1). Nevertheless, the mean annual disturbance rate for all plots combined did not differ significantly between time periods ($F = 0.35$, $P = 0.71$). Furthermore, mean disturbance rates of island (SP3, 4 and 5) and mainland (all other) plots were not significantly different ($F = 2.0$, $P = 0.17$).

We detected an average of 1.51 major growth release per tree per century (SD = 1.07) and 7.20 moderate releases per tree per century (SD = 3.06) in all plots combined. Over the last ca. 250 years, periods of simultaneous gap formation, as indicated by increased frequency of growth releases, were recorded in the 1790s, 1850s, 1910s, 1950s and 1980s (Fig. 3.2). Moderate growth releases were recorded continuously over the whole studied period, whereas major releases were mostly recorded in the 20th century (Fig. 3.2).

3.5.2 Gap size

Mean gap size was 39 ± 44 m2 with the GNM protocol and 42 ± 67 m^2 with the GSM protocol. Maximum gap size was higher with the GSM protocol than with the GNM protocol (750 m^2 vs 444 m^2 respectively) (App. C and App. D). The total gap size distribution (all three periods pooled) followed a power distribution

(GNM: y = 257.06 x-2.747, R^2 = 0.95; GSM: y = 122.96 x-2.015, R^2 = 0.87), with about 85% of the gaps smaller than 50 m^2 (Fig. 3.3). The use of two gap delineation procedures did not produce statistically different distributions (bootstraped Kolmogorov-Smirnov test between GNM and GSM: D = 0.02; P = 0.99). Gap size distributions also did not differ between time periods (App. E).

Table 3.1 Annual disturbance rates (as percent area disturbed per year) for three consecutive 20-year periods in each sampling plot (SP). Total disturbance rate is for the 60 years combined (1942-2001). Mean (± SD) disturbance rate for all SPs is also provided for each time period. Note 1: SD of the total mean disturbance rate was computed from all disturbance rates from all time periods. Note 2: The disturbance rate is the same regardless of the delimitation procedure used (gap number maximization (GNM) or gap size maximization (GSM)).

	1942-1961	1962-1981	1982-2001	mean disturbance rate
SP1	0.78	2.07	0.87	1.24
SP2	1.20	0.98	1.91	1.36
SP3	0.99	0.56	0.51	0.69
SP4	1.08	0.56	0.70	0.78
SP5	0.36	0.57	1.49	0.81
SP6	0.54	0.50	0.73	0.59
SP7	0.66	1.74	2.27	1.56
SP8	0.88	0.99	0.69	0.85
SP9	1.86	0.71	0.51	1.03
SP10	0.60	0.99	1.45	1.01
SP11	0.66	0.76	0.52	0.65
Mean±SD	0.87±0.41	0.95±0.51	1.06±0.62	0.96±0.51

Maximum crown radius was larger in deciduous species (mean = 5.1 m, 5.5 m and 5.9 m for yellow birch, sugar maple and red maple trees of 20-40 cm DBH respectively) than in coniferous species (mean = 2.5 m and 2.6 m for balsam fir and white spruce trees of 20-40 cm DBH, respectively).

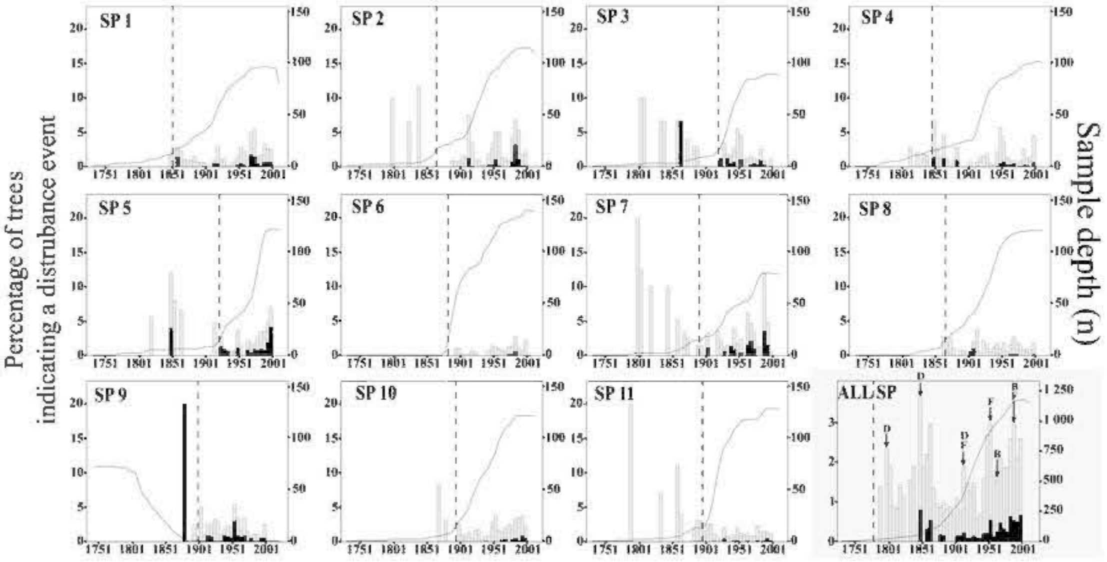

Figure 3.2 Percentage of trees, per 5-year interval, having recorded a major (black) or a moderate (grey) release for each of the 11 sampling plots and for all plots combined. Sample depth is indicated on the right-hand side y-axis. Vertical dashed lines indicate the threshold below which results were not interpreted (set at 15 individuals after Fraver & White (2005) and Firm et al. (2009)). Arrows indicate decades of known moderate disturbance events having occurred in the study area, as recorded in the literature (F = forest tent caterpillar; B = blowdown; D = drought).

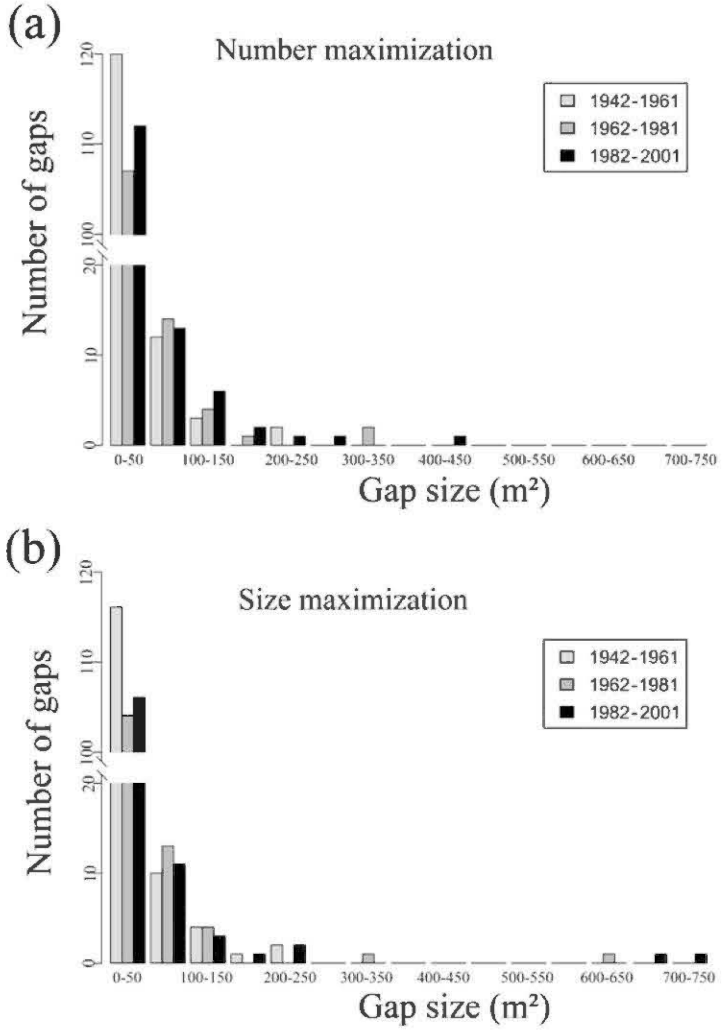

Figure 3.3 Number of gaps per 50 m² size class and time periods: 1942-1961 (light grey), 1962-1981 (dark grey), 1982-2001 (black) for the combined 11 sampling plots for the gap number maximization (a) and gap size maximization (b) procedures.

3.5.3 Effect of gap dynamics, DBH and stand age on species composition

The first RDA axis, linked to mean gap size, disturbance rate and stand age, explained 40% of the variability in species composition (*F* = 5.1; *P* = 0.03) (Fig. 3.4). Plots dominated by sugar maple (SP1, SP2, SP7, and SP9) tended to have larger gaps and higher disturbance rates than plots dominated by yellow birch and balsam fir (SP4, SP5, and SP6) (App. A and Fig. 3.4). Plots dominated by sugar maple were also slightly older (Fig. 3.4). The second RDA axis, with eastern hemlock and eastern white cedar at one end, and red oak and white spruce at the other end, was related to mean DBH of the dominant trees and mean gap size, but only explained 7% of the variability in species composition and was not significant (*F* = 0.9; *P* = 0.44).

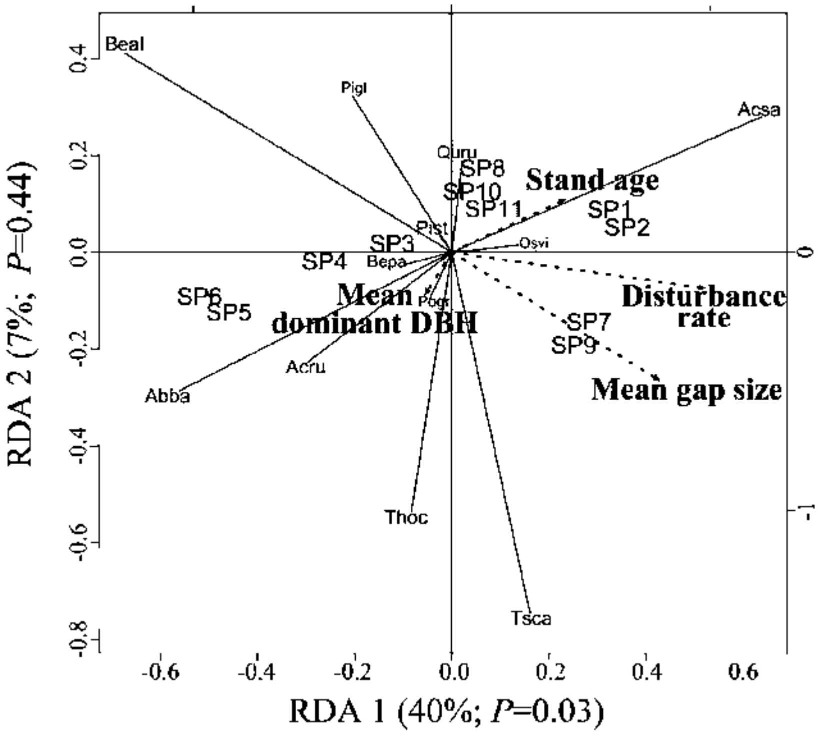

Figure 3.4 Redundancy analysis (RDA) relating species to disturbance rate using the gap number maximization procedure, mean gap size, mean DBH of dominant trees and plot age (stand age) for all sampling plots (SP). Acsa: *Acer saccharum* Marsh.; Beal: *Betula alleghanieusis* Britton; Abba: *Abies balsamea* (L.) Mill.; Tsca: *Tsuga canadeusis* (L.) Carr.; Acru: *Acer rubrum* L.; Pigl: *Picea glauca* (Moench) Voss; Thoc: *Thuja occidentalis* L.; Bepa: *Betula papyrifera* Marsh.; Osvi: *Ostrya virginiana* (Mill.) K. Koch; Quru: *Quercus rubra* L.; Pogr: *Populus graudidentata* Michx.; Pist: *Pinus strobus* L.

3.6 Discussion

3.6.1 Disturbance rate

The mean annual gap disturbance rate in our study area at the northern limit of the temperate deciduous forest (0.96%) was similar to gap disturbance rates found ca. 300-1200 km to the south in eastern USA (1%, Runkle 1982; 0.96%, Fraver et al. 2009). This finding does not support our hypothesis 1 that the disturbance rate would be higher at the northern limit of temperate deciduous forests than in more central locations of its range. The observed disturbance rate was more than 50% lower than that reported in the only other study conducted at the northern limit of temperate deciduous forests, but ca. 560 km to the east (2.2%, Payette et al. 1990). This study was based on a single plot located on top of a hill and was thus likely more prone to wind disturbance than our study sites located on flat landscapes. Nevertheless, variability in mean annual gap disturbance rate between the 11 plots we studied (0.66-2.27%) included the value recorded by Payette et al. (1990) and shows that our larger sample size enabled us to better represent natural variability.

Peaks in gap formation were recorded in the 1790s, 1850s, 1910s, 1950s and 1980s in our study area (Fig. 3.2), pointing towards synchronous tree mortality caused by large-scale biotic (e.g., insect outbreaks) and abiotic (e.g., blowdown or drought) disturbances. Indeed, forest tent caterpillar (*Malacosoma disstria* Hubner) outbreaks were recorded in our study area in the 1910s, 1950s and 1980s (Cooke & Lorenzetti 2006). A dendrochronological reconstruction revealed that severe droughts occurred in eastern Canada in 1794, 1849 and 1916 (Girardin et al. 2004). Intermediate blowdowns were recorded in the study area in 1962, 1983 and 2006 (Roy et al. 2010). We did not observe the 2006 blowdown as we sampled old-growth stands with no evidence of recent stand-replacing disturbances. The 1962 blowdown did not either correspond to a peak in gap formation, possibly because it was much smaller than the 1983 blowdown (557 ha in 1962 vs 3276 ha in 1983; Roy et al. 2010), resulting in reduced probability of detection.

3.6.2 Gap size

Mean gap size was smaller in our study area (39-42 m²) than in other temperate deciduous forests, e.g. in European beech forests (141-297 m²; Rugani et al. 2013; Hobi et al. 2015) and Japanese temperate forests dominated by *Quercus serrata* and *Fagus japonica* (70-190 m²; Yamamoto 1992a; Abe et al. 1995; Tanaka & Nakashizuka 1997). In our study area, 94% of gaps were smaller than 100 m², whereas this size class only represented 60-70% of the gaps reported for North American and European temperate deciduous forests (Runkle 1982; Petritan et al. 2013; Rugani et al. 2013; Hobi et al. 2015). Moreover, we measured extended gaps, whereas the aforementioned studies measured strict canopy gaps. In addition, maximum gap size was smaller in our study area (444-750 m²) than in other studies (800-1000 m²) (Yamamoto 1992b; Rugani et al. 2013; Hobi et al. 2015). A border effect could have led us to underestimate gap sizes. For example, the largest gap we recorded (750 m²) was located at the edge of a plot and could have actually been larger (App. C). Nevertheless, the size of our sampling plots was comparable to those reported in most other studies, thus warranting the comparison.

Mean crown size of the main deciduous species was similar in our study area and in more centrally-located temperate deciduous forests. Indeed, crown radiuses varied between 3.8 and 6 m for 20-40 cm DBH yellow birch, sugar maple and red maple trees sampled in Wisconsin (Webster & Lorimer (2005), whereas we measured mean radiuses of 5.1, 5.5 and 5.9 cm for the same species and DBH. Our second hypothesis suggesting that smaller gap size in the north could be explained by smaller crown size must thus be rejected. The choice between alternative gap identification procedures, one maximizing gap number and another one maximizing gap size, did not affect gap size distribution, indicating the robustness of the results.

Plots with high proportions of balsam fir and yellow birch tended to be younger and to have lower disturbance rates and smaller mean gap sizes compared to plots dominated by sugar maple (Fig. 3.4). Balsam fir is short-lived compared to sugar maple and yellow birch, and it has a smaller crown size compared to deciduous species. Moreover, balsam fir is frequently under the canopy in the sugar maple – yellow birch biome and is rarely a dominant species. Thus, the death of balsam fir trees occurs more often, but does not necessarily create canopy openings. Nevertheless, when balsam fir trees indeed create canopy gaps, they tend to be smaller than those created by deciduous trees (Kneeshaw & Bergeron 1998; Pham et al. 2004; Kneeshaw & Prévost 2007). This supports our hypothesis 3a that a higher proportion of conifers would lead to a lower disturbance rate, due to their smaller crowns and lower average height, and therefore refutes our alternative hypothesis 3b that a higher proportion of conifers could increase the disturbance rate. Our plots with balsam fir were dominated by yellow birch, and this could further explain their smaller gap size and lower disturbance rate. Indeed, wind-firmness is similar for yellow birch and sugar maple of small diameters (DBH < 15 cm), but for larger diameters, yellow birch is more wind-firm than sugar maple (Canham et al. 2001; Nolet et al. 2012). Wind-firmness could explain partial branch-by-branch dieback of yellow birch trees noted during fieldwork (personal observation), suggesting that old and large yellow birch trees do not create large canopy openings, but rather multiple small gaps caused by branch shedding.

3.7 Conclusion

Temperate forests at their northern distribution limit exhibited smaller and more numerous canopy gaps, but the same annual gap disturbance rate as temperate forests in the central part of their distribution range in north-eastern USA. This difference is important to consider in ecosystem-based forest management plans aiming to emulate natural gap disturbance regimes in tolerant hardwood stands of the northern part of the temperate deciduous forest, as smaller gaps favor shade tolerant species like sugar maple. Ecosystem-based forest management plans should rely more on selection cuts than in the central part of the biome where larger gaps can be emulated by larger cuts. Nevertheless, occasional larger-scale cuts (> 100 m^2) will still be necessary to reproduce the effects of episodic blowdown events and this could help maintain intermediate shade-tolerant species like yellow birch. However, the focus of the current study on mesic old-growth stands may question the generality of the observed patterns. Further work will be needed to document gap dynamics across different substrate types and stand ages.

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3.9 References

Abe, S., Masaki, T. & Nakashizuka, T. 1995. Factors influencing sapling composition in canopy gaps of a temperate deciduous forest. *Vegetatio* 120: 21-31.

Baddeley, A. & Turner, R. 2005. Spatstat: an R package for analyzing spatial point patterns. *Journal of Statistical Software* 12: 1-42.

Bégin, E. 2011. *Caractérisation des régimes de perturbations par le chablis et des vents extrèmes dans l'érablière à bouleau jaune du Québec.* Unpublished M.Sc. thesis, UQAM, Montréal, Qc.

Bergeron, Y. 2000. Species and stand dynamics in the mixed woods of Quebec's southern boreal forest. *Ecology* 81: 1500-1516.

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.

Blackburn, G.A., Abd Latif, Z. & Boyd, D.S. 2014. Forest disturbance and regeneration: a mosaic of discrete gap dynamics and open matrix regimes? *Journal of Vegetation Science* n/a-n/a.

Borcard, D., Gillet, F. & Legendre, P. 2011. *Numerical Ecology with R*. Springer, New-York.

Brown, J.L. 1981. *Les forêts du Témiscamingue, Québec: écologie et photo-interprétation*. Laboratoire d'écologie forestière, Université Laval.

Canham, C.D., Papaik, M.J. & Latty, E.F. 2001. Interspecific variation in susceptibility to windthrow as a function of tree size and storm severity for northern temperate tree species. *Canadian Journal of Forest Research* 31: 1-10.

Cooke, B.J. & Lorenzetti, F. 2006. The dynamics of forest tent caterpillar outbreaks in Québec, Canada. *Forest Ecology and Management* 226: 110-121.

Copenheaver, C.A., Seiler, J.R., Peterson, J.A., Evans, A.M., McVay, J.L. & White, J.H. 2014. Stadium Woods: A dendroecological analysis of an old-growth forest fragment on a university campus. *Dendrochronologia* 32: 62-70.

Curtis, J.T. & McIntosh, R.P. 1951. An upland forest continuum in the prairie-forest border region of Wisconsin. *Ecology* 32: 476-496.

D'Amato, A.W. & Orwig, D.A. 2008. Stand and landscape-level disturbance dynamics in old-growth forests in western Massachusetts. *Ecological Monographs* 78: 507-522.

Dahir, S.E. & Lorimer, C.G. 1996. Variation in canopy gap formation among developmental stages of northern hardwood stands. *Canadian Journal of Forest Research* 26: 1875-1892.

Després, T., Asselin, H., Doyon, F. & Bergeron, Y. 2014. Structural and spatial characteristics of old-growth temperate deciduous forests at their northern distribution limit. *Forest Science* 60: 871–880.

Drever, C.R., Messier, C., Bergeron, Y. & Doyon, F. 2006. Fire and canopy species composition in the Great Lakes–St. Lawrence forest of Témiscamingue, Québec. *Forest Ecology and Management* 231: 27-37.

Drobyshev, I.V. 2001. Effect of natural disturbances on the abundance of Norway spruce (*Picea abies* (L.) Karst.) regeneration in nemoral forests of the southern boreal zone. *Forest Ecology and Management* 140: 151-161.

Firm, D., Nagel, T.A. & Diaci, J. 2009. Disturbance history and dynamics of an old-growth mixed species mountain forest in the Slovenian Alps. *Forest Ecology and Management* 257: 1893-1901.

Fraver, S. & White, A.S. 2005. Disturbance dynamics of old-growth *Picea rubens* forests of northern Maine. *Journal of Vegetation Science* 16: 597-610.

Fraver, S., White, A.S. & Seymour, R.S. 2009. Natural disturbance in an old-growth landscape of northern Maine, USA. *Journal of Ecology* 97: 289-298.

Girardin, M.P., Tardif, J., Flannigan, M.D. & Bergeron, Y. 2004. Multicentury reconstruction of the Canadian Drought Code from eastern Canada and its relationship with paleoclimatic indices of atmospheric circulation. *Climate Dynamics* 23: 99-115.

Henry, J.D. & Swan, J.M.A. 1974. Reconstructing forest history from live and dead plant material- An approach to the study of forest succession in southwest New Hampshire. *Ecology* 55: 772-783.

Hobi, M.L., Commarmot, B. & Bugmann, H. 2015. Pattern and process in the largest primeval beech forest of Europe (Ukrainian Carpathians). *Journal of Vegetation Science* 26: 323-336.

Holmes, R.L. 1983. Computer-assisted quality control in tree-ring dating and measurement. *Tree-Ring Bulletin* 1983: 51-67.

Keeton, W.S., Kraft, C.E. & Warren, D.R. 2007. Mature and old-growth riparian forests: Structure, dynamics, and effects on adirondack stream habitats. *Ecological Applications* 17: 852-868.

Keeton, W.S., Whitman, A.A., McGee, G.C. & Goodale, C.L. 2011. Late-successional biomass development in northern hardwood-conifer forests of the northeastern United States. *Forest Science* 57: 489-505.

Khakimulina, T., Fraver, S. & Drobyshev, I. 2015. Mixed-severity natural disturbance regime dominates in an old-growth Norway spruce forest of northwest Russia. *Journal of Vegetation Science* n/a-n/a.

Kneeshaw, D.D. & Bergeron, Y. 1998. Canopy gap characteristics and tree replacement in the Southeastern boreal forest. *Ecology* 79: 783-794.

Kneeshaw, D.D. & Prévost, M. 2007. Natural canopy gap disturbances and their role in maintaining mixed-species forests of central Quebec, Canada. *Canadian Journal of Forest Research* 37: 1534-1544.

Leak, W.B. 1987. Comparison of standard and actual tree-growth trends for deciduous and coniferous species in New Hampshire. *Canadian Journal of Forest Research* 17: 1297-1300.

Legendre, P. & Gallagher, E. 2001. Ecologically meaningful transformations for ordination of species data. *Oecologia* 129: 271-280.

Lorimer, C.G., Dahir, S.E. & Singer, M.T. 1999. Frequency of partial and missing rings in *Acer saccharum* in relation to canopy position and growth rate. *Plant Ecology* 143: 189-202.

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.

Nolet, P., Doyon, F. & Bouffard, D. 2012. Predicting stem windthrow probability in a northern hardwood forest using a wind intensity bio-indicator approach. *Open Journal of Forestry* 2: 77.

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

Payette, S., Filion, L. & Delwaide, A. 1990. Disturbance regime of a cold temperate forest as deduced from tree-ring patterns: the Tantaré Ecological Reserve, Quebec. *Canadian Journal of Forest Research* 20: 1228-1241.

Peterson, C.J., Krueger, L.M., Royo, A.A., Stark, S. & Carson, W.P. 2013. Disturbance size and severity covary in small and mid-size wind disturbances in Pennsylvania northern hardwoods forests. *Forest Ecology and Management* 302: 273-279.

Petritan, A.M., Nuske, R.S., Petritan, I.C. & Tudose, N.C. 2013. Gap disturbance patterns in an old-growth sessile oak (*Quercus petraea* L.)–European beech (*Fagus sylvatica* L.) forest remnant in the Carpathian Mountains, Romania. *Forest Ecology and Management* 308: 67-75.

Pham, A.T., Grandpré, L.D., Gauthier, S. & Bergeron, Y. 2004. Gap dynamics and replacement patterns in gaps of the northeastern boreal forest of Quebec. *Canadian Journal of Forest Research* 34: 353-364.

Purves, D.W. 2009. The demography of range boundaries versus range cores in eastern US tree species. *Proceedings: Biological Sciences* 276: 1477-1484.

Rankin, W.T. & Tramer, E.J. 2002. The gap dynamics of canopy trees of a *Tsuga canadensis* forest community. *Northeastern Naturalist* 9: 391-406.

Robitaille, A. & Saucier, J.P. 1998. *Paysages régionaux du Québec méridional*. Les publications du Québec, Québec.

Roy, M.-E., Doyon, F., Nolet, P. & Bouffard D. 2010. *Historique des perturbations et réponse de la végétation forestière dans l'érablière à bouleau jaune de l'ouest au Témiscamingue au cours du 20ième siècle*. Institut québécois d'aménagement de la forêt feuillue, Ripon, Québec.

Rugani, T., Diaci, J. & Hladnik, D. 2013. Gap dynamics and structure of two old-growth beech forest remnants in Slovenia. *PLoS ONE* 8: e52641.

Runkle, J.R. 1981. Gap regeneration in some old-growth forests of the Eastern United States. *Ecology* 62: 1041-1051.

Runkle, J.R. 1982. Patterns of disturbance in some old-growth mesic forests of Eastern North America. *Ecology* 63: 1533-1546.

Runkle, J.R. 2013. Thirty two years of change in an old-growth Ohio beech-maple forest. *Ecology* 94: 1165-1175

Sekhon, J.C. 2011. Multivariate and propensity score matching software with automated balance optimization: The matching package for R. *Journal of Statistical Software* 42: 1-52.

Seymour, R.S., White, A.S. & de Maynadier, P.G. 2002. Natural disturbance regimes in northeastern North America - evaluating silvicultural systems using natural scales and frequencies. *Forest Ecology and Management* 155: 357-367.

Stokes, M.A. & Smiley, T.L. 1968. *An introduction to tree-ring dating*. University of Chicago Press, Chicago, USA.

Tanaka, H. & Nakashizuka, T. 1997. Fifteen years of canopy dynamics analyzed by aerial photographs in a temperate deciduous forest, Japan. *Ecology* 78: 612-620.

Tyrrell, L.E. & Crow, T.R. 1994. Structural characteristics of old-growth hemlock-hardwood forests in relation to age. *Ecology* 75: 370-386.

Villeneuve, N. 1994. *Les écosystmes forestiers exceptionnels au Québec*. Gouvernement du Québec.

Villeneuve, N. & Brisson, J. 2003. Old-growth forests in the temperate deciduous zone of Quebec: Identification and evaluation for conservation and research purposes. *The Forestry Chronicle* 79: 559-569.

Webster, C.R. & Lorimer, C.G. 2005. Minimum opening sizes for canopy recruitment of midtolerant tree species: A retrospective approach. *Ecological Applications* 15: 1245-1262.

Westveld, M. 1956. Natural Forest Vegetation Zones of New England. *Journal of Forestry* 54: 332-338.

Yamamoto, S.-I. 1992a. Gap characteristics and gap regeneration in primary evergreen broad-leaved forests of western Japan. *Botanical Magazine-Tokyo* 105: 29-45.

Yamamoto, S.I. 1992b. The gap theory in forest dynamics. *Botanical Magazine-Tokyo* 105: 375-383.

Zeibig, A., Diaci, J. & Wagner, S. 2005. Gap disturbance patterns of a *Fagus sylvatica* virgin forest remnant in the mountain vegetation belt of Slovenia. *Forest Snow and Landscape Research* 79: 69-80.

Zhang, Y., Bergeron, Y., Zhao, X.-H. & Drobyshev, I. 2014. Stand history is more important than climate in controlling red maple (*Acer rubrum* L.) growth at its northern distribution limit in western Quebec, Canada. *Journal of Plant Ecology*.

CHAPITRE IV

CAN SUSTAIN OLD-GROWTH ATTRIBUTES WHILE MANAGING NORTHERN DECIDUOUS FOREST?

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Article à soumettre

4.1 Abstract

Northern temperate deciduous forests are characterized by a natural disturbance regime dominated by small canopy gaps and, to a lesser extent, partial windthrow. Large-scale catastrophic disturbances are rare, and thus old-growth stands likely represented a high proportion of preindustrial landscapes. We used simulation modelling based on empirical data to assess the relationship between old-growth forest attributes (i.e., species composition, dead biomass and biomass of trees > 200 years-old) and various disturbance regimes involving different frequency and intensity of natural (gaps and windthrow) and anthropogenic (partial cutting) disturbances using LANDIS-II. A limited effect of partial cutting on old-growth attributes was observed, especially with a partial cutting rate > 0.6 % per year, resulting in a 44% decrease of the biomass of old trees (> 200 years-old) and a 10.2% deficit of dead biomass, compared to scenarios with natural disturbances only. However, the species composition did not differ between scenarios with and without partial cutting. These results suggest that specific retention measures of older (larger) live and dead trees of all sizes should be applied to favor the preservation of old-growth attributes at the landscape scale.

4.2 Résumé

Les forêts tempérées feuillues nordiques sont caractérisées par un régime de perturbations naturelles dominé par des trouées de petites tailles et dans une moindre mesure des chablis partiels. Les perturbations catastrophiques de grande ampleur sont rares, et donc les paysages préindustriels devaient être composés principalement de vieux peuplements. Nous avons utilisé un modèle basé sur des données empiriques pour simuler la relation entre les attributs de vieille forêt (c.-à-d., composition spécifiques, biomasse morte et biomasse des arbres plus vieux que 200 ans) et différents régimes de perturbations naturelles (trouées et chablis) et anthropiques (coupe partielle) à plusieurs fréquences et intensités à l'aide de LANDIS-II. Un effet limité des coupes partielles sur les attributs de vieille forêt a été observé, et plus spécifiquement lorsque le taux de coupe partielle était supérieur à 0,6% par an, ce qui résultait en une perte de 44% de la biomasse de vieux arbres (> 200 ans) et en un déficit de 10,2% de biomasse morte, comparativement aux scénarios avec uniquement des perturbations naturelles. Cependant, la composition spécifique ne différait pas entre les scénarios avec et sans coupe partielle. Ces résultats suggèrent qu'une mesure particulière de rétention de vieux arbres vivants (soit plus large) et de bois mort de toutes tailles devrait être appliquée pour favoriser la préservation des attributs de vieille forêt à l'échelle du paysage.

4.3 Introduction

Large-scale catastrophic natural disturbances are rare in temperate deciduous forests, and old-growth forests represented a high proportion of the preindustrial landscape (Frelich & Lorimer 1991; Burrascano et al. 2013). Sustainable management of temperate deciduous forests is thus particularly challenging, if one goal is to maintain a proportion of old-growth forests in the landscape within the limits of the preindustrial range of variability (Burton et al. 1999; Bauhus et al. 2009; Wirth et al. 2009). Old-growth temperate deciduous forests are generally characterized by a wide range of tree sizes, an heterogeneous spatial organization, and high amounts of necromass mostly composed of coarse woody debris (Burrascano et al. 2013; Després et al. 2014). Old-growth forest attributes are known to contribute to maintaining biodiversity as they provide unique micro-habitats for a wide variety of organisms like bryophytes, wildlife and insects (Berg et al. 1994; Ódor & Standovár 2001; Burrascano et al. 2008). Without specifically designed practices, managed forests are likely to lose old-growth attributes in the long term (Hale et al. 1999; McGee et al. 1999; Spies 2004).

Ecosystem-based forest management reproduces the spatiotemporal patterns created by natural disturbances (Johnson et al. 1995; Gauthier et al. 2009). As each forest biome has a distinct natural disturbance regime, implementing ecosystem-based forest management requires a specific set of harvesting methods to reproduce the imprint left on the landscape by the local natural disturbance regime (Mladenoff & Pastor 1993). At the northern distribution limit of temperate deciduous forests in eastern North America, the natural disturbance regime is mainly characterized by canopy gaps and partial windthrow (Payette et al. 1990; Seymour et al. 2002; Bégin 2011; Després et al. under review). Selection cutting is generally used to emulate gaps (Angers et al. 2005), as it focuses on the removal of large-diameter dominant trees, which are usually responsible for gap creation (Keeton 2006). When added to gaps, intermediate disturbances such as partial windthrow can modify the forest structure by broadening the disturbance gradient and by leaving high densities of residual living trees (Woods 2004; Splechtna et al. 2005; Keeton et al. 2011; Cowden et al. 2014). Large canopy openings created by intermediate disturbances favor the recruitment of intermediate shade-tolerant species (Kern et al. 2013), such as yellow birch (*Betula alleghaniensis* Britton) and red oak (*Quercus rubra* L.) (Larsen & Johnson 1998; Canham et al. 1999; Hanson & Lorimer 2007; Beaudet et al. 2011).

Forest management using partial cutting could help sustain some old-growth forest attributes such as species composition, age structure and amount of dead biomass (Bauhus et al. 2009). Indeed, partial windthrow and partial cutting both target large dominant trees (Nolet et al. 2012; ministère des Ressources naturelles 2013). However, the end result will be markedly different if partial cutting substitutes windthrow, or if it adds to it. If partial cutting is added to windthrow, the total disturbance rate will be higher, which might result in a loss of old-growth forests.

In this study, we used forest landscape modeling to assess the effect of combining different disturbance regimes in the maintenance of old-growth forest attributes (i.e., species composition, age structure and amount of dead biomass). We modeled different scenarios representing combinations of small- and medium-scale natural disturbances and forest harvesting. We hypothesized that partial cutting can substitute windthrow up to a certain threshold, passed which the combined disturbance regime (cutting + windthrow) will cause a loss in old-growth forest attributes (Angers et al. 2005; Cimon-Morin et al. 2010). We also hypothesized that intermediate disturbances create conditions leading to the maintenance of intermediate shade-tolerant species in the landscape (Woods 2004).

4.4 Material and methods

4.4.1 Study area

The study area is located within the sugar maple (*Acer saccharum* Marsh.) – yellow birch bioclimatic domain of western Quebec, Canada (46°70' – 47°22' N, 78°49' – 78°89' W), characterized by humo-ferric podzols (Brown 1981). The most abundant forest community in the area is sugar maple – yellow birch, with fewer occurrences of yellow birch – balsam fir (*Abies balsamea* (L.) Mill.) or hemlock (*Tsuga canadensis* (L.) Carr.), and balsam fir – eastern white cedar (*Thuja occidentalis* L.) communities (Brown 1981). Climate is continental with cold winters and warm summers. Mean annual temperature is 4.2°C and total annual precipitation is 1044 mm with an average of 29% falling as snow (Environnement Canada 2011).

Small canopy openings (mean size 39 m^2) created by the death of one or a few trees dominate the natural disturbance regime in the study area (Després et al. under review). Partial windthrow occurs from time to time (mean size: 8 ha; max size: 200 ha), with an estimated cycle between 15 and 300 years (Bégin 2011). Large-scale catastrophic disturbances are rare, with fire cycle estimated at several hundred years for the post-settlement period (Drever et al. 2006) and a few millennia for catastrophic windthrow (Bégin 2011).

4.4.2 Experimental design and landscape initialization

We used LANDIS-II (version 6.0) to model the forest landscape (Scheller et al. 2007). LANDIS-II is a dynamic, spatially explicit model based on life history attributes (e.g. Steenberg et al. 2011; Sturtevant et al. 2012; Duveneck et al. 2014). It simulates cohort succession, seed dispersal, natural disturbances, harvesting, growth and mortality. The landscape is subdivided into cells that interact with each other within "ecoregions" of homogeneous climate and soil conditions. We simulated a simplified landscape with only one site condition based on the most common site type found in the study area, which is mesic humo-ferric podzols (Brown 1981). We created a 10 x 10 km map (100 km^2), subdivided into 0.25 ha cells (25 x 25 m). Initial forest conditions (cohort age and species composition) were assigned to each cell by randomly drawing from field measurements obtained from 11 old-growth 0.25 ha plots sampled in the Témiscamingue area (Després et al. 2014). Each of those 11 plots was subdivided into 4 subplots, for a total of 44 possible initial conditions. Simulations were ran on a 600-year horizon to encompass at least one life cycle for every species (App. F), with outputs compiled and reported every 10 years.

We simulated three different disturbance regimes: (1) gaps only; (2) gaps and partial windthrow; and (3) gaps, partial windthrow and partial cutting. To do so, we used the Biomass Succession extension (version 3.1) (Scheller & Mladenoff 2004), the Base Wind extension (version 2.0) (Scheller & Mladenoff 2004) and the Biomass Harvest extension (version 2.1) (Gustafson et al. 2000) of LANDIS-II. Partial windthrow and partial cutting were simulated using different frequency/severity combinations along a gradient of landscape turnover rates, ending up with 40 scenarios, replicated 3 times each (Table 4.1). Després et al. (under review) determined the annual disturbance rate by gap dynamics to be 0.96 ± 0.51% in the study area. We thus targeted three different disturbance rates (0.5%, 1% and 1.5% per year) to evaluate a range of forest management systems as suggested in a previous study (Seymour et al. 2002). We tested the European and American selection cutting systems, and two different shelterwood cutting systems (with 3 and 4 cohorts). Catastrophic disturbances like wildfire and catastrophic windthrow were not simulated because they have a very long cycle in our study area (Grenier et al. 2005; Drever et al. 2006). Model description and parameter estimations are described in the supplementary material (App. G and App. H).

Gap dynamics – Because LANDIS-II is not specifically designed to generate gaps, we built a prescription using the Biomass Harvest extension to simulate gap dynamics. The entire studied landscape was considered as one management area to make sure that all cells could be affected by gap disturbances at any time step, according to the following scheme. First, for each species, four equivalent age classes (juvenile, young, mature, old) were created by dividing the species longevity by four. Then, every 10 years, 19.2% of the biomass of the oldest class was removed, as well as 9.6% of the biomass of the young and mature classes, so that 9.6% of all cells were disturbed per decade (Table 4.1), equivalent to a 0.96% annual gap disturbance rate

Table 4.1 Disturbance regimes modeled with LANDIS-II. Each scenario was replicated three times.

Disturbance regime	*Disturbance rate Targeted (Realized) (% area disturbed per decade)*			*Severity/ type*	*Rotation period (years)*	*Specifications*
Gaps		9.6 (4.5)			10	9.6% of the 2nd and 3rd quarter of maximum age + 19.2% of the 4th quarter
Gaps + partial windthrow		9.6 (9.6)		Low	15	5-20% of the oldest cohort
		9.6 (9.5)		Moderate	75	21-40% of the oldest cohort
		9.6 (9.5)		High	300	40-60% of the oldest cohort
Gaps + partial windthrow (for all three severities) + partial cutting	5 (2.5)	10 (10)	15 (12)	European selection cutting	10	Trees larger than the minimum harvest size
	10% (5)	20 (10)	30 (12.3)	American selection cutting	20	Trees larger than the minimum harvest size
	15 (11)	30 (18)	45 (25.2)	Shelterwood cutting (4 cohorts)	30	Trees larger than the minimum harvest size
	20 (14.6)	40 (25.6)	60 (37.2)	Shelterwood cutting (3 cohorts)	40	Trees larger than the minimum harvest size

(Després et al. under review). The youngest age class (juvenile) was always left undisturbed in the gaps-only scenario because gaps mostly affect older trees.

Partial windthrow – We simulated three different partial windthrow regimes, with rotation periods of 15, 75 and 300 years (Table 4.1), corresponding to the lower, middle and upper values of the range of partial windthrow cycles recorded in the study area (Roy et al. 2010; Bégin 2011). The three scenarios used the same event size distribution with a minimum size of 1 pixel (625 m²), a maximum size of 200 ha and a mean size of 8 ha (Bégin 2011). However, severity varied to maintain the same annual disturbance rate in the three different partial windthrow regimes (Table 4.1). Partial windthrow was set to mostly affect older cohorts (Seymour et al. 2002).

Partial cut – Partial cutting was generated using the Biomass Harvest extension V2.1. To represent a variety of silvicultural options, we simulated four different rotation periods: 10, 20, 30 and 40 years. They were applied in combination with three harvest levels in order to result, once combined, into three targeted annual disturbance rates: 0.5 %, 1.0% and 1.5 % (Table 4.1). Based on current forestry practices in Quebec, a tree needs to have a minimum of 20 cm of diameter at breast height (dbh) to be selected for partial cutting. However, as tree size is not used in LANDIS-II per se, we used field data to develop a relationship between tree age and diameter, combining species by shade tolerance class (tolerant, mid-tolerant, intolerant), and then converted diameter to age for each species (data not shown). For each partial cutting scenario, all three partial windthrow scenarios were tested.

As the Biomass Harvest extension in LANDIS-II can only harvest once per time step in a given cell, partial cuts and gaps were combined in a sole prescription by adding their respective biomass removal directives.

4.4.3 Dead biomass

LANDIS-II monitors the dead biomass left on site. However, as the main harvesting method applied to tolerant hardwood stands is cut-to-length (Bolton & D'Amato 2011; Lussier & Meek 2014), an important portion of the biomass is left on the cutblock and is not exported from the site (Tritton et al. 1987; Fraver et al. 2002). Indeed, in average 50 % of the living material composed of leaves, bark, branches and limbs is left on site after harvesting (Thiffault et al. 2014). Therefore, to more accurately simulate dead biomass generated under the partial cutting scenarios, only half of the total amount of biomass harvested was considered exported from the cell.

4.4.4 Data analysis

We performed three replicates of each scenario, but differences between replicates were very small for all studied variables (see App. I). Therefore, we used the means of the three replicates in data analyses. We compiled LANDIS-II map outputs using the raster library in R (R Core Team 2015). At each time step, we computed dead biomass deficit, which we defined as the difference between the mean dead biomass in the scenarios with natural disturbances only (i.e., gaps and gaps and partial windthrow) and in the scenarios with partial cutting.

4.5 Results

4.5.1 Species composition

Total aboveground tree biomass for the entire landscape varied little between scenarios, showing a cyclic pattern that tended to stabilize around 140 T/ha towards the end of simulation time (Fig. 4.1). Final composition after 600 years did not differ between scenario families (gaps; gaps + partial windthrow; gaps + partial windthrow + partial cutting). Indeed, the relative importance of the two dominant species in the initial landscape, sugar maple and yellow birch, was maintained in all scenarios through the simulation horizon, these species representing respectively 43% and 26% of the total biomass (Fig. 4.2). The two shade-intolerant species, white birch and large-toothed aspen, were marginal in the initial landscape and disappeared over simulation time in all scenarios. White pine was also marginal in the initial landscape and either disappeared or remained at a marginal level (0.001 % of the total biomass). The abundance of eastern hemlock, white spruce and red oak increased with simulation time in all scenarios. The trend was more pronounced for red oak, a mid-tolerant species. Biomass of red maple and balsam fir remained more or less stable during simulation time for all scenarios.

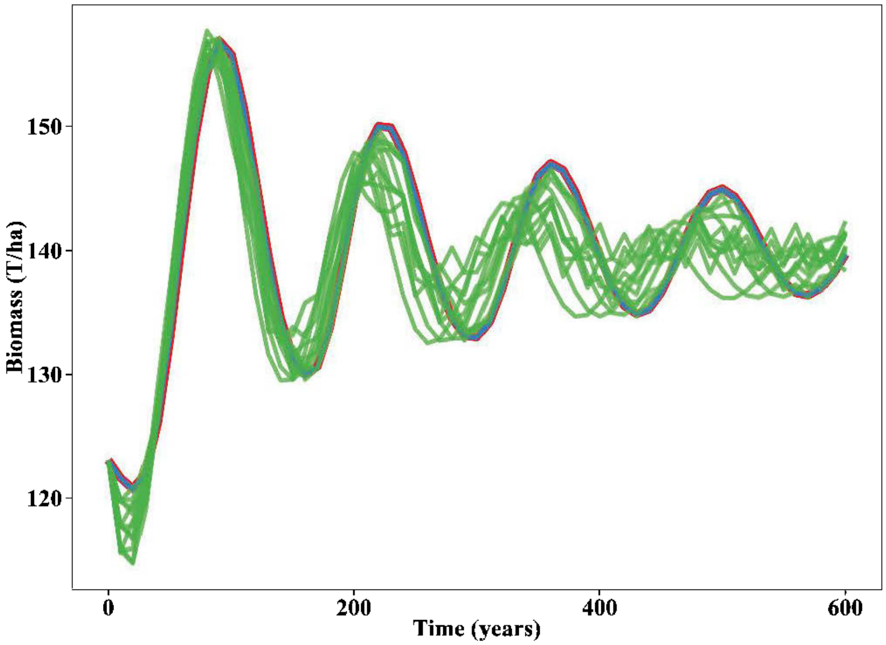

Figure 4.1 Total aboveground tree biomass (T/ha) over 600 years of simulation for each of the 40 scenarios grouped by disturbance type: gaps only (red), gaps and partial windthrow (blue), and gaps, partial windthrow and partial cutting (green).

4.5.2 Age structure

Trees older than 200 years only represented a mean of 0.4% (SD = 0.16) of the total biomass in all scenarios, as averaged over the last 100 years of simulation (Fig. 4.3). However, in the partial cutting scenarios, biomass of trees older than 200 years was significantly higher for scenarios with harvesting rates ≤ 0.60% per year (0.64 ± 15 T/ha), compared to scenarios with harvesting rates > 0.60% per year (0.28 ± 0.09 T/ha) (t = 5.5, df = 11, p < 0.001) (Fig. 4.4).

In the scenarios with partial cutting, the biomass of mature trees (> 50 years-old, all species combined) averaged over the last 100 years of simulation time decreased with increasing disturbance rate (Fig. 4.5a). The biomass of young trees (≤ 50 years, all species combined) showed the opposite trend and increased with increasing disturbance rate (Fig. 4.5b).

The relative proportion of the total biomass for mid-tolerant species was similar in the scenarios without disturbance, with gaps only, and with gaps and partial windthrow (Fig. 4.6), and showed a cyclical pattern. Mid-tolerant species between 76 and 200 years-old represented 65% of the total biomass of mid-tolerant species in the last 100 years of simulation. Regeneration (0-25 years-old) was constant in all scenarios, averaging about 6% over the last 100 years of simulation. Old trees (> 200 years-old) represented 0.1% and 0.06% of the total biomass for yellow birch and for red oak, respectively, in all scenarios for the last 100 years of simulation (Fig. 4.6).

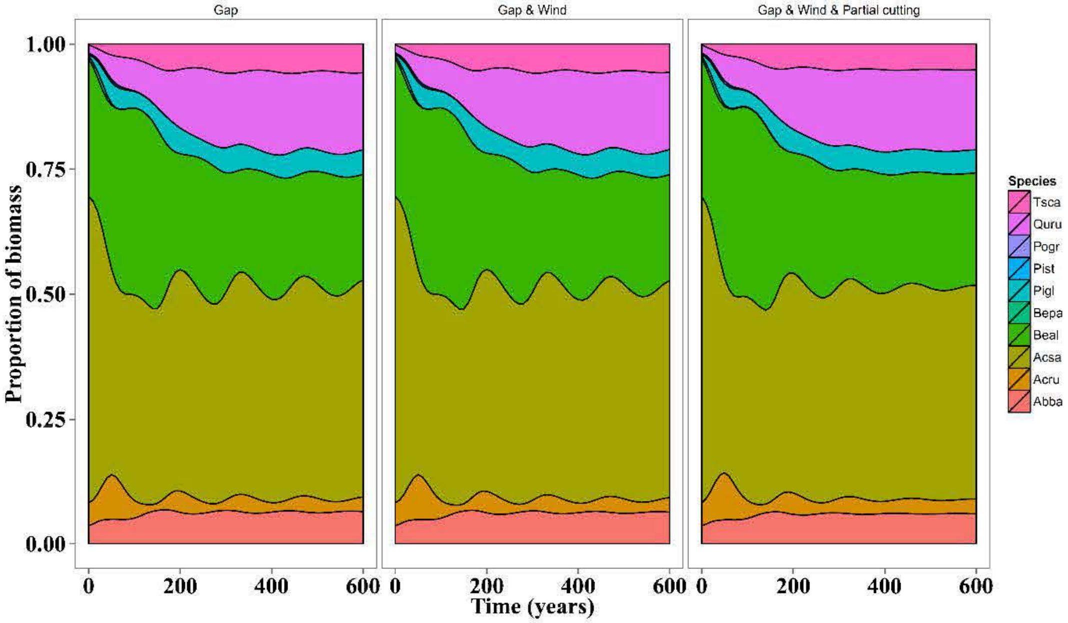

Figure 4. 2. Relative proportion of the total biomass for all tree species sampled during 600 years of simulation for each disturbance type: gaps only, gaps + partial windthrow (mean of the 3 scenarios), and gaps + partial windthrow + partial cutting (mean of the 36 scenarios). Species abbreviations are: Abba: *Abies balsamea* (L.) Mill; Acru: *Acer rubrum* L.; Acsa: *Acer saccharum* Marsh.; Beal: *Betula alleghaniensis* Britton; Bepa: *Betula papyrifera* Marsh; Pogr: *Populus grandidentata* Michx.; Pigl: *Picea glauca* (Moench) Voss; Pist: *Pinus strobus* L.; Quru: *Quercus rubra* L.; Tsca: *Tsuga canadensis* (L.) Carr.

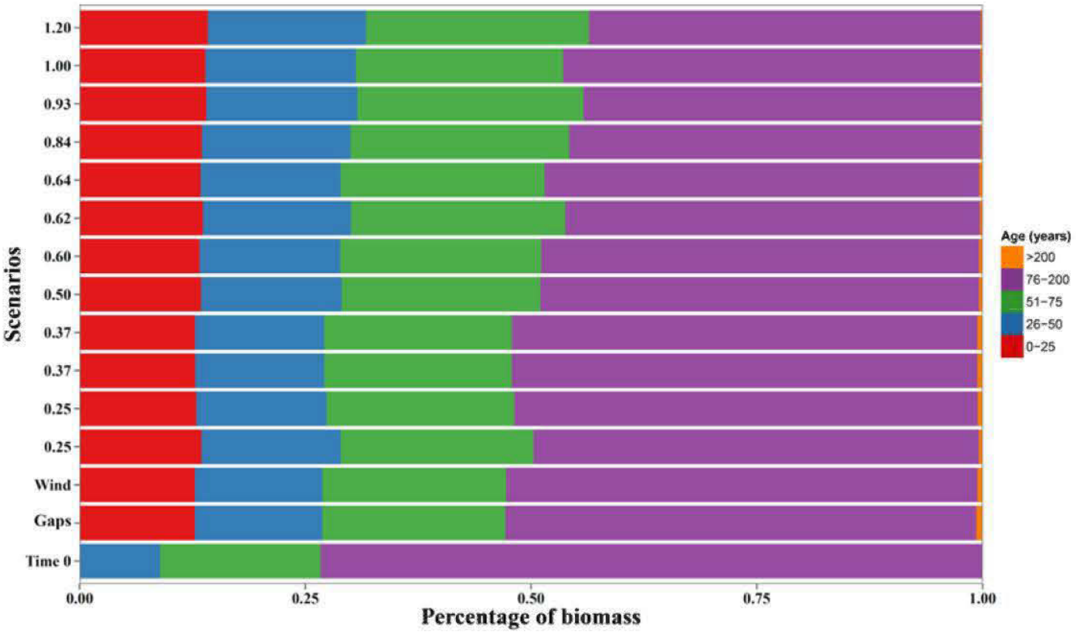

Figure 4.3 Percentage of the total biomass by age class at initial simulation time (Time 0) and the mean of the last 100 years of simulation for the different scenarios: gaps only (gaps), gaps + partial windthrow (wind), and gaps + partial windthrow + partial cutting, from lowest to highest realized disturbance rate (0.25% to 1.20%). The mean of the three partial windthrow rotations (15, 75 and 300 years) was computed for the partial windthrow and partial cutting scenarios.

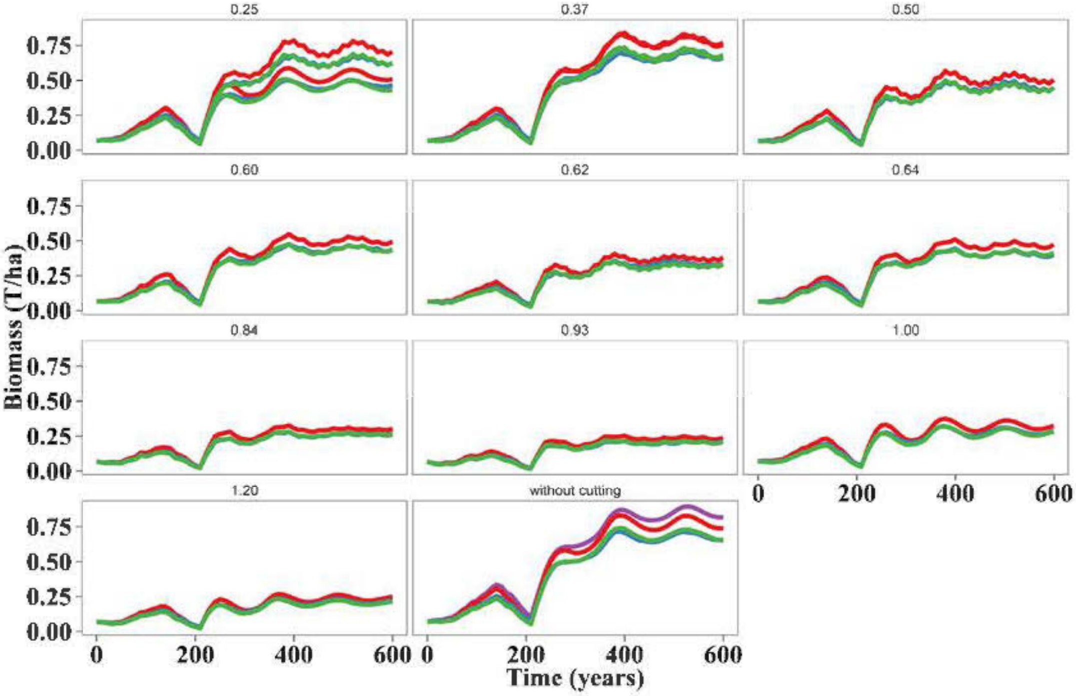

Figure 4. 4 Biomass of trees older than 200 years during 600 years of simulation time for scenarios with and without partial cutting. Ten different disturbance rates are shown for the partial cutting scenarios (from 0.25 to 1.20% per year) and the three windthrow rotation periods are shown with different colors: 15 years in red, 75 years in green, 300 years in blue. The gaps only scenario is shown in purple.

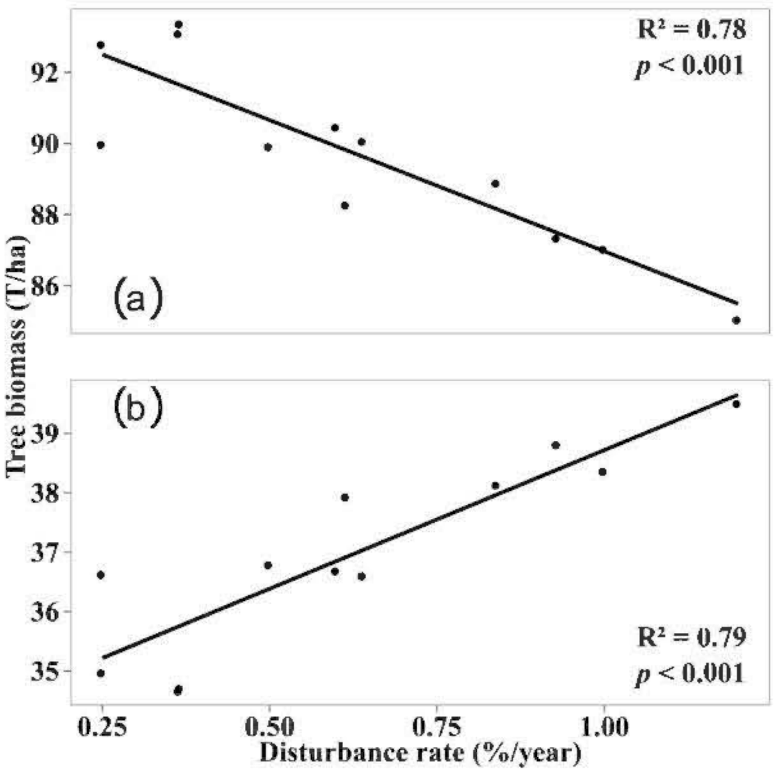

Figure 4.5 . Biomass of mature trees (> 50 years) (a) and young trees (≤ 50 years) (b) relative to disturbance rate for the 12 scenarios with partial cutting and a partial windthrow rotation of 75 years.

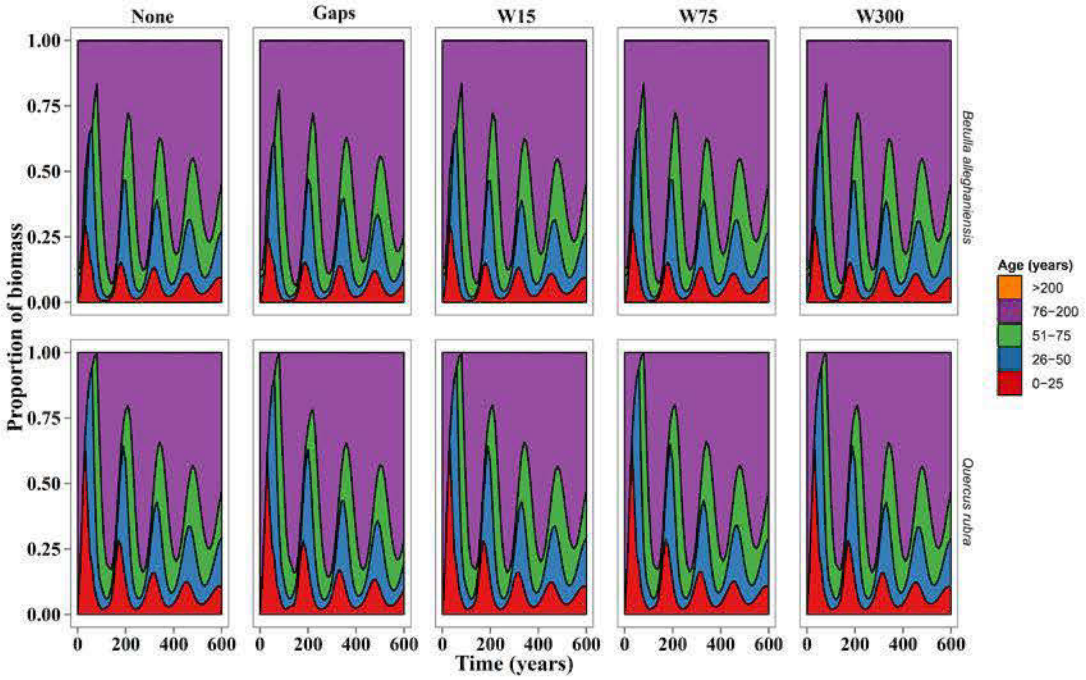

Figure 4.6 Relative proportion of the total biomass for 5 age classes during 600 years of simulation for two intermediate shade-tolerant species (*Betula alleghaniensis* and *Quercus rubra*) according to 5 different scenarios: no disturbance (none), gaps only (gaps), and gaps + partial windthrow with rotation periods of 15, 75 and 300 years (W15, W75 and W300).

4.5.3 Dead biomass

All partial cutting scenarios generally showed a deficit of dead biomass compared to scenarios without harvesting (Fig. 4.7). The mean dead biomass deficit over the last 100 years of simulation across all partial cutting scenarios was 10.2 ± 2.2%. However, while the deficit was constant during simulation time for some scenarios (e.g., 0.50 and 0.84% realized disturbance rate), the pattern was more cyclic for other scenarios, sometimes even showing brief excesses of dead biomass (e.g., 0.64 and 1.00% realized disturbance rate).

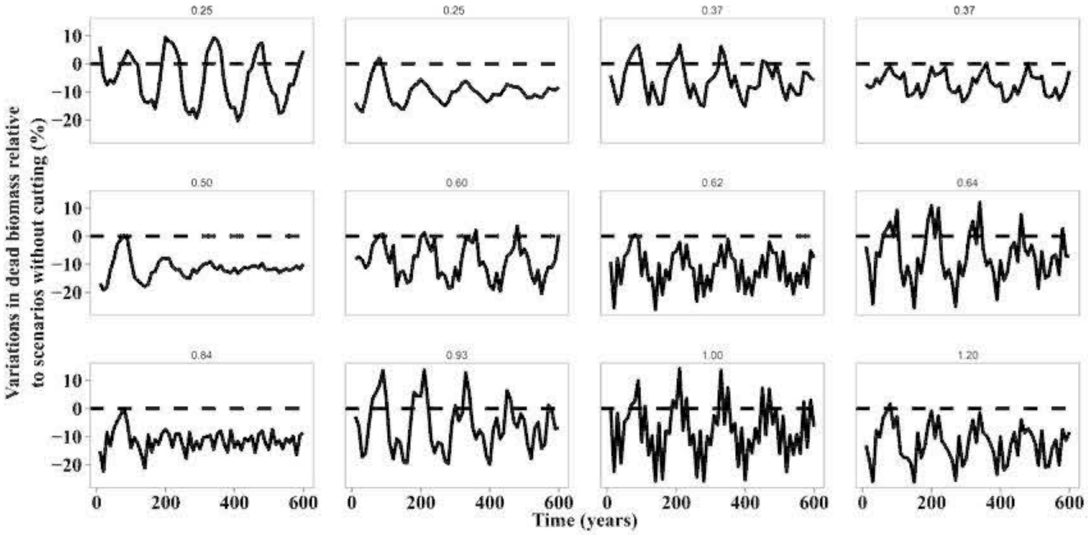

Figure 4. 7 Dead biomass variation (in percentage) during 600 years of simulation for all partial cutting scenarios (sorted by % annual disturbance rate), relative to mean dead biomass in all scenarios without cutting (i.e., mean of gap only and mean of gap + three partial winthrow scenarios) (dashed line). For partial cutting scenarios, the mean of the three partial windthrow rotations (15, 75 and 300 years) was computed (continuous line).

4.6 Discussion

It was impossible to reach the targeted disturbance rate in all scenarios (Table 4.1). For many cells, the low biomass of old trees (> 200 years-old) likely limited the ability of the model to reach the harvest level prescribed to generate gaps and partial cutting (Table 4.1 and Fig. 4.2). Thus, while the range of realized disturbance rates is comparable to what was parameterized, the values are lower (0.25-1.2% per year, compared to 0.5-1.5% per year). That being said, mean total aboveground biomass for all scenarios (140 T/ha) is similar to the aboveground biomass measured in the field (143 T/ha, Fig. H.1), but lower than values recorded in more southerly located old-growth temperate deciduous forests in eastern North America (up to 370 T/ha; Muller & Liu 1991; Brown et al. 1997).

4.6.1 Maintaining old-growth forest attributes with partial cutting

The biomass of old trees (> 200 years-old) was more than two times higher in the partial cutting scenarios with low harvesting rates (0.25-0.60% per year), compared to those with higher harvesting rates (0.60-1.20% per year). This confirms our hypothesis that partial cutting can substitute windthrow up to a certain threshold which is here a partial cutting rate of 0.60 % per year. Partial cutting scenarios with low harvesting rates (≤ 0.60% per year) had a limited effect on the forest structure and seemed to substitute to gaps and partial windthrow. However, partial cutting with higher harvesting rates (> 0.60 to 1.20 % per year) had an effect on the forest structure, as they were, at least partly, added to natural disturbances. Thus, forests harvested more intensively are more likely to lose live-tree structural complexity which is an important old-growth attribute (McGee et al. 1999; Zenner 2004; Burrascano et al. 2013).

Partial cutting scenarios produced a mean deficit of 10.2% of dead biomass compared to scenarios with natural disturbances only, but the deficit did not show a clear trend with harvesting intensity. Such a dead biomass deficit could have a negative effect on micro-habitats which could cause a loss of biodiversity and old-growth forest ecosystem services (Hodge & Peterken 1998; Fraver et al. 2002; Angers et al. 2005; Burrascano et al. 2013).

In our simulations, we observed a loss of structural elements with the decrease of very old and dead biomass. Reservation, retention and restoration could be used to prevent such losses (Franklin et al. 1997; Mitchell & Beese 2002; Seymour et al. 2002; Keeton 2006). Reservation aims to conserve large patches of old-growth forest at the landscape scale, retention aims to leave dominant trees uncut, and restoration aims to increasing old-growth structural attributes from secondary forest succession.

4.6.2 Sensitivity of mid-tolerant species to natural disturbances

The biomass of mid-tolerant species (yellow birch and red oak, in our case) did not vary between the different natural disturbance scenarios (Fig. 4.6). This is contrary to our hypothesis that intermediate disturbances would create condition more favorable to intermediate shade-tolerant species. Indeed, in our simulation, mid-tolerant species did not seem sensitive to the increase of canopy opening created by partial windthrow, compared to small gaps only. Different studies have shown the importance of large canopy openings to maintain mid-tolerant species (Webster & Lorimer 2005; Duchesne & Prévost 2012). Our choice of shade classes could have biased our results, as mid-tolerant species were able to persist even in a landscape without any disturbance (App. H). However, changing shade classes did not change the response to natural disturbances (App. H). Thus, light availability (canopy opening) does not seem to be the only variable explaining the establishment and persistence of mid-tolerant species in temperate deciduous stands, and other life history traits could be important, like growth or survival rates (Papaik et al. 2005). Indeed, mid-tolerant species could persist in the landscape if they grow faster than shade-tolerant species or if they have higher survival rates.

4.6.3 Model limitations

LANDIS-II does not handle gap disturbances natively, and we had to simulate gaps using the Biomass Harvest extension, which works at the stand level. Thus, LANDIS-II removed a percentage of the stand which is defined by a cell size of 625 m^2 and could not create realistic gaps like a tree-level model could do. Even if LANDIS-II was set to remove the disturbance rate found at the northern limit of the sugar maple – yellow birch forest (mean: 0.96 ± 0.51 % per year, Després et al. under review), it could not create small gaps (mean: 39 ± 44 m², Després et al. under review).Such an overestimated gap size could have had a positive effect on the biomass of mid-tolerant species. Similarly, dead biomass did not retroact on species establishment or tree growth rate within the Biomass Succession extension. Thus, we could not perfectly quantify the effects of harvesting on forest dynamics. It could have been possible using the Forest Carbon extension (Dymond et al. 2012), but a lot more parameters would have been necessary that were not available for our study area. Finally, LANDIS-II provides biomass, cohort richness and age outputs, whereas other ecological parameters could possibly better describe old-growth forest attributes, such as diameter structure or species richness.

4.7 Conclusion

Simulations of old-growth sugar maple – yellow birch forests showed that partial cutting with at rates between 0.61 and 1.20% per year resulted in a loss of old-growth stands (> 200 years-old) and reduced dead biomass, although it did not alter species composition. Thus, for forest management to be sustainable in such forests, the partial cutting rate should not exceed 0.60% per year. This is representative of the current partial cutting rate in the study area (ministère des Ressources naturelles 2013). However, our results showed that differences between natural old-growth forests and managed forests could be reduced by leaving some live trees older than 200 years (i.e., with a diameter > 40 cm) on cutting sites, along with coarse woody debris of different sizes.

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4.9 References

Angers, V.A., Messier, C., Beaudet, M. & Leduc, A. 2005. Comparing composition and structure in old-growth and harvested (selection and diameter-limit cuts) northern hardwood stands in Quebec. *Forest Ecology and Management* 217: 275-293.

Bauhus, J., Puettmann, K. & Messier, C. 2009. Silviculture for old-growth attributes. *Forest Ecology and Management* 258: 525-537.

Beaudet, M., Harvey, B.D., Messier, C., Coates, K.D., Poulin, J., Kneeshaw, D.D., Brais, S. & Bergeron, Y. 2011. Managing understory light conditions in boreal mixedwoods through variation in the intensity and spatial pattern of harvest: A modelling approach. *Forest Ecology and Management* 261: 84-94.

Bégin, E. 2011. *Caractérisation des régimes de perturbations par le chablis et des vents extrèmes dans l'érablière à bouleau jaune du Québec.* Unpublished M.Sc. thesis, UQAM, Montréal, Qc.

Berg, A., Ehnstrom, B., Gustafsson, L., Hallingback, T., Jonsell, M. & Weslien, J. 1994. Threatened plant, animal, and fungus species in swedish forests: Distribution and habitat associations. *Conservation Biology* 8: 718-731.

Bolton, N.W. & D'Amato, A.W. 2011. Regeneration responses to gap size and coarse woody debris within natural disturbance-based silvicultural systems in northeastern Minnesota, USA. *Forest Ecology and Management* 262: 1215-1222.

Brown, J.L. 1981. *Les forêts du Témiscamingue, Québec: écologie et photo-interprétation.* Laboratoire d'écologie forestière, Université Laval.

Brown, S., Schroeder, P. & Birdsey, R. 1997. Aboveground biomass distribution of US eastern hardwood forests and the use of large trees as an indicator of forest development. *Forest Ecology and Management* 96: 37-47.

Burns, R.M., Honkala, B.H. & tech. coords. 1990. *Silvics of North America: 1. Conifers; 2. Hardwoods.* U.S. Department of Agriculture, Forest Service, Washington, DC.

Burrascano, S., Keeton, W.S., Sabatini, F.M. & Blasi, C. 2013. Commonality and variability in the structural attributes of moist temperate old-growth forests: A global review. *Forest Ecology and Management* 291: 458-479.

Burrascano, S., Lombardi, F. & Marchetti, M. 2008. Old-growth forest structure and deadwood: Are they indicators of plant species composition? A case study from central Italy. *Plant Biosystems* 142: 313-323.

Burton, P.J., Kneeshaw, D.D. & Coates, K.D. 1999. Managing forest harvesting to maintain old growth in boreal and sub-boreal forests. *The Forestry Chronicle* 75: 623-631.

Canham, C.D., Kobe, R.K., Latty, E.F. & Chazdon, R.L. 1999. Interspecific and intraspecific variation in tree seedling survival: effects of allocation to roots versus carbohydrate reserves. *Oecologia* 121: 1-11.

Cimon-Morin, J., Ruel, J.-C. & Darveau, M. 2010. Short term effects of alternative silvicultural treatments on stand attributes in irregular balsam fir-black spruce stands. *Forest Ecology and Management* 260: 907-914.

Cowden, M.M., Hart, J.L., Schweitzer, C.J. & Dey, D.C. 2014. Effects of intermediate-scale wind disturbance on composition, structure, and succession in *Quercus* stands: Implications for natural disturbance-based silviculture. *Forest Ecology and Management* 330: 240-251.

Després, T., Asselin, H., Doyon, F. & Bergeron, Y. 2014. Structural and spatial characteristics of old-growth temperate deciduous forests at their northern distribution limit. *Forest Science* 60: 871–880.

Després, T., Asselin, H., Doyon, F., Drobyshev, I. & Bergeron, Y. under review. Gap disturbance regime of old-growth temperate deciduous forests at their northern range limit. *Journal of Vegetation Science* In Review.

Drever, C.R., Messier, C., Bergeron, Y. & Doyon, F. 2006. Fire and canopy species composition in the Great Lakes–St. Lawrence forest of Témiscamingue, Québec. *Forest Ecology and Management* 231: 27-37.

Duchesne, L. & Prévost, M. 2012. Canopy disturbance and intertree competition: implications for tree growth and recruitment in two yellow birch–conifer stands in Quebec, Canada. *Journal of Forest Research* 1-11.

Duveneck, M.J., Scheller, R.M., White, M.A., Handler, S.D. & Ravenscroft, C. 2014. Climate change effects on northern Great Lake (USA) forests: A case for preserving diversity. *Ecosphere* 5: art23.

Dymond, C.C., Scheller, R.M. & Beukema, S. 2012. A new model for simulating climate change and carbon dynamics in forested landscapes. *Jounral of Ecosystems and Management* 13: 1-2.

Environnement Canada 2011. Canadian Climate Normals 1981-2010 Station Data. Atmospheric Environment Service, Downsview, Ontario, Canada. http://climate.weather.gc.ca/climate_normals/index_e.html.

Farrar, J.L. 1995. *Trees in Canada*. Natural Resources Canada, Canadian Forest Service, Ontario, Canada.

Fortin, M. & Langevin, L. 2010. *ARTÉMIS-2009 : un modèle de croissance basé sur une approche par tiges individuelles pour les forêts du Québec*. Direction de la recherche forestière, Gouvernement du Québec, Québec.

Franklin, J.F., Berg, D.R., Thornburgh, D.A. & Tappeiner, J.C. 1997. Alternative silvicultural approaches to timber harvesting: variable retention harvest systems. In: Kohm, K.A. & Franklin, J.F. (eds.) *Creating a forestry for the 21st century. The science of ecosystem management*, pp. 111-139. Washington, DC, Island Press.

Fraver, S., Wagner, R.G. & Day, M. 2002. Dynamics of coarse woody debris following gap harvesting in the Acadian forest of central Maine, U.S.A. *Canadian Journal of Forest Research* 32: 2094-2105.

Frelich, L.E. & Lorimer, C.G. 1991. A simulation of landscape-level stand dynamics in the northern hardwood region. *Journal of Ecology* 79: 223-233.

Gauthier, S., Vaillancourt, M.-A., Leduc, A., De Grandpré, L., Kneeshaw, D., Morin, H., Drapeau, P. & Bergeron, Y. 2009. *Ecosystem management in the boreal forest*. Presses de l'Université du Québec, Québec, Canada.

Grenier, D.J., Bergeron, Y., Kneeshaw, D. & Gauthier, S. 2005. Fire frequency for the transitional mixedwood forest of Timiskaming, Quebec, Canada. *Canadian Journal of Forest Research* 35: 656-666.

Gustafson, E.J., Shifley, S.R., Mladenoff, D.J., Nimerfro, K.K. & He, H.S. 2000. Spatial simulation of forest succession and timber harvesting using LANDIS. *Canadian Journal of Forest Research* 30: 32-43.

Hale, C.M., Pastor, J. & Rusterholz, K.A. 1999. Comparison of structural and compositional characteristics in old-growth and mature, managed hardwood forests of Minnesota, U.S.A. *Canadian Journal of Forest Research* 29: 1479-1489.

Hanson, J.J. & Lorimer, C.G. 2007. Forest structure and light regimes following moderate wind storms: Implications for multi-cohort management. *Ecological Applications* 17: 1325-1340.

Hodge, S.J. & Peterken, G.F. 1998. Deadwood in British forests: priorities and a strategy. *Forestry* 71: 99-112.

Humbert, L., Gagnon, D., Kneeshaw, D. & Messier, C. 2007. A shade tolerance index for common understory species of northeastern North America. *Ecological Indicators* 7: 195-207.

Johnson, E.A., Miyanishi, K. & Weir, J.M.H. 1995. Old-growth, disturbance, and ecosystem management. *Canadian Journal of Botany* 73: 918-926.

Keeton, W.S. 2006. Managing for late-successional/old-growth characteristics in northern hardwood-conifer forests. *Forest Ecology and Management* 235: 129-142.

Keeton, W.S., Whitman, A.A., McGee, G.C. & Goodale, C.L. 2011. Late-successional biomass development in northern hardwood-conifer forests of the northeastern United States. *Forest Science* 57: 489-505.

Kern, C.C., D'Amato, A.W. & Strong, T.F. 2013. Diversifying the composition and structure of managed, late-successional forests with harvest gaps: What is the optimal gap size? *Forest Ecology and Management* 304: 110-120.

Larsen, D.R. & Johnson, P.S. 1998. Linking the ecology of natural oak regeneration to silviculture. *Forest Ecology and Management* 106: 1-7.

Lupien, P. 2004. *Guide des feuillus nobles en Basse-Mauricie : guide de mise en valeur* Shawinigan : Syndicat des producteurs de bois de la Mauricie, Québec, Canada.

Lussier, J.-M. & Meek, P. 2014. Managing heterogeneous stands using a multiple-treatment irregular shelterwood method. *Journal of Forestry* 112: 287-295.

McGee, G.G., Leopold, D.J. & Nyland, R.D. 1999. Structural characteristics of old-growth, maturing, and partially cut northern hardwood forests. *Ecological Applications* 9: 1316-1329.

Ministère des Ressources naturelles 2013. *Le guide sylvicole du Québec - Tome II : Les concepts et l'application de la sylviculture.* Les Publications du Québec, Québec.

Mitchell, S.J. & Beese, W.J. 2002. The retention system: reconciling variable retention with the principles of silvicultural systems. *The Forestry Chronicle* 78: 397-403.

Mladenoff, D.J. & Pastor, J. 1993. Sustainable forest ecosystems in the northern hardwood and conifer forest region: concepts and management. In: Aplet, G.H., Johnson, N., Olson, J.T. & Sample, V.A. (eds.) *Defining sustainable forestry*, pp. 145-180. Island Press, Washington, DC.

Muller, R.N. & Liu, Y. 1991. Coarse woody debris in an old-growth deciduous forest on the Cumberland Plateau, southeastern Kentucky. *Canadian Journal of Forest Research* 21: 1567-1572.

Nolet, P., Doyon, F. & Bouffard, D. 2012. Predicting stem windthrow probability in a northern hardwood forest using a wind intensity bio-indicator approach. *Open Journal of Forestry* 2: 77.

Ódor, P. & Standovár, T. 2001. Richness of bryophyte vegetation in near-natural and managed beech stands: The effects of management-induced differences in dead wood. *Ecological Bulletins* 219-229.

Papaik, M.J., Canham, C.D., Latty, E.F. & Woods, K.D. 2005. Effects of an introduced pathogen on resistance to natural disturbance: beech bark disease and windthrow. *Canadian Journal of Forest Research* 35: 1832-1843.

Paré, D., Bernier, P., Lafleur, B., Titus, B.D., Thiffault, E., Maynard, D.G. & Guo, X. 2013. Estimating stand-scale biomass, nutrient contents, and associated uncertainties for tree species of Canadian forests. *Canadian Journal of Forest Research* 43: 599-608.

Payette, S., Filion, L. & Delwaide, A. 1990. Disturbance regime of a cold temperate forest as deduced from tree-ring patterns: the Tantaré Ecological Reserve, Quebec. *Canadian Journal of Forest Research* 20: 1228-1241.

R Core Team 2015. R: A language and environment for statistical computing. In: R Foundation for Statistical Computing, Vienna, Austria.

Roy, M.-E., Doyon, F., Nolet, P. & Bouffard D. 2010. *Historique des perturbations et réponse de la végétation forestière dans l'érablière à bouleau jaune de l'ouest au Témiscamingue au cours du 20ième siècle.* Institut québécois d'aménagement de la forêt feuillue, Ripon, Québec.

Scheller, R.M., Domingo, J.B., Sturtevant, B.R., Williams, J.S., Rudy, A., Gustafson, E.J. & Mladenoff, D.J. 2007. Design, development, and application of LANDIS-II, a spatial landscape simulation model with flexible temporal and spatial resolution. *Ecological Modelling* 201: 409-419.

Scheller, R.M. & Mladenoff, D.J. 2004. A forest growth and biomass module for a landscape simulation model, LANDIS: design, validation, and application. *Ecological Modelling* 180: 211-229.

Scheller, R.M. & Mladenoff, D.J. 2007. An ecological classification of forest landscape simulation models: tools and strategies for understanding broad-scale forested ecosystems. *Landscape Ecology* 22: 491-505.

Seymour, R.S., White, A.S. & de Maynadier, P.G. 2002. Natural disturbance regimes in northeastern North America - evaluating silvicultural systems using natural scales and frequencies. *Forest Ecology and Management* 155: 357-367.

Spies, T.A. 2004. Ecological concepts and diversity of old-growth forests. *Journal of Forestry* 102: 14-20.

Splechtna, B.E., Gratzer, G. & Black, B.A. 2005. Disturbance history of a European old-growth mixed-species forest: A spatial dendro-ecological analysis. *Journal of Vegetation Science* 16: 511-522.

Steenberg, J.W.N., Duinker, P.N. & Bush, P.G. 2011. Exploring adaptation to climate change in the forests of central Nova Scotia, Canada. *Forest Ecology and Management* 262: 2316-2327.

Sturtevant, B.R., Miranda, B.R., Shinneman, D.J., Gustafson, E.J. & Wolter, P.T. 2012. Comparing modern and presettlement forest dynamics of a subboreal wilderness: Does spruce budworm enhance fire risk? *Ecological Applications* 22: 1278-1296.

Thiffault, E., Béchard, A., Paré, D. & Allen, D. 2014. Recovery rate of harvest residues for bioenergy in boreal and temperate forests: A review. *Wiley Interdisciplinary Reviews: Energy and Environment* n/a-n/a.

Tritton, L., Martin, C.W., Hornbeck, J. & Pierce, R. 1987. Biomass and nutrient removals from commercial thinning and whole-tree clearcutting of central hardwoods. *Environmental Management* 11: 659-666.

Ward, B.C., Mladenoff, D.J. & Scheller, R.M. 2005. Simulating landscape-level effects of constraints to public forest regeneration harvests due to adjacent residential development in northern Wisconsin. *Forest Science* 51: 616-632.

Webster, C.R. & Lorimer, C.G. 2005. Minimum opening sizes for canopy recruitment of midtolerant tree species: A retrospective approach. *Ecological Applications* 15: 1245-1262.

Wirth, C., Gleixner, G. & Heimann, M. 2009. *Old-growth forests: Function, fate and value.* Springer, Verlag, Berlin, Heidelberg.

Woods, K.D. 2004. Intermediate disturbance in a late-successional hemlock-northern hardwood forest. *Journal of Ecology* 92: 464-476.

Zenner, E.K. 2004. Does old-growth condition imply high live-tree structural complexity? *Forest Ecology and Management* 195: 243-258.

CHAPITRE V

CONCLUSION GENERALE

La dynamique naturelle des forêts tempérées feuillues a été relativement bien étudié à travers le monde (Runkle 1982; Fraver et al. 2009; Svoboda et al. 2010; Burrascano et al. 2013; Nagel et al. 2014). Cependant, en Amérique du Nord, les études réalisées à la limite nordique de répartition des forêts tempérées feuillues sont rares (Payette et al. 1990). Or, la mise en place de l'aménagement forestier écosystémique nécessite de connaître la dynamique forestière naturelle afin de s'en inspirer (Grumbine 1994). L'objectif de cette étude était de caractériser la dynamique naturelle de vieilles forêts tempérées feuillues à leur limite nordique de répartition dans l'Est de l'Amérique du Nord.

Tout d'abord, 11 vieux peuplements du sous-domaine bioclimatique de l'érablière à bouleau jaune de l'Ouest ont été caractérisés (Chapitre 2). Ensuite, la dynamique des trouées a été reconstituée aux échelles du peuplement et du paysage (Chapitre 3). Enfin, l'impact de l'aménagement forestier sur le maintien des attributs de vieilles forêts a été évalué à l'échelle du paysage (Chapitre 4).

La structure, la composition spécifique et la dynamique spatiale des vieilles forêts tempérées feuillues à leur limite nordique de répartition diffèrent en plusieurs points de ce qui a été observée plus au centre de l'aire de répartition du biome (Chapitre 2). En effet, la structure diamétrale de la forêt tempérée feuillue au centre de l'aire de répartition suit d'abord une exponentielle négative ou une distribution de Weibull indiquant un recrutement continu (Rubin et al. 2006), avant de changer pour une sigmoïde inversée dans les plus vieux peuplements indiquant une faible mortalité des arbres matures (Lorimer et al. 2001; Westphal et al. 2006). Nous avons montré que la forêt tempérée feuillue conserve une distribution diamétrale de Weibull à sa limite nordique de répartition, même dans les vieux peuplements. Néanmoins, il faut souligner que la forme de la distribution diamétrale est dépendante de l'échelle à laquelle elle est étudiée (Manion & Griffin 2001). Une distribution diamétrale qui suit une sigmoïde inversée à l'échelle du peuplement peut montrer une structure différente à l'échelle de la placette-échantillon (Manion & Griffin 2001). La richesse spécifique n'augmente pas avec l'âge des peuplements, contrairement à ce qui serait attendu d'un processus stochastique comme les trouées (Hubbell 2001). Cette différence peut être expliquée par la tendance de l'érable à sucre à se succéder à lui-même, engendrant des vieux peuplements d'érable à sucre presque purs. La structure d'âge montre un recrutement constant pour certains peuplements tel qu'attendu (Fraver et al. 2009), alors que d'autres montrent plutôt un recrutement par pics suggérant la présence de perturbations intermédiaires. Cependant, l'ouverture créée par les perturbations intermédiaires ne semble pas assez grande pour permettre l'établissement de nouvelles espèces. Enfin, la répartition spatiale aléatoire des cohortes d'âges, d'espèces et de bois mort vont dans le sens de plusieurs autres études menées en forêt tempérée feuillue (Chokkalingam & White 2001; Keeton 2006; Curzon & Keeton 2010). Ceci résulterait du manque de grandes perturbations dans les vieux peuplements. Ainsi, la différence de structure avec des forêts issues du centre de l'aire de répartition est importante et nécessite un aménagement forestier adapté avec, par exemple, des coupes de jardinage.

La dynamique des trouées diffère entre la forêt tempérée feuillue à sa limite nordique de répartition par rapport au centre de son aire de répartition (Chapitre 3). En effet, la distribution de taille des trouées dans l'aire centrale de répartition de la forêt tempérée varie en moyenne de 70 à 297 m^2 (Yamamoto 1992a; Abe et al. 1995; Rugani et al. 2013; Hobi et al. 2015). Or, à la limite nordique de répartition de la forêt tempérée feuillue au Témisacamingue, la taille moyenne des trouées est de seulement 39 m^2. La création d'aussi petites trouées pourrait être causée par la chute de grosses branches comme celles du bouleau jaune. En effet, le bouleau jaune est plus sensible aux perturbations produite par le vent que l'érable à sucre (Canham et al. 2001). Le taux de perturbation par les trouées est sensiblement le même dans les forêts tempérées feuillues au centre et à la limite nordique de leur aire de répartition dans l'Est de l'Amérique du Nord, soit environ 1% par an (Runkle 1982; Dahir & Lorimer 1996;

Fraver et al. 2009). Ainsi, pour un même taux de perturbation, les trouées plus petites à la limite nordique ont une fréquence plus élevée. Ceci pourrait être dû aux hivers plus long et rigoureux qui fragilisent les arbres et favoriseraient la création de trouées. La petite taille moyenne des trouées (39 m^2) mise en relation avec la répartition spatiale aléatoire des arbres (cf. Chapitre 2) montre à nouveau la nécessité de faire des coupes de jardinage dans le cadre d'un aménagement écosystémique. De plus, il y avait peu de variation du taux de renouvellement forestier entre les 11 peuplements étudiés du domaine bioclimatique de l'érablière à bouleau jaune de l'Ouest. Ainsi, lors de la mise en place de l'aménagement forestier écosystémique dans de vieux peuplements d'érablière à bouleau jaune, il faudra appliquer les mêmes prescriptions, soit des coupes partielles avec des trouées de petite taille (39 m^2).

La modélisation de la dynamique de vieilles érablières à bouleau jaune à l'échelle du paysage à l'aide de LANDIS-II montre que les coupes partielles affectant plus de 0.60% du territoire sur une base annuelle entraînent une diminution des attributs de vieilles forêts (Chapitre 4). En effet, au-delà d'un taux annuel de perturbation de 0.60% par coupes partielles, la biomasse des arbres de plus de 200 ans chute de 44% par rapport à des coupes partielles affectant de 0.25 à 0.60% du territoire chaque année. De plus, les coupes partielles causent un déficit moyen de 10.2% de biomasse morte, peu importe le taux annuel de prélèvement. Or, le bois mort, et plus particulièrement sa diversité de taille, est une caractéristique essentielle des vieilles forêts (Hodge & Peterken 1998; Angers et al. 2005; Burrascano et al. 2013). La perte de vieux arbres et de biomasse morte entraîne une diminution de la complexité structurelle des vieilles forêts (Zenner 2004). Des recommandations pour l'aménagement forestier durable afin d'éviter la perte des attributs de vieilles forêts seraient de limiter la coupe d'arbres de plus de 200 ans (c'est-à-dire avec un diamètre de plus de 40 cm) et de laisser un total de 60% de la biomasse coupée sur place, incluant des débris ligneux de différentes tailles.

L'objectif de cette étude, qui était de caractériser la dynamique naturelle de vieilles forêts tempérées feuillues à leur limite nordique de répartition dans l'Est de l'Amérique du Nord, a été atteint. Cependant quelques incertitudes demeurent. Est-ce que les petites trouées sont causées par le dépérissement branche par branche des arbres? De même, le mécanisme permettant la persistance des espèces semi-tolérantes à l'ombre comme le bouleau jaune ou le chêne rouge n'a pas été clairement établi. En effet, ces espèces ont besoin d'ouvertures minimales de 100 à 250 m^2 pour s'établir (Webster & Lorimer 2005), ce que ne permettent pas les trouées répertoriés dans l'aire d'étude (cf. Chapitre 3). Cependant, la modélisation n'a pas permis de mettre en évidence le rôle de la taille des ouvertures dans le maintien des espèces semi-tolérantes à l'ombre. En effet, dans le scénario sans aucune perturbation, les espèces semi-tolérantes à l'ombre arrivaient à se maintenir dans le paysage. Ainsi, l'établissement et le maintien dans le paysage des espèces semi-tolérantes à l'ombre pourraient dépendre des perturbations intermédiaires, comme les chablis partiels, mais également de traits de vie comme le taux de croissance ou le taux de survie (Papaik et al. 2005).

5.1 Recommandations pour l'aménagement forestier écosystémique

Nous avons montré que la dynamique naturelle de la forêt tempérée feuillue diffère au centre et à la limite nordique de son aire de répartition. Ainsi, la mise en place de l'aménagement écosystémique à la limite nordique de la forêt tempérée feuillue nécessite des dispositions particulières quant au type, à la taille et à la fréquence des coupes. En effet, les trouées, qui sont la principale perturbation naturelle en forêt tempérée feuillue, font en moyenne 39 m^2, sont réparties de manière aléatoire et affectent 0,96 % du territoire en moyenne chaque année (Chapitre 3). Cependant, des ouvertures de grande taille, de l'ordre de 250 à 600 m^2, plus rares, permettent le maintien des espèces semi-tolérantes à l'ombre comme le bouleau jaune ou le chêne rouge (Webster & Lorimer 2005). De plus, la modélisation a montré que lorsque des coupes partielles affectent plus de 0,60% du territoire sur une base annuelle, il y a une érosion de certains attributs des forêts anciennes comme une diminution de biomasse morte et de la biomasse des arbres de plus de 200 ans (> 40 cm de diamètre). Pour limiter ces pertes d'attributs des forêts anciennes, il faudrait limiter la coupe des arbres les plus vieux et laisser du bois mort de différentes tailles après coupe (Chapitre 4). En effet, laisser du bois mort de différentes tailles permet de maintenir un plus grand nombre de micro-habitats qui favorisent le maintien de la biodiversité (Ódor & Standovár 2001; Heilmann-Clausen & Christensen 2004). La préservation de la biomasse des très vieux arbres et du bois mort sont deux enjeux qui sont actuellement pris en compte dans l'aménagement forestier pratiqué au Témiscamingue par le biais des coupes de jardinages (ministère des Ressources naturelles de la Faune et des Parcs 2003). En effet, les coupes de jardinage et les coupes progressives irrégulières sont deux types d'aménagement qui s'inspirent de la dynamique naturelle des vieilles érablières en créant de petites trouées et en protégeant la régénération préétablie.

Les vieilles forêts ne sont pas composées exclusivement de peuplement à l'équilibre, mais de peuplement à différents stades de succession, incluant des peuplements multi-âge (Frelich & Lorimer 1991b). Ainsi, ces recommandations d'aménagement valent pour les vieilles forêts tempérées feuillues climaciques pour lesquelles l'aménagiste souhaite préserver les attributs de forêts anciennes.

5.2 Perspectives

Cette étude est une première étape dans l'obtention des conditions de base nécessaires à la réalisation de l'aménagement forestier écosystémique dans le domaine bioclimatique de l'érablière à bouleau jaune de l'Ouest. L'étude d'autres types de peuplements à différents âges dans la même région permettrait une vision plus globale du fonctionnement de ce paysage. Un échantillonnage aléatoire au sein de vieux peuplements de différente structure (de taille et de quantité de bois mort) permettrait une meilleure représentation de la dynamique naturelle du territoire. De même, l'étude des perturbations intermédiaires, comme le chablis partiel, dans le maintien des espèces semi-tolérantes à l'ombre semble l'une des prochaines étapes essentielles à une vision globale de la dynamique naturelle de la forêt tempérée feuillue à sa limite nordique de répartition. L'importance des perturbations intermédiaires a déjà été démontré dans le centre de l'aire de répartition de la forêt feuillue tempérée (Seymour et al. 2002; Keeton et al. 2011), mais pas à sa limite nordique de répartition. Ayant montré la différence de dynamique des trouées entre le centre et la limite nordique de répartition de la forêt tempérée feuillue, il serait intéressant de vérifier si la dynamique des perturbations intermédiaires diffère également.

En plus de l'étude des arbres, une étude de la faune et du reste de la flore, avec une attention particulière sur l'impact du bois mort dans cet écosystème, permettrait de mieux définir le type d'aménagement qui serait le plus propice à conserver les attributs de forêt ancienne. Il ne faut pas non plus oublier que des communautés autochtones vivent sur ces territoires et que leurs connaissances et leurs besoins devraient être inclus dans l'approche écosystémique. De plus, de nouvelles études situées dans le sous-domaine bioclimatique de l'érablière à bouleau jaune de l'Est seraient intéressantes pour voir la différence avec l'Ouest.

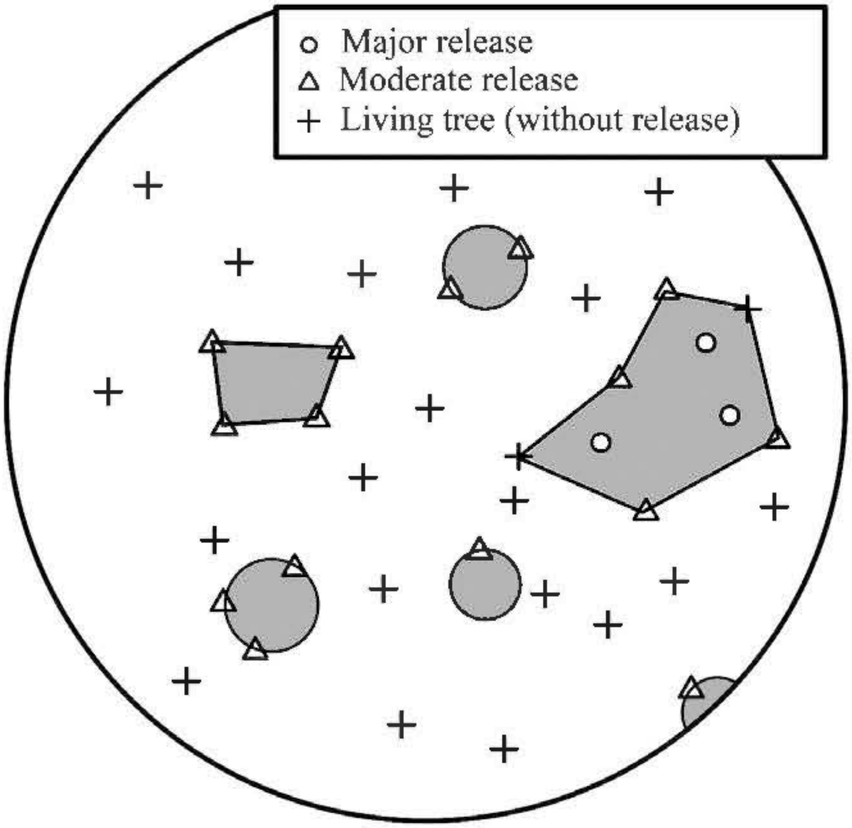
APPENDIX A

SPECIES IMPORTANCE VALUES FOR EACH SAMPLING PLOT (SP). ACSA: *ACER SACCHARUM* MARSH.; BEAL: *BETULA ALLEGHANIENSIS* BRITTON; ABBA: *ABIES BALSAMEA* (L.) MILL.; TSCA: *TSUGA* CANADENSIS (L.) CARR.; ACRU: *ACER RUBRUM* L.; PIGL: *PICEA GLAUCA* (MOENCH) VOSS; THOC: *THUJA OCCIDENTALIS* L.; BEPA: *BETULA PAPYRIFERA* MARSH.; OSVI: *OSTRYA VIRGINIANA* (MILL.) K. KOCH; QURU: *QUERCUS RUBRA* L.; POGR: *POPULUS GRANDIDENTATA MICHX.; PIST: PINUS STROBUS* L. AGE REPRESENT THE 90^{TH} PERCENTILE OF THE AGE DISTRIBUTION OF SUCCESSFULLY-AGED TREES.

Sampling plot	Age	Acsa	Beal	Abba	Tsca	Acru	Pigl	Thoc	Bepa	Osvi	Quru	Pogr	Pist
SP1	184	90.22	5.28	.	.	.	.	.	.	2.95	1.54	.	.
SP2	167	94.88	3.55	.	.	.	.	.	.	1.57	.	.	.
SP3	119	54.60	29.59	7.46	0.73	1.16	5.26	1.20	.	.	.	.	.
SP4	195	36.72	46.21	10.63	2.14	2.16	2.14	.	.	.	.	.	.
SP5	99	15.44	39.68	25.98	.	17.58	.	.	.	.	.	1.33	.
SP6	134	8.13	63.49	16.51	2.91	0.45	1.42	0.92	6.17	.	.	.	.
SP7	151	77.22	7.77	.	15.01	.	.	.	.	.	.	.	.
SP8	147	62.92	33.44	.	.	.	1.31	.	.	.	2.32	.	.
SP9	129	75.86	8.74	.	7.69	.	.	7.72	.	.	.	.	.
SP10	117	70.93	25.61	1.44	.	0.59	1.43	.	.	.	.	.	.
SP11	111	77.08	18.27	1.13	.	1.25	1.71	.	.	.	.	.	0.56

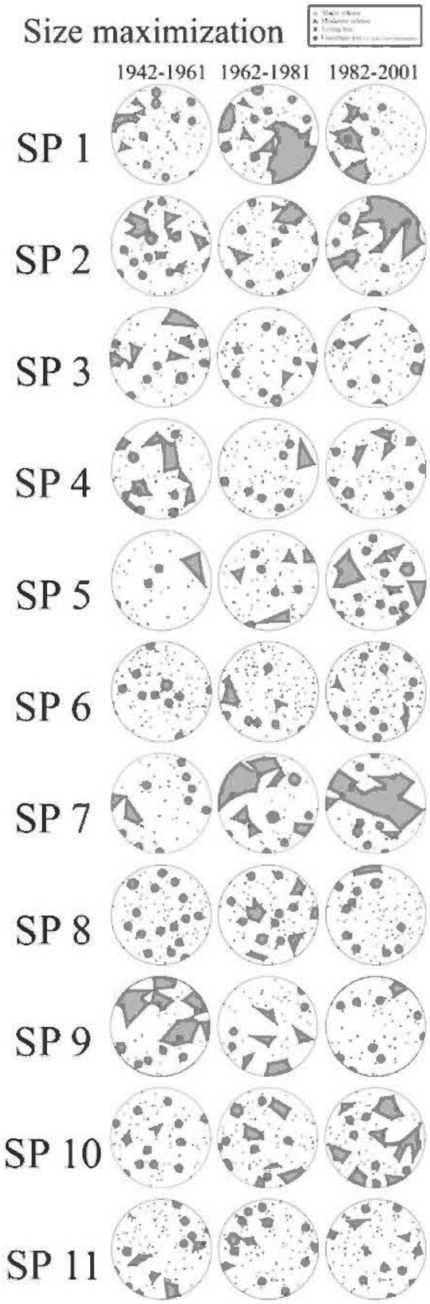
APPENDIX B

EXAMPLES OF GAP DELINEATION. EACH SYMBOL IS A LIVING TREE. GAP AREAS ARE IN GREY.



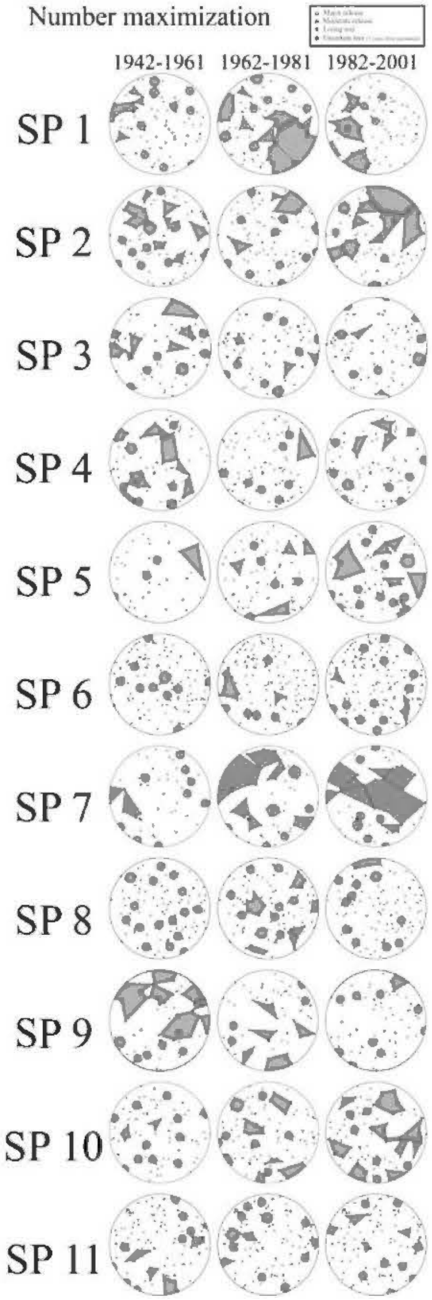
APPENDIX C

GAP RECONSTRUCTIONS USING THE GAP SIZE MAXIMIZATION PROCEDURE FOR THREE 20-YEAR PERIODS AND FOR THE 11 SAMPLING PLOTS. ALL PLOTS ARE 0.25 HA IN SIZE.



APPENDIX D

GAP RECONSTRUCTIONS USING THE GAP NUMBER MAXIMIZATION PROCEDURE FOR THREE 20-YEAR PERIODS AND FOR THE 11 SAMPLING PLOTS. ALL PLOTS ARE 0.25 HA IN SIZE.



APPENDIX E

KOLMOGOROV-SMIRNOV TEST COMPARING GAP SIZE DISTRIBUTIONS OBTAINED FROM THE GAP SIZE MAXIMIZATION (GSM) AND THE GAP NUMBER MAXIMIZATION (GNM) DELINEATION PROCEDURES FOR EACH TIME PERIOD. MISSING VALUES WERE FOR THE SAME GAP DISTRIBUTION (GSM OR GNM) AT THE SAME TIME PERIOD AND GAVE *D* = 0 AND *P* = 1.

	1942-1961	1962-1981	1982-2001
1942-1961	.	$D_{GSM} = 0.09$ $P_{GSM} = 0.41$	$D_{GSM} = 0.03$ $P_{GSM} = 0.99$
1962-1981	$D_{GNM} = 0.08$ $P_{GNM} = 0.47$	.	$D_{GSM} = 0.06$ $P_{GSM} = 0.77$
1982-2001	$D_{GNM} = 0.06$ $P_{GNM} = 0.70$	$D_{GNM} = 0.05$ $P_{GNM} = 0.88$	.

APPENDIX F

TREE SPECIES LIFE HISTORY PARAMETERS USED IN LANDIS-II.

Species	Longevity	Sexual maturity	Shade tolerance	Effective seed dispersal distance	Maximum seed dispersal distance	Vegetative reproduction probability	Minimum vegetative reproduction age	Maximum vegetative reproduction age
Abies balsamea	150	25	5	60	160	0	0	0
Acer rubrum	200	10	3	100	200	0.5	10	100
Acer saccharum	300	30	4	100	200	0.25	10	60
Betula alleghaniensis	320	40	3	100	400	0.25	10	40
Betula papyrifera	200	15	2	200	5000	0.5	10	200
Populus grandidentata	150	10	1	500	5000	0.9	1	100
Picea glauca	250	30	4	30	200	0.1	30	250
Pinus strobus	400	25	2	60	250	0	0	0
Quercus rubra	300	50	3	15	1000	0.75	10	150
Tsuga canadensis	450	20	5	30	100	0	0	0

APPENDIX G

LANDIS-II BIOMASS SUCCESSION – DYNAMIC INPUTS

Within the LANDIS-II Biomass Succession extension (Scheller & Mladenoff 2004), succession patterns emerge from complex interactions among cohorts of tree species, both at the pixel-level, through intra- and inter-specific competition, and at the landscape-level, mainly through the processes of seed dispersal and differential post-disturbance survivorship. Those interactions are largely influenced by three subsets of parameters: maximum aboveground biomass (BMAX), maximum aboveground net primary productivity (ANPPMAX) and species establishment probabilities (SEP) (Table G.1). Values were assigned to each species.

Table G.1 Establishment probability (ProbEst), Maximum Annual Net Primary Productivity ($ANPP_{max}$) and Maximum Biomass ($Biomass_{max}$) parameters used in LANDIS-II for each species.

Species	ProbEst	$ANPP_{max}$	$Biomass_{max}$
Abies balsamea	0.3	850	9200
Acer rubrum	0.35	1137	15500
Acer saccharum	0.89	700	20100
Betula alleghaniensis	0.77	1139	20200
Betula papyrifera	0.17	987	14700
Populus grandidentata	0.34	462	9200
Picea glauca	0.38	1106	12200
Pinus strobus	0.15	1538	14000
Quercus rubra	0.44	1882	18800
Tsuga canadensis	0.28	686	13000

Competition intensity is largely influenced by the maximum aboveground biomass (BMAX) that the environment can support at the pixel level. Alongside with the aboveground biomass already present on site, the BMAX determines the “growing space” still available. Each species must be assigned a BMAX value (in g/m2), which defines the maximum allowable aboveground biomass for the species. The BMAX for all species combined is equal to the BMAX of the species with the highest value.
A maximum possible aboveground net primary productivity (ANPPMAX; in g/m2/yr) must also be assigned to each species. That value partly determines the speed at which the available “growing space” is filled by each established cohort. It is modulated (lowered) by the amount of intra- and inter-specific competition, as well as by cohort age. ANPPMAX estimates for each species combination were drawn from closed canopy forests, prior to the onset of any age-related decline in productivity (Scheller & Mladenoff 2004).

Finally, succession at a given site is largely influenced by the cohorts that can actually establish though simulation time. The shade tolerance of a given species and the light conditions that prevail at a given time step partly determine if that species can establish a new cohort, provided that seeds reach the site. To take into account the differential capacities of species to establish at a given site, the species establishment probabilities (SEP) modulate the probability of a cohort establishing itself granted that light conditions are adequate and seeds reach a given pixel.

The BMAX were obtained from Artemis-2009, which is the empirically based stand development operational model used in Quebec (Fortin & Langevin 2010). It includes a series of submodels that simulate individual stems' establishment, growth, and mortality. It was based on and calibrated with measurements from the network of temporary sample plots of the Quebec Ministry of Forests, Wildlife and Parcs.

First, a subset of temporary plots was selected to conform with the homogeneous environmental conditions simulated in the present study (FE32 which represents the following ecotype: sugar maple – yellow birch on shallow to deep deposits of moderate texture and mesic drainage). Then we computed the average maximum of basal area that could be reached in all temporary plots of the subset, as simulated by Artemis-2009 with all species combined. Because the LANDIS-II Biomass Succession extension requires that a BMAX value be assigned for each individual species and because the available Artemis-2009 outputs did not contain pure species stands, we hypothesized that all species could reach that same maximum basal area (28.8 m2/ha), in equivalent aboveground biomass. To convert basal area in aboveground biomass, we used stand-level allometric equations from Paré et al. (2013). As a result, different BMAX values were obtained among species, but they were all based on the same basal area.

Maximum aboveground primary productivity (ANPPMAX) values were obtained from an ongoing modelling experiment conducted by the Canadian Forest Service as part of the Integrated Assessment of the Forest Change project using the PICUS gap model. Contrary to LANDIS-II, PICUS is a stand-level gap model that explicitly simulates individual stems in a tridimensional stand structure. It is a hybrid model that incorporates stem interactions and physiological processes, which is of particular importance as ANPPMAX values correspond to hypothetical growth in optimal conditions, i.e., without competition, just before senescence. We used PICUS because it was impossible to obtain empirical observations or Artemis-2009 outputs corresponding to those conditions. The main environmental inputs of PICUS include, but are not limited to, mean surface temperature (monthly), mean precipitations (monthly), mean photosynthetically active radiation (monthly), vapor pressure deficit, N-deposition (annual), CO2 concentration, soil pH, and soil water holding capacity. Species inputs include, but are not limited to biomass, regeneration, seed production, mortality, growth, and environmental response. There are currently 78 different parameters for each species. To compute ANPPMAX at the stand level we simulated pure stands from bare ground. Then for each species simulation, we computed the ANPP by subtracting the biomass produced at time t+1 from that at time t and extracted the maximum ANPP during the course of simulation.

Species Establishment Probabilities (SEP) were more difficult to estimate objectively. The working definition of SEP in the LANDIS-II Biomass Succession extension is: The probability of a cohort establishing granted that seeds reached the site and that there is adequate light conditions. To acknowledge the inherent subjectivity associated with that parameter, we chose to use expert knowledge from a sample of 10 experts. To minimize personal and/or collective biases, we included 5 local practitioners with intimate knowledge of the region, as well as 5 academic or governmental researchers, and asked them to estimate from the best of their knowledge the SEP as described in the definition above. For the purpose of the present study, we used the mean value calculated from their answers.

The LANDIS-II species parameters include species longevity, seed dispersal, shade class, etc. (Burns et al. 1990; Farrar 1995; Lupien 2004; Humbert et al. 2007) (App. F). We used the Landis-II-Site V2.3 tool to calibrate the shade class parameter (App. H).

APPENDIX H

SHADE CLASS IN LANDIS-II

We sampled 11 old-growth plots in the sugar maple – yellow birch bioclimatic domain, and computed the biomass of each species in every plot (Fig. H.1). We used those sample plots as a referential. The definition of shade class in LANDIS-II is a sensitive parameter. The shade class definition allows LANDIS-II to determine which amount of biomass is necessary to change from an open canopy (shade class = 0) to a totally closed canopy (shade class = 5). This parameter is expressed as a percentage of the maximum biomass of each species defined in Table H.1. Thus, the lower the shade class definition threshold, the stronger the competition for light.

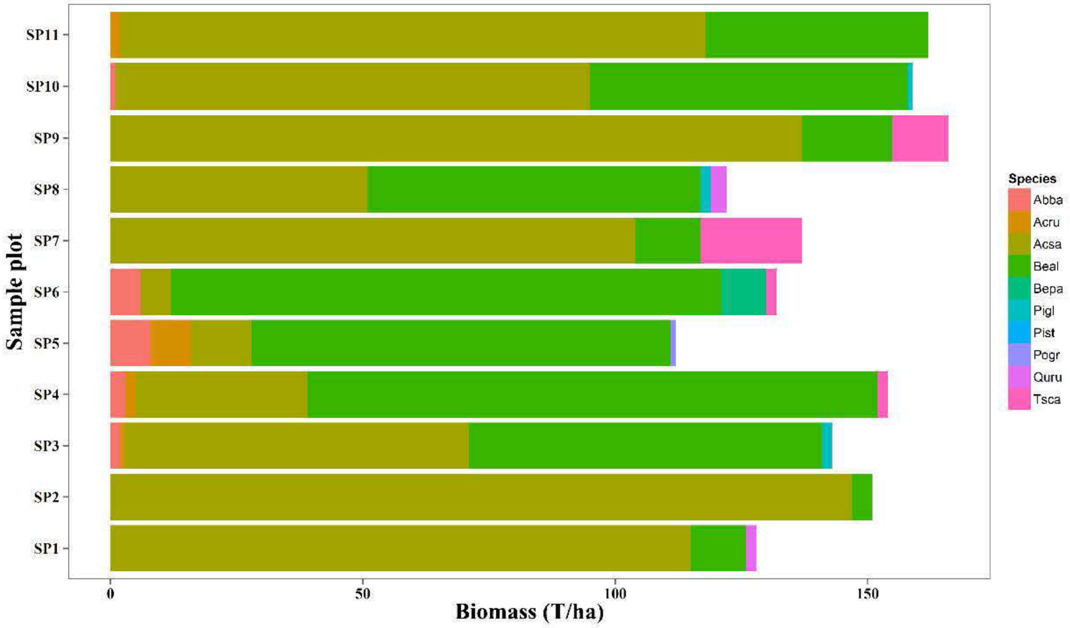


Figure H.1 Biomass by species for 11 old-growth sugar maple – yellow beach stands. See Figure 4.2 for species abbreviations.

We tested two different shade classifications: a ‘balanced’ one which gradually passes from class 0 to class 5, and a more ‘conservative’ one which increases faster from class 0 to class 5 (Table H.1). The tests were performed using LANDIS-Site V2.3 (Fig H.2). After 1000 years of simulation, sugar maple and yellow birch were still present in the stands using the ‘balanced’ shade classes. With the ‘conservative’ shade classes, sugar maple was dominant (ca. 75% of the total biomass) and yellow birch decreased by half (from 30 % at time 0 to less than 15% after 1000 years of simulation). The decrease of yellow birch and the increase of sugar maple in the conservative shade class definition were expected in the absence of disturbances (senescence only). However, had we used the conservative shade classes in LANDIS-II, the total amount of biomass would have been higher than in the sample plots (170 T/ha versus 140 T/ha). Moreover, with the conservative shade classes, yellow birch

Table H.1 Percentage of the lower threshold of biomass in a cell relative to the maximum possible biomass (App. G.1) to enter in the shade class indicated in column 1 for ‘balanced’ or ‘conservative’ shade species simulations. If the percentage of present biomass is under 10% the site shade class is considered 0 (open), if it is higher than 60% for the shade conservative simulation or 80% for the balanced simulation, the site shade class is consider 5 (closed).

Site shade class	Percent Max Biomass ‘conservative’ shade classes	Percent Max Biomass ‘balanced’ shade classes
1	10%	10%
2	20%	25%
3	30%	40%
4	40%	60%
5	60%	80%

would have always represented only a third of the sugar maple biomass, even without disturbance (Fig. H.3). Thus, we chose to use the 'balanced' shade classes in LANDIS-II to more realistically represent the total biomass in the landscape and have a better representativeness of yellow birch (Fig. H.1).

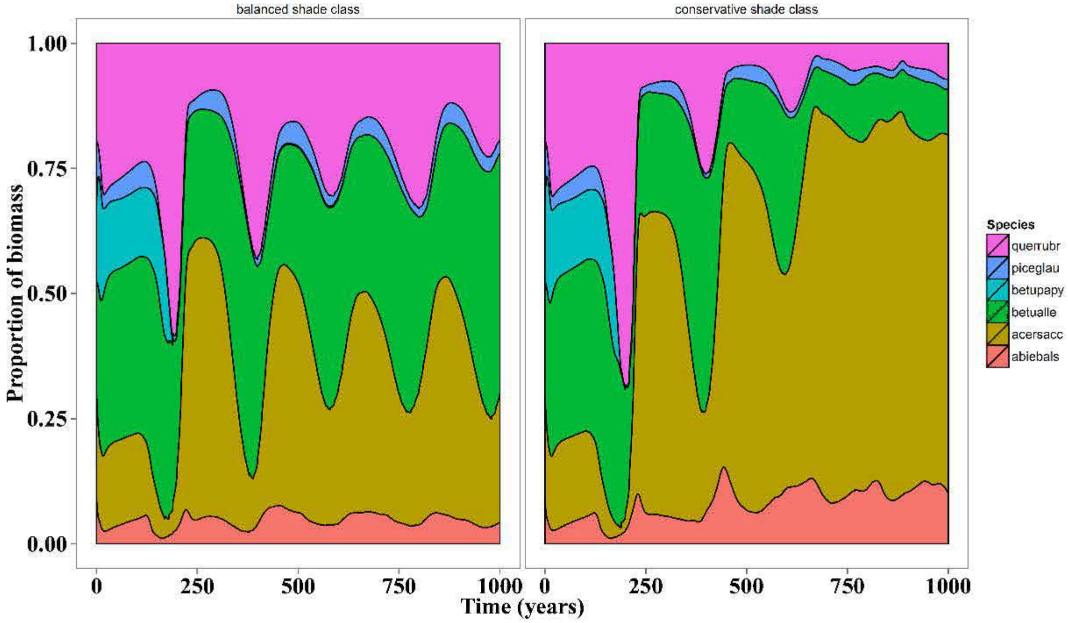


Figure H.2 Biomass proportion of 6 species (See Figure 4.2 for species abbreviations) using LANDIS-Site for the 'balanced' and the 'conservative' shade classes described in Table. H.1.

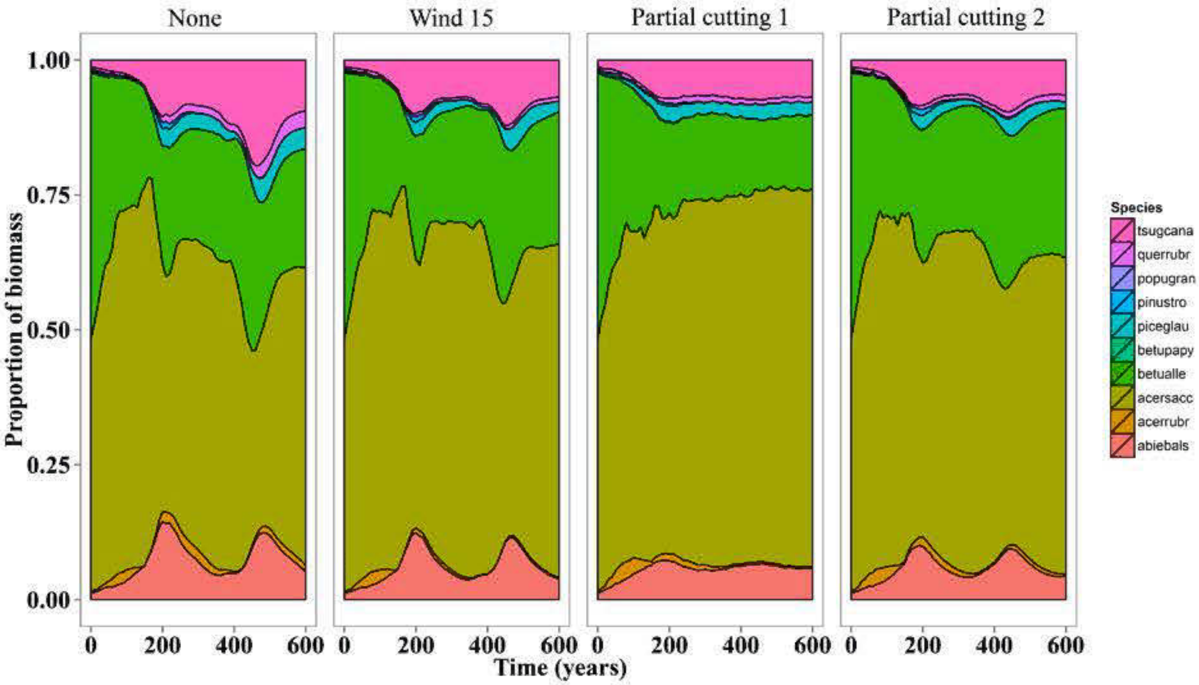


Figure H.3 Biomass proportion per species for four scenarios (without disturbance (None), with partial windthrow under a 15 years rotation (Wind 15) and with partial cutting with an intensity of 60% every 40 years (Partial cutting 1) and 20% every 20 years (Partial cutting 2)) using the 'conservative' shade classes (see Table H.1). See Figure 4.2 for species abbreviations.

APPENDIX I

STANDARD DEVIATION BETWEEN THE THREE REPLICATES FOR THE LIVING BIOMASS PER AGE CLASS AND THE TOTAL DEAD BIOMASS. THE STANDARD DEVIATION (SD) WAS COMPUTED FOR EACH SCENARIO (AND AGE CLASS FOR THE LIVING BIOMASS) AT EVERY TIME STEP. MINIMAL, MAXIMAL AND MEAN SD VALUES ARE PRESENTED OVER ALL 40 SCENARIOS AND 60 TIME STEPS. THE DATA RANGE OF EACH VARIABLE (MIN-MAX) IS ALSO PROVIDED.

	Data range (min / max) (in T/ha)	Min SD	Max SD	Mean SD
Living biomass per age class	99 /143	0.013	0.159	0.096
Dead biomass	30 / 47	0.033	0.133	0.075

BIBLIOGRAPHIE GÉNÉRALE

Abe, S., Masaki, T. & Nakashizuka, T. 1995. Factors influencing sapling composition in canopy gaps of a temperate deciduous forest. *Vegetatio* 120: 21-31.

Alessandrini, A., Biondi, F., Di Filippo, A., Ziaco, E. & Piovesan, G. 2011. Tree size distribution at increasing spatial scales converges to the rotated sigmoid curve in two old-growth beech stands of the Italian Apennines. *Forest Ecology and Management* 262: 1950-1962.

Angers, V.A., Messier, C., Beaudet, M. & Leduc, A. 2005. Comparing composition and structure in old-growth and harvested (selection and diameter-limit cuts) northern hardwood stands in Quebec. *Forest Ecology and Management* 217: 275-293.

Beaudet, M. & Messier, C. 1998. Growth and morphological responses of yellow birch, sugar maple, and beech seedlings growing under a natural light gradient. *Canadian Journal of Forest Research* 28: 1007-1015.

Bégin, E. 2011. *Caractérisation des régimes de perturbations par le chablis et des vents extrèmes dans l'érablière à bouleau jaune du Québec.* Unpublished M.Sc. thesis, UQAM, Montréal, Qc.

Bergeron, Y., Cyr, D., Drever, C.R., Flannigan, M., Gauthier, S., Kneeshaw, D., Lauzon, È., Leduc, A., Goff, H.L., Lesieur, D. & Logan, K. 2006. Past, current, and future fire frequencies in Quebec's commercial forests: implications for the cumulative effects of harvesting and fire on age-class structure and natural disturbance-based management. *Canadian Journal of Forest Research* 36: 2737-2744.

Bergeron, Y. & Fenton, N.J. 2012. Boreal forests of eastern Canada revisited: old growth, nonfire disturbances, forest succession, and biodiversity. *Botany* 90: 509-523.

Bergeron, Y. & Harvey, B. 1997. Basing silviculture on natural ecosystem dynamics: An approach applied to the southern boreal mixedwood forest of Quebec. *Forest Ecology and Management* 92: 235-242.

Bergeron, Y., Leduc, A., Harvey, B.D. & Gauthier, S. 2002. Natural fire regime: A guide for sustainable management of the Canadian boreal forest. *Silva Fennica* 36: 81-95.

Boulfroy, E. & Lessard, G. 2009. Atelier sur les projets pilotes d'aménagement écosystémique des forêts. *CERFO.*

Brown, J.L. 1981. *Les forêts du Témiscamingue, Québec: écologie et photo-interprétation.* Laboratoire d'écologie forestière, Université Laval.

Bugmann, H. 2001. A Review of Forest Gap Models. *Climatic Change* 51: 259-305.

Burrascano, S., Keeton, W.S., Sabatini, F.M. & Blasi, C. 2013. Commonality and variability in the structural attributes of moist temperate old-growth forests: A global review. *Forest Ecology and Management* 291: 458-479.

Busing, R.T. 1991. A spatial model of forest dynamics. *Plant Ecology* 92: 167-179.

Canham, C.D., Coates, K.D., Bartemucci, P. & Quaglia, S. 1999. Measurement and modeling of spatially explicit variation in light transmission through interior cedar-hemlock forests of British Columbia. *Canadian Journal of Forest Research* 29: 1775-1783.

Canham, C.D., Denslow, J.S., Platt, W.J., Runkle, J.R., Spies, T.A. & White, P.S. 1990. Light regimes beneath closed canopies and tree-fall gaps in temperate and tropical forests. *Canadian Journal of Forest Research* 20: 620-631.

Canham, C.D., Papaik, M.J. & Latty, E.F. 2001. Interspecific variation in susceptibility to windthrow as a function of tree size and storm severity for northern temperate tree species. *Canadian Journal of Forest Research* 31: 1-10.

Chokkalingam, U. & White, A. 2001. Structure and spatial patterns of trees in old-growth northern hardwood and mixed forests of northern Maine. *Plant Ecology* 156: 139-160.

Cooke, B.J. & Lorenzetti, F. 2006. The dynamics of forest tent caterpillar outbreaks in Québec, Canada. *Forest Ecology and Management* 226: 110-121.

Cowden, M.M., Hart, J.L., Schweitzer, C.J. & Dey, D.C. 2014. Effects of intermediate-scale wind disturbance on composition, structure, and succession in *Quercus* stands: Implications for natural disturbance-based silviculture. *Forest Ecology and Management* 330: 240-251.

Currie, W.S. & Bergen, K. 2008. *Ecosystems: Forest: Temperate*. Elsevier, Oxford.

Curzon, M.T. & Keeton, W.S. 2010. Spatial characteristics of canopy disturbances in riparian old-growth hemlock – northern hardwood forests, Adirondack Mountains, New York, USA. *Canadian Journal of Forest Research* 40: 13-25.

Cyr, D., Gauthier, S., Bergeron, Y. & Carcaillet, C. 2009. Forest management is driving the eastern North American boreal forest outside its natural range of variability. *Frontiers in Ecology and the Environment* 7: 519-524.

D'Amato, A.W. & Orwig, D.A. 2008. Stand and landscape-level disturbance dynamics in old-growth forests in western Massachusetts. *Ecological Monographs* 78: 507-522.

Dahir, S.E. & Lorimer, C.G. 1996. Variation in canopy gap formation among developmental stages of northern hardwood stands. *Canadian Journal of Forest Research* 26: 1875-1892.

Doyon, F. & Sougavinski, S. 2002. Caractérisation du régime de perturbations naturelles de la forêt feuillue du Nord-Est de l'Amérique du Nord. In: pp. 123. Institut québécois d'aménagement de la forêt feuillue.

Drever, C.R., Bergeron, Y., Drever, M.C., Flannigan, M., Logan, T. & Messier, C. 2009. Effects of climate on occurrence and size of large fires in a northern hardwood landscape: historical trends, forecasts, and implications for climate change in Témiscamingue, Québec. *Applied Vegetation Science* 12: 261-272.

Drever, C.R., Messier, C., Bergeron, Y. & Doyon, F. 2006. Fire and canopy species composition in the Great Lakes–St. Lawrence forest of Témiscamingue, Québec. *Forest Ecology and Management* 231: 27-37.

Environnement Canada 2011. Canadian Climate Normals 1981-2010 Station Data. Atmospheric Environment Service, Downsview, Ontario, Canada. http://climate.weather.gc.ca/climate_normals/index_e.html.

Fraver, S., White, A.S. & Seymour, R.S. 2009. Natural disturbance in an old-growth landscape of northern Maine, USA. *Journal of Ecology* 97: 289-298.

Frelich, L.E. & Lorimer, C.G. 1991a. Natural disturbance regimes in hemlock-hardwood forests of the Upper Great-Lakes region. *Ecological Monographs* 61: 145-164.

Frelich, L.E. & Lorimer, C.G. 1991b. A simulation of landscape-level stand dynamics in the northern hardwood region. *Journal of Ecology* 79: 223-233.

Gauthier, S., Vaillancourt, M.-A., Leduc, A., De Grandpré, L., Kneeshaw, D., Morin, H., Drapeau, P. & Bergeron, Y. 2008. *Aménagement écosystémique en forêt boréale*. Presses de l'Université du Québec, Québec, Canada.

Gauthier, S., Vaillancourt, M.-A., Leduc, A., De Grandpré, L., Kneeshaw, D., Morin, H., Drapeau, P. & Bergeron, Y. 2009. *Ecosystem management in the boreal forest*. Presses de l'Université du Québec, Québec, Canada.

Goff, F.G. & West, D. 1975. Canopy-understory interaction effects on forest population structure. *Forest Science* 21: 98-108.

Goodburn, J.M. & Lorimer, C.G. 1999. Population structure in old-growth and managed northern hardwoods: an examination of the balanced diameter distribution concept. *Forest Ecology and Management* 118: 11-29.

Gram, W.K., Sork, V.L., Marquis, R.J., Renken, R.B., Clawson, R.L., Faaborg, J., Fantz, D.K., Le Corff, J., Lill, J. & Porneluzi, P.A. 2001. Evaluating the effects of ecosystem management: A case study in a Missouri Ozark forest. *Ecological Applications* 11: 1667-1679.

Gravel, D., Beaudet, M. & Messier, C. 2010. Large-scale synchrony of gap dynamics and the distribution of understory tree species in maple–beech forests. *Oecologia* 162: 153-161.

Grenier, D.J., Bergeron, Y., Kneeshaw, D. & Gauthier, S. 2005. Fire frequency for the transitional mixedwood forest of Timiskaming, Quebec, Canada. *Canadian Journal of Forest Research* 35: 656-666.

Grenon, F., Jetté, J.-P. & Leblanc, M. 2010. Manuel de référence pour l’aménagement écosystémique des forêts au Québec – Module 1 - Fondements et démarche de la mise en oeuvre. In: pp. 51. Centre d’enseignement et de recherche en foresterie de Sainte-Foy inc. et ministère des Ressources naturelles et de la Faune, Direction de l’environnement et de la protection des forêts, Québec.

Grumbine, R.E. 1994. What is ecosystem management ? *Conservation Biology* 8: 27-38.

Hanson, J.J. & Lorimer, C.G. 2007. Forest structure and light regimes following moderate wind storms: Implications for multi-cohort management. *Ecological Applications* 17: 1325-1340.

Haynes, R.W., Bormann, B.T., Lee, D.C. & Martin, J.R. 2006. *Northwest Forest Plan—The First 10 Years (1994-2003): Synthesis of Monitoring and Research Results*. U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, Portland, Oregon.

Heilmann-Clausen, J. & Christensen, M. 2004. Does size matter?: On the importance of various dead wood fractions for fungal diversity in Danish beech forests. *Forest Ecology and Management* 201: 105-117.

Hobi, M.L., Commarmot, B. & Bugmann, H. 2015. Pattern and process in the largest primeval beech forest of Europe (Ukrainian Carpathians). *Journal of Vegetation Science* 26: 323-336.

Hodge, S.J. & Peterken, G.F. 1998. Deadwood in British forests: priorities and a strategy. *Forestry* 71: 99-112.

Hong, S.H. 2008. Forest landscape models: Definitions, characterization, and classification. *Forest Ecology and Management* 254: 484-498.

Hubbell, S.P. 2001. *The unified neutral theory of biodiversity and biogeography*. Princeton University Press.

Jardon, Y., Morin, H. & Dutilleul, P. 2003. Périodicité et synchronisme des épidémies de la tordeuse des bourgeons de l'épinette au Québec. *Canadian Journal of Forest Research* 33: 1947-1961.

Johnson, E.A., Miyanishi, K. & Weir, J.M.H. 1995. Old-growth, disturbance, and ecosystem management. *Canadian Journal of Botany* 73: 918-926.

Keeton, W.S. 2006. Managing for late-successional/old-growth characteristics in northern hardwood-conifer forests. *Forest Ecology and Management* 235: 129-142.

Keeton, W.S., Whitman, A.A., McGee, G.C. & Goodale, C.L. 2011. Late-successional biomass development in northern hardwood-conifer forests of the northeastern United States. *Forest Science* 57: 489-505.

Koukoulas, S. & Blackburn, G.A. 2005. Spatial relationships between tree species and gap characteristics in broad-leaved deciduous woodland. *Journal of Vegetation Science* 16: 587-596.

Landres, P.B., Morgan, P. & Swanson, F.J. 1999. Overview of the use of natural variability concepts in managing ecological systems. *Ecological Applications* 9: 1179-1188.

Lorimer, C.G. 1989. Relative Effects of Small and Large Disturbances on Temperate Hardwood Forest Structure. *Ecology* 70: 565-567.

Lorimer, C.G., Dahir, S.E. & Nordheim, E.V. 2001. Tree mortality rates and longevity in mature and old-growth hemlock-hardwood forests. *Journal of Ecology* 89: 960-971.

Lorimer, C.G., Frelich, L.E. & Nordheim, E.V. 1988. Estimating gap origin probabilities for canopy trees. *Ecology* 69: 778-785.

Manion, P.D. & Griffin, D.H. 2001. Large landscape scale analysis of tree death in the Adirondack Park, New York. *Forest Science* 47: 542-549.

McCarthy, J. 2001. Gap dynamics of forest trees: A review with particular attention to boreal forests. *Environmental Reviews* 9: 1-59.

Messier, C., Posada, J., Aubin, I. & Beaudet, M. 2009. Functional relationships between old-growth forest canopies, understorey light and vegetation dynamics. In: Wirth, C., Gleixner, G. & Heimann, M. (eds.) *Old-growth forests*, pp. 115-139. Springer, Berlin Heidelberg.

Ministère des Ressources naturelles de la Faune et des Parcs 2003. *Manuel d'aménagement forestier*. Gouvernement du Québec, Québec.

Mladenoff, D.J. 2004. LANDIS and forest landscape models. *Ecological Modelling* 180: 7-19.

Mladenoff, D.J. & Pastor, J. 1993. Sustainable forest ecosystems in the northern hardwood and conifer forest region: concepts and management. In: Aplet, G.H., Johnson, N., Olson, J.T. & Sample, V.A. (eds.) *Defining sustainable forestry*, pp. 145-180. Island Press, Washington, DC.

MRNF 2010. *Ressources et industries forestières - Portrait statistique*. Québec, Canada.

Nagel, T.A., Svoboda, M. & Kobal, M. 2014. Disturbance, life history traits, and dynamics in an old-growth forest landscape of southeastern Europe. *Ecological Applications* 24: 663-679.

Ódor, P. & Standovár, T. 2001. Richness of bryophyte vegetation in near-natural and managed beech stands: The effects of management-induced differences in dead wood. *Ecological Bulletins* 219-229.

Papaik, M.J., Canham, C.D., Latty, E.F. & Woods, K.D. 2005. Effects of an introduced pathogen on resistance to natural disturbance: beech bark disease and windthrow. *Canadian Journal of Forest Research* 35: 1832-1843.

Payette, S. 1992. Fire as a controlling process in the North American boreal forest. In: Shugart, H.H., Leemans, R. & Bonan, G.B. (eds.) *A systems analysis of the global boreal forest*, pp. 144-169. Cambridge University Press, Cambridge.

Payette, S., Filion, L. & Delwaide, A. 1990. Disturbance regime of a cold temperate forest as deduced from tree-ring patterns: the Tantaré Ecological Reserve, Quebec. *Canadian Journal of Forest Research* 20: 1228-1241.

Payette, S., Morneau, C., Sirois, L. & Desponts, M. 1989. Recent Fire History of the Northern Quebec Biomes. *Ecology* 70: 656-673.

Perera, A.H., Buse, L.J. & Weber, M.G. 2004. *Emulating Natural Forest Landscape Disturbances: Concepts and Applications*. Columbia University Press, New-York.

Perry, G.L.W. & Enright, N.J. 2006. Spatial modelling of vegetation change in dynamic landscapes: a review of methods and applications. *Progress in Physical Geography* 30: 47-72.

Peterson, C.J. & Pickett, S.T.A. 1991. Treefall and resprouting following catastrophic windthrow in an old-growth hemlock-hardwoods forest. *Forest Ecology and Management* 42: 205-217.

Pickett, S.T.A. & White, P.S. 1985. *Patch dynamics: a synthesis*. Academic Press, INC., Orlando, FL.

Pilon, V. & Payette, S. 2015. Sugar maple (*Acer saccharum*) forests at their northern distribution limit are recurrently impacted by fire. *Canadian Journal of Forest Research* 45: 452-462.

Piovesan, G., Alessandrini, A., Baliva, M., Chiti, T., D'andrea, E., De Cinti, B., Di Filippo, A., Hermanin, L., Lauteri, M. & Scarascia Mugnozza, G. 2010. Structural patterns, growth processes, carbon stocks in an Italian network of old-growth beech forests. *L'Italia Forestale e Montana* 65: 557-590.

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

Rubin, B.D., Manion, P.D. & Faber-Langendoen, D. 2006. Diameter distributions and structural sustainability in forests. *Forest Ecology and Management* 222: 427-438.

Rugani, T., Diaci, J. & Hladnik, D. 2013. Gap dynamics and structure of two old-growth beech forest remnants in Slovenia. *PLoS ONE* 8: e52641.

Runkle, J.R. 1982. Patterns of disturbance in some old-growth mesic forests of Eastern North America. *Ecology* 63: 1533-1546.

Runkle, J.R. 1985. Disturbance regimes in temperate forests. In: Pickett, S.T.A. & White, P.S. (eds.) *The ecology of natural disturbance and patch dynamics*, pp. 17-33. Academic Press Inc., London.

Scheller, R.M. & Mladenoff, D.J. 2007. An ecological classification of forest landscape simulation models: tools and strategies for understanding broad-scale forested ecosystems. *Landscape Ecology* 22: 491-505.

Seidl, R., Rammer, W. & Blennow, K. 2014a. Simulating wind disturbance impacts on forest landscapes: Tree-level heterogeneity matters. *Environmental Modelling & Software* 51: 1-11.

Seidl, R., Rammer, W. & Spies, T.A. 2014b. Disturbance legacies increase the resilience of forest ecosystem structure, composition, and functioning. *Ecological Applications* 24: 2063-2077.

Seymour, R.S., White, A.S. & de Maynadier, P.G. 2002. Natural disturbance regimes in northeastern North America - evaluating silvicultural systems using natural scales and frequencies. *Forest Ecology and Management* 155: 357-367.

Svoboda, M., Fraver, S., Janda, P., Bače, R. & Zenáhlíková, J. 2010. Natural development and regeneration of a Central European montane spruce forest. *Forest Ecology and Management* 260: 707-714.

Tanaka, H. & Nakashizuka, T. 1997. Fifteen years of canopy dynamics analyzed by aerial photographs in a temperate deciduous forest, Japan. *Ecology* 78: 612-620.

Taylor, A.R., Chen, H.Y.H. & VanDamme, L. 2009. A review of forest succession models and their suitability for forest management planning. *Forest Science* 55: 23-36.

Tyrrell, L.E. & Crow, T.R. 1994. Structural characteristics of old-growth hemlock-hardwood forests in relation to age. *Ecology* 75: 370-386.

Webster, C.R. & Lorimer, C.G. 2005. Minimum opening sizes for canopy recruitment of midtolerant tree species: A retrospective approach. *Ecological Applications* 15: 1245-1262.

Westphal, C., Tremer, N., Oheimb, G.v., Hansen, J., Gadow, K.v. & Härdtle, W. 2006. Is the reverse J-shaped diameter distribution universally applicable in European virgin beech forests? *Forest Ecology and Management* 223: 75-83.

Whitmore, T.C. 1989. Canopy Gaps and the Two Major Groups of Forest Trees. *Ecology* 70: 536-538.

Woods, K.D. 2004. Intermediate disturbance in a late-successional hemlock-northern hardwood forest. *Journal of Ecology* 92: 464-476.

Yaffee, S.L., Phillips, A.F., Frentz, I.C., Hardy, P.W., Maleki, S.M. & Thorpe, B.E. 1996. *Ecosystem management in the United States: an assessment of current experience*. Island Press, Washington.

Yamamoto, S.-I. 1992a. Gap characteristics and gap regeneration in primary evergreen broad-leaved forests of western Japan. *Botanical Magazine-Tokyo* 105: 29-45.

Yamamoto, S.I. 1992b. The gap theory in forest dynamics. *Botanical Magazine-Tokyo* 105: 375-383.

Zeibig, A., Diaci, J. & Wagner, S. 2005. Gap disturbance patterns of a *Fagus sylvatica* virgin forest remnant in the mountain vegetation belt of Slovenia. *Forest Snow and Landscape Research* 79: 69-80.

Zenner, E.K. 2004. Does old-growth condition imply high live-tree structural complexity? *Forest Ecology and Management* 195: 243-258.

Zhang, L., Gove, J.H., Liu, C. & Leak, W.B. 2001. A finite mixture of two Weibull distributions for modeling the diameter distributions of rotated-sigmoid, uneven-aged stands. *Canadian Journal of Forest Research* 31: 1654-1659.