UNIVERSITÉ DU QUÉBEC À MONTRÉAL

COEXISTENCE ET SYLVICULTURE DE L'ÉRABLE À SUCRE ET DU HÊTRE À GRANDES FEUILLES DANS UN CONTEXTE DE CHANGEMENTS GLOBAUX

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RÉSUMÉ

La présente étude visait à mieux comprendre la dynamique de la coexistence entre l'érable à sucre (*Acer saccharum* Marsh.) et le hêtre à grandes feuilles (*Fagus grandifolia* Ehrh.) dans un contexte de changements globaux et à évaluer des pratiques sylvicoles pouvant être adaptées à cet écosystème dans ce contexte en perpétuel changement. Dans le premier chapitre, nous nous sommes intéressés à l'effet de la fertilisation sur la croissance et la régénération de ces deux espèces dans un contexte où plusieurs auteurs émettent l'hypothèse d'une baisse de fertilité des sols - en raison des précipitations acides - qui défavoriserait l'érable aux par rapport au hêtre à grandes feuilles. Les données provenant d'une dispositif de fertilisation (chaulage) ne montrent que des effets négligeables de ce traitement sur la dynamique entre les deux essences, alors que des traitements de récolte et d'élimination des gaules de hêtre ont des effets beaucoup plus marqués. Nos résultats ne semblent pas démontrer que la richesse des sols est un facteur limitant la croissance et la régénération de l'érable à sucre dans la région à l'étude.

Dans le deuxième chapitre, nous nous sommes penchés sur l'évolution comparée de la croissance de l'érable à sucre et du hêtre sur une période d'environ 60 ans par dendrochronologie. Nos résultats démontrent clairement une chute abrupte de la croissance de l'érable par rapport au hêtre à partir de 1986. Sans pouvoir l'affirmer avec certitude, nous émettons l'hypothèse que cette baisse de croissance serait due à un événement de redoux suivi d'un gel sévère en janvier 1986, puis suivi par une sécheresse en 1988. Non seulement l'érable à sucre n'a pas recouvré sa croissance 20 ans plus tard, mais il semble avoir été affecté de nouveau par un autre événement extrême. Comme les événements extrêmes sont appelés à être de plus en plus fréquents, mais qu'ils peuvent avoir des effets en apparence subtils, nous prônons le développement d'approches de modélisation novatrices qui permettront de prendre en compte les effets de tels événements.

Dans le troisième chapitre, nous nous sommes intéressés à l'aménagement équienne comme outil potentiel pour l'adaptation aux changements globaux puisque ce mode d'aménagement est presqu'inutilisé dans les érablières du Québec. L'aménagement

équienne présente l'avantage de favoriser une grande diversité - tant à l'échelle du peuplement que du paysage - qui est souvent vue comme un élément important de la résilience des forêts face aux changements globaux. Malgré l'absence de littérature sur le sujet, il existe une forte croyance à l'effet que l'aménagement inéquienne est préférable à l'aménagement équienne pour favoriser la résilience des forêts. Nous avons ainsi procédé à une revue de littérature recensant les articles scientifiques à travers le monde qui comparent les deux modes d'aménagement au niveau écologique. Il ressort de cette revue qu'aucune des deux approches ne semble supérieure à l'autre du point de vue écologique, chacune ayant ses avantages et inconvénients. Comme les réponses obervées sur les effets de l'aménagement équienne et inéquienne sont très spécifiques aux espèces, cette revue supporte qu'une diversité d'approches sylvicoles sont nécessaires pour maintenir une diversité d'habitats. Par le fait même, notre étude ouvre la voie pour les aménagistes à l'utilisation d'un outil sylvicole supplémentaire – l'aménagement équienne, qui était quasiment proscrit dans certains types de forêts (ex. : les forêts de feuillus nobles) - pour faire face aux changements globaux.

Pris dans leur ensemble, les résultats des chapitres de la thèse supportent l'utilisation mesurée de l'aménagement équienne dans les érablières pour, entre autres, favoriser l'érable à sucre aux dépens du hêtre et la résilience de cet écosystème dans son ensemble. Enfin, nous jetons les bases d'une approche permettant de doser le niveau d'interventionnisme de l'humain dans sa volonté de faciliter l'adaptation des écosystèmes forestiers aux changements globaux.

INTRODUCTION GÉNÉRALE

La coexistence des espèces intrigue les écologistes depuis des décennies (ex. (Whittaker, 1965); elle a été étudié dans plusieurs milieux (ex. Christie and Armesto, 2003; Lusk and Smith, 1998; Wright, 2002; Yamamoto et al., 1995), et pour plusieurs taxa (ex. Martin, 1988; Novotny et al., 2002; Pfennig et al., 2006). Aussi, la coexistence des espèces est un champ de recherche en lui-même. Par exemple, Zobel (1992) identifie sept concepts (complémentaires ou exclusifs) permettant d'expliquer la coexistence d'espèces. Dans les dernières années, la théorie du modèle neutre (Hubbell, 1997) est certes celle qui a attiré le plus d'attention (Gravel et al., 2006). Cette théorie est à l'opposé de celle des niches et considère les espèces comme équivalentes au niveau fonctionnel et elle prend en compte les dynamiques aux échelles de la population locale et de la métacommunauté. Toutefois pour qu'une coexistence s'installe, une stabilité est requise dans les forces qui structurent les communautés (Clark et al 2007). Or, cette stabilité, spécialement avec les changements globaux, est fortement remise en question.

Depuis plusieurs décennies, les scientifiques tentent d'expliquer la coexistence de l'érable à sucre et du hêtre à grandes feuilles (CEEH) dans les forêts tempérées du nord-est américain. On parle de coexistence plus que de succession (e.g. Forcier, 1975) parce que les deux essences sont très tolérantes à l'ombre et qu'aucune ne semble dominer au point de marginaliser l'autre tant à l'échelle du peuplement que du paysage, et ce sur une longue période (plusieurs siècles). C'est la définition que nous retiendrons pour cette thèse. Poulson et Platt (1996) ont proposé un modèle de coexistence allogénique, dépendant de la grandeur et de la fréquence des trouées. Ce modèle se situe dans le même courant que celui des études de Runkle (1981) et Canham (1988, 1989) qui ont aussi étudié le succès de la régénération de ces deux essences en fonction de diverses caractéristiques des trouées. Bien que les résultats de ces études ne soient pas toujours concordants, ils tendent généralement à démontrer que le hêtre a une meilleure capacité à survivre sous couvert et que l'érable à sucre a une meilleure capacité à augmenter sa croissance en hauteur en présence d'une trouée. Par contre, Beaudet et al. (2007) n'observent pas de changements marqués de la performance de la régénération des deux essences selon un gradient de lumière après une importante ouverture créée par un verglas. Ce résultat est en contradiction avec celui de Canham (1989) qui a observé une meilleure réponse de la part de l'érable à des petites trouées que de la part du hêtre. Nolet et al. (2008) observent un plus grand succès pour l'érable à sucre après coupe totale qu'après coupe partielle et émettent l'hypothèse qu'il existe un seuil de lumière à partir duquel l'érable à sucre est plus performant que le hêtre à grandes feuilles. Ce seuil serait toutefois beaucoup plus élevé que celui proposé par Poulson et Platt (1996). (Gravel et al., 2011) observent un changement sur 40 ans dans le succès relatif de l'établissement des deux essences, passant d'un avantage pour l'érable à un avantage pour le hêtre à grandes feuilles sans toutefois pouvoir en expliquer les causes. Arii et Lechowicz (2002) ont quant à eux démontré que les conditions de sol avaient aussi un effet important sur le succès de régénération des deux essences, le hêtre évitant les sites les plus secs et l'érable évitant les sites plus pauvres (pH acide et teneur en calcium plus faibles) sous la canopée de hêtre. Ce dernier résultat, l'effet de la canopée du hêtre sur les caractéristiques des sols, va dans le sens d'une coexistence autogénique et est donc en contradiction avec le modèle de Poulson et Platt. D'autres auteurs ont aussi vu des relations entre les caractéristiques de sol et le succès relatif des deux essences en régénération (Duchesne et al., 2005; Nolet et al., 2008) alors que d'autres n'en ont pas observées (Gravel et al., 2011).

Parallèlement aux études sur la CEEH, de très nombreuses études se sont penchées sur le dépérissement de la cime ou le déclin de la croissance de l'érable à sucre observé à différentes périodes dans le nord-est américain et au Canada depuis quelques décennies (Millers et al., 1989). Il n'est pas toujours facile de dissocier les phénomènes de dépérissement et déclin puisqu'ils sont intimement liés (Houston, 1999). La quantification de ces phénomènes prend différentes formes. Par exemple, sur le plateau des Appalaches, les érables morts peuvent représenter de 25 à 30% de la surface terrière en érable sur les certains sites les plus susceptibles (Hallett et al., 2006). Bauce and Allen (1991) observent une diminution de croissance en surface terrière de l'érable dans l'état de New York de l'ordre d'environ 40% entre 1962 et 1987. Duchesne et al. (2002) ont aussi observé de telles chutes de croissance dans certains sites du Réseau d'étude et de surveillance des écosystèmes forestiers (RESEF) du Québec. Kolb et McCormick (1993) montrent une baisse de croissance en surface terrière d'environ 75% sur 20 ans dans des érablières de la Pennsylvanie. Ce ne sont pas toutes les régions qui sont touchées par le déclin/dépérissement; par exemple, Lane et Reed (1993) n'observent aucun signe de déclin à long terme pour l'érable dans le nord des États-Unis. Dans l'ouest du Québec, des données récentes semblent indiquer que la croissance en diamètre de l'érable à sucre est toujours en déclin (Labrecque et al., 2006).

Ce déclin/dépérissement a été associé à de nombreux facteurs, tels la défoliation par les insectes (Cooke and Lorenzetti, 2006), les maladies (Houston, 1999), les facteurs climatiques (Auclair et al., 1996; Payette et al., 1996), les dépôts acides (Adams, 1999), la densité des peuplements (Bauce and Allen, 1991), l'âge des peuplements (Auclair et al., 1996) et la colonisation par l'érable de sites qui lui sont peu propices (Horsley et al., 2000). Il demeure que les chercheurs semblent s'accorder sur le fait qu'il n'y a pas qu'une seule cause liée au déclin de l'érable à sucre. Toutefois, c'est sur l'importance relative de ces facteurs ou leur caractère (facteur prédisposant, initiateur, aggravant (Manion, 1981) que les opinions divergent. Les facteurs liés aux peuplements (densité, âge et qualité de site) sont considérés comme des facteurs prédisposant en ce sens qu'ils ne sont pas à l'origine du dépérissement, mais le favorisent. Les défoliations par les insectes (Gavin et al., 2008) ont des effets marqués sur la croissance de l'érable, mais je n'ai trouvé aucune étude qui présentait cette cause comme étant la principale cause du déclin/dépérissement de l'érable à sucre. Les défoliations par les insectes semblent souvent agir en concomitance avec des événements climatiques extrêmes. Pour plusieurs auteurs, les événements climatiques extrêmes seraient la cause principale des déclins observés (Auclair et al., 1997; Bauce and Allen, 1991; Gavin et al., 2008); les sécheresses et les événements de gel-dégel sont les phénomènes les plus souvent cités. Enfin pour plusieurs autres chercheurs, les dépôts acides, en diminuant la quantité d'éléments nutritifs disponibles dans le sol pour la végétation, seraient la principale cause de dépérissement des érablières (Adams, 1999; Moore et al., 2012; Sharpe et al., 2002). Le débat sur l'importance des dépôts acides sur la santé et la dynamique des érablières a d'ailleurs donné lieu à des échanges virulents dans la littérature scientifique (Messier et al., 2011; Sharpe et al., 2002).

En général, les corpus de littérature sur la CEEH et le dépérissement des érablières sont très indépendants, peu d'auteurs faisant le lien entre les deux sujets (voir toutefois Duchesne et al., 2005 et Nolet et al., 2008). Cela s'explique probablement par le fait que les études traitant de la CEEH ont en commun qu'elles ne regardent que le succès relatif de la régénération (semis et gaules) d'une essence par rapport à l'autre. Bien qu'il soit extrêmement pertinent de s'intéresser à la régénération pour connaître comment évolue la dominance entre les deux essences, il est surprenant que peu d'études (voir Runkle, 2013) se soient penchées sur la performance relative des deux essences à des stades plus avancés (DHP de 10 cm et plus). Cette performance à des stades plus avancés, certes influencée par le dépérissement, est susceptible d'influencer la composition en essences dans la canopée, qui , à son tour, peut avoir une influence sur le succès de régénération des deux essences.

Afin de mieux comprendre l'évolution de la CEEH dans un contexte de changements globaux, la présente étude vise à préciser l'effet des variables climatiques et du statut nutritionnel, appelés à évoluer avec les changements climatiques et les dépôts acides (deux des éléments les plus importants des changements globaux), sur la CEEH, et ce, à différents stades de développement des individus, pas seulement au stade de la régénération. La prise en compte de différentes classes de taille des individus dans l'étude de la CEEH apparaît importante pour deux raisons distinctes. Premièrement, les individus dominants de la canopée ne sont pas soumis aux mêmes conditions de croissance que les individus sous la canopée que ce soit en termes de radiation, de température, de pression atmosphérique ou de vitesse de vent (ex. Baldocchi et al., 2002). N'étant pas soumis aux mêmes conditions, les individus de différentes tailles ne réagiront pas nécessairement de la même façon à des changements de conditions (ex. : disponibilité en eau – Mérian and Lebourgeois, 2011 - ou en éléments nutritifs). Deuxièmement, le stade de développement ontogénique peut avoir un effet marqué sur l'allocation des ressources (Delagrange et al., 2004). Il est donc logique de croire que des individus de tailles différentes ne sont pas nécessairement influencés de la même façon par des changements de conditions de croissance. Par exemple, des jeunes tiges en plein développement pourraient avoir des besoins en éléments nutritifs du sol plus grands que des arbres dominants qui, en grande partie, recyclent les éléments nutritifs (Vadeboncoeur, 2010). Autre exemple, des plus petits individus ayant des systèmes racinaires moins bien développés pourraient avoir plus de difficultés à tolérer un déficit en eau.

Par ailleurs, les changements globaux ne sont pas les seuls facteurs à influencer la CEEH puisque d'autres facteurs, tels les épidémies d'insectes (Cooke and

Lorenzetti, 2006), le broutage par les chevreuils (Sage et al., 2003), et l'aménagement forestier (Nolet et al., 2008), peuvent aussi influencer cette coexistence, et ce, de façon indépendante ou non des changements globaux. L'aménagement forestier, et plus spécifiquement la sylviculture, peut toutefois constituer une opportunité pour rendre les forêts plus résilientes face aux changements globaux. Toutefois dans la très grande majorité des juridictions qui couvrent l'aire de distribution de l'érable à sucre et du hêtre à grandes feuilles, la sylviculture est peu diversifiée puisque l'aménagement inéquienne (coupe de jardinage) y est fortement recommandé, sinon obligatoire, ne laissant que très peu de place à l'aménagement équienne. Pourtant, l'aménagement équienne, spécialement s'il est bien agencé avec d'autres formes d'aménagement, semble présenter certains avantages en termes de résilience des peuplements forestiers, car il favorise souvent une diversité en essences forestières et permet de ré-initialiser un peuplement forestier à partir de jeunes tiges vigoureuses. Dans un contexte de changements globaux, une diversification de la sylviculture favoriserait probablement la résilience des écosystèmes présentement dominés par ces deux essences. Or, l'aménagement équienne se bute à des préjugés quant à ses impacts écologiques – peut-être parce qu'utilisé de façon trop dominante dans certaines régions. Si ces préjugés sont fondés ou demeurent des préjugés, il sera difficile d'entrevoir l'aménagement équienne comme une option valable pour favoriser la résilience des forêts

Ainsi, dans le Chapitre 1, j'étudierai la comment la CEEH est influencée par des changements dans le statut nutritionnel du sol en relation avec la taille des individus. Dans le Chapitre 2 de ma thèse, je me pencherai sur les effets du climat sur la CEEH en fonction de la taille des individus étudiés (contrairement à Gravel et al. (2011) par exemple qui s'étaient concentrés sur les gaules). Finalement, dans le Chapitre 3, j'évaluerai, à partir d'une revue de littérature, comment l'aménagement équienne et inéquienne se comparent quant à leurs impacts écologiques dans les forêts du monde entier.

Mes hypothèses générales sont donc les suivantes:

- Comme de nombreuses études tendent à démontrer un effet positif important de la fertilité des sols sur l'érable à sucre, la fertilisation devrait favoriser la croissance et la régénération de l'érable à sucre aux dépens du hêtre à grandes feuilles.
- Comme de nombreuses études ont relaté une baisse de croissance de l'érable à sucre, et ce un peu partout sur son aire de distribution, un moment charnière relié au début de cette baisse devrait être observé;
- Comme l'aménagement équienne est perçu de façon négative au Québec (en forêt feuillue noble plus particulièrement) et dans plusieurs autres juridictions, une revue de littérature exhaustive comparant les effets écologiques de l'aménagement équienne et inéquienne devrait démontrer des effets écologiques beaucoup plus négatifs pour l'aménagement équienne.

CHAPITRE I

LIMING HAS A LIMITED EFFECT ON SUGAR MAPLE-AMERICAN BEECH DYNAMICS COMPARED TO BEECH SAPLING ELIMINATION AND CANOPY OPENING.[1]

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[1] Ce chapitre a été accepté, tel que présenté, dans la Revue canadienne de la Recherche forestière. Les co-auteurs sont : Sylvain Delagrange, Kim Bannon, Christian Messier et Daniel Kneeshaw.

1.1 Abstract

Sugar maple (SM, *Acer saccharum* Marsh.)-dominated forests of North America are increasingly affected by many human-induced modifications in environmental conditions. As a remedy, adapted silvicultural treatments are needed. Even though it is generally accepted that SM health is related to soil fertility and that there is an extensive literature on SM-American beech (AB, *Fagus grandifolia* Ehrh.) regeneration stand dynamics related to light availability, the interaction between these two factors has rarely been studied. Our main objective was thus to verify the possible role of a light-soil interaction on SM-AB stand dynamics. We used a factorial design with three factors (harvest intensity, liming and beech sapling elimination) to test this interaction. Our results showed that the radial growth of SM and AB tree and sapling growth was positively affected by canopy opening but not by liming. Liming did not favour AB seedlings while it favoured SM in specific canopy opening situations confirming, albeit partially, the light-soil interaction hypothesis. Overall, liming had very limited effects on SM-AB stand dynamics compared to canopy opening and AB sapling elimination treatments. We do not advocate the extensive use of liming as other silvicultural strategies tested provided more promising results to favour SM over AB.

1.2 Introduction

For decades, forest ecologists have attempted to understand the mechanisms that drive changes in forest composition in order to predict future conditions. This understanding is crucial in an era of global change, given that silvicultural treatments can either help forests to adapt to novel ecological conditions (e.g. West et al., 2009) or decrease forest resilience when improper actions are taken. The forests of northeastern North America that are dominated by sugar maple (SM, *Acer saccharum* Marsh.) represent an example of an ecosystem that requires both deeper understanding and adapted silviculture, as evidence shows that this ecosystem has already been affected by changes in environmental conditions (e.g. Auclair et al., 1996; Driscoll et al., 2003). Despite many studies that have been carried out on the dynamics of sugar maple-dominated ecosystems in the last few decades, limited links have been made between two major research perspectives: the first one, driven mainly by abiotic factors (e.g. soil fertility), focuses on sugar maple decline and the second one driven, mainly by biotic factors, focuses on sugar maple-American beech (AB, *Fagus grandifolia* Ehrh.) coexistence.

SM decline has been reported in many studies over recent decades. This decline, which is closely linked to SM dieback (Houston, 1999), has affected SM stands in many parts of its distribution. For example, Hallett et al. (2006) reported that dead SM represent about 25% to 30% of SM basal area on the Allegheny Plateau of the northeastern USA. Moreover, many studies have reported decreases in basal areal increment in recent decades: a decrease of approximately 30% in the state of New York (Bauce and Allen, 1991) and in the province of Québec (Duchesne et al., 2002), and as great as 75% in Pennsylvania (Kolb and McCormick, 1993).

While it is generally accepted that SM decline is due to many concomitant factors - insect defoliation (Cooke and Lorenzetti, 2006), diseases (Houston 1999), climatic events (Auclair et al., 1996; Payette et al., 1996), soil fertility depletion is the factor that has received the most attention. Many studies (Duchesne et al., 2002; Hallett et al., 2006; Kolb and McCormick, 1993) have shown a relationship between sugar maple decline and current soil nutrient status (mainly with Mg and Ca). However, these studies could not determine a causal relationship because they did not directly link SM decline to any change in soil nutrient status. To overcome this problem, many studies have tested whether fertilization would increase SM performance. In a meta-analysis, Vadeboncoeur (2010) showed that fertilization with Ca (alone or in combinations with other elements) generally has a positive effect on SM performance. However, results were highly variable as some authors observed marked positive effects (Long et al., 2011; Moore and Ouimet, 2006; Wilmot et al., 1996), others observed no effects (Fyles et al., 1994; Gasser et al., 2010), and still others noted negative effects (Côté et al., 1995). In another recent meta-analysis, Reid and Watmough (2014) also observed strong variation in the effects of liming and ash fertilization on hardwood growth.

On the biotic side, many studies published since the early 1980's focused on SM-AB coexistence. While some divergent results have been reported, a consensus seems to emerge – especially among studies focussing on the regeneration dynamics between the two species, that a slight increase in the frequency and size of gaps favours SM over AB. For example, Runkle (1981) showed that the SM-AB dynamics differed among sites given that species self-replacement occurred on some sites while reciprocal replacement of SM by AB regeneration occurred on others. Canham (1988) observed a stronger growth response of SM than AB to small canopy gaps, which he attributed to a greater increase in leaf area and better leaf display for sugar maple in gaps compared to those beneath closed canopies. He subsequently showed that beech saplings are better able to withstand canopy competition (Canham, 1990). Brisson et al. (1994) predicted that in an old-growth SM dominated stand, AB abundance would strongly increase if the high proportion of AB that was observed in the sapling layer persists. The authors further suggested that light was a possible limiting factor for SM seedling survival. Poulson and Platt (1996) observed that an increase in the number of gap openings and available vertical light in the recent decades shifted SM-AB dynamics, leading to an advantage of SM over AB.

In subsequent decades, a number of studies arrived at different conclusions. Beaudet et al. (2007), who worked on the same site as Brisson et al. (1994), noticed no significant changes in the relative performance of SM and AB seedlings after large openings were created by a severe ice storm. Nolet et al. (2008) showed openings that were much larger than those described by Poulson and Platt (1996) or Canham (1988) were required to favour SM over AB in the sapling stage. Nelson and Wagner (2014) observed that shelterwood harvests are not sufficient to favour SM over AB at the seedling stage unless a silvicultural treatment is applied to eliminate the AB sapling layer. To understand how SM can be promoted at the expense of AB is actually an important issue because SM has a much greater economic value.

Studying the combined effect of stand disturbance history and soil nutrient status on current SM and AB regeneration, Nolet et al. (2008) put forward a hypothesis that would help to reconcile differences in findings from studies that were related to SM-AB dynamics with those that were related to the effect of soil fertility on SM decline. Their hypothesis considers a light-soil interaction and is two-fold. First, as light increases, SM performance relative to that of AB improves and, beyond a certain threshold, SM even exceeds AB growth. While other authors had found similar results, Nolet et al. (2008) add that this threshold is much higher than previously found and that large openings are required for SM to outperform AB. The second part of the light-soil interaction hypothesis predicts that the light threshold is higher on less fertile sites, meaning that on poorer soils, SM will require more light to outperform AB. This second part is in agreement with many findings showing SM to be more sensitive to changes in soil fertility than AB (Kobe et al., 2002; Long et al., 1997). This hypothesis is supported physiologivally as nutrients (e.g calcium) are involved in several leaf mechanisms including stomata opening and synthesis of membanes and cell walls (McLaughlin and Wimmer, 1999). Furthermore, Nolet et al. (2008) were not explicit about how their hypothesis might apply to various stages of stem development. However, the consideration of stem size in the study of SM-AB dynamics appears to be important for two distinct reasons. First, dominant individuals in the canopy are not subject to the same growth conditions as individuals under the canopy (poles, saplings and seedlings) in terms of radiation, temperature, air pressure or wind speed (e.g., Baldocchi et al. 2002). Second, the stage of development of the individual (or size) can have a marked effect on resource allocation (Delagrange et al., 2004). It is therefore logical to assume that individuals of different sizes are not necessarily influenced in the same way by changes in growth conditions (Mérian and Lebourgeois, 2011). A better understanding of how the response of the various stages of stem development to canopy opening and fertilization differ is crucial to develop sound silvicultural treatments.

Using an experimental design that was established in 2006, our objectives were i) to test the light-soil interaction hypothesis advanced by Nolet et al. (2008) and ii) to propose adapted silvicultural treatments to favour SM at the expense of AB.

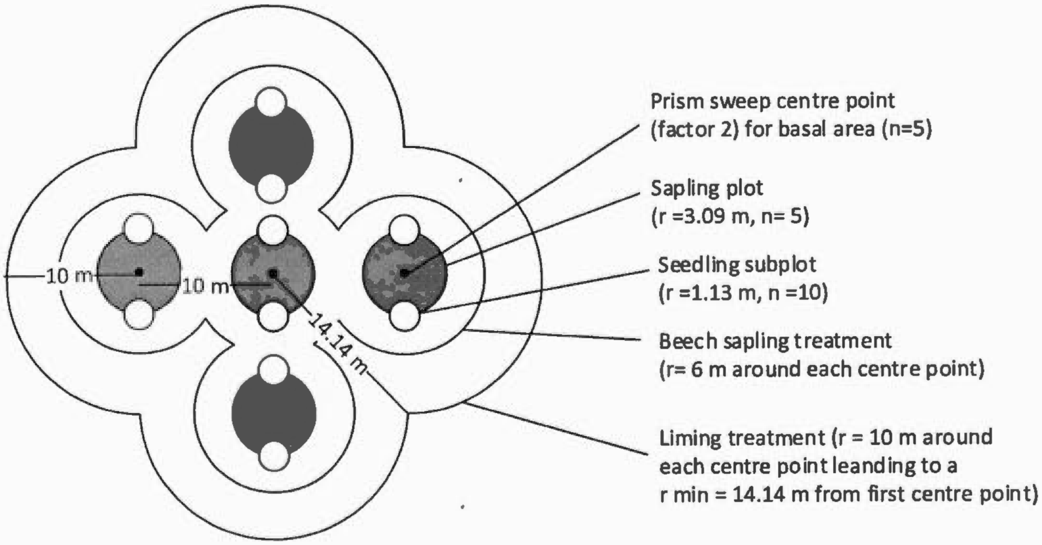
1.3 Methods

1.3.1 Study area

The study area is located northeast of Duhamel (Quebec, Canada) close to Gagnon Lake (46°07'40" N, 75°09'24" W.), which is in the eastern portion of the Simon Lake landscape unit in the western sugar maple–yellow birch (*Betula alleghaniensis* Britton) bioclimatic region (Saucier et al., 2009).The landscape contains numerous hills with elevations rarely exceeding 350 m asl (Robitaille and Saucier, 1998). Mean annual temperature is 3.7 °C, the mean annual precipitation is about 1000 mm (including 250 mm as snow), and the number of degree-days above 0 °C is 2716 (Environment Canada, 2014). Surface geology of the study area is characterized by thin to moderately thin glacial till, which is composed of metamorphic rocks, such as gneiss. The parent material is topped by sandy Dystric Brunisols (Soil Landscapes of Canada Working Group (SLCWG), 2010). The forest canopy is dominated by sugar maple in association with yellow birch, American beech, American basswood (*Tilia americana* L.), ironwood or American hop-hornbeam (*Ostrya virginiana* (Miller) K. Koch), eastern hemlock (*Tsuga canadensis* (L.) Carrière), and balsam fir (*Abies balsamea* (L.) Miller). The region is recognized for its relatively low pH and Ca levels (Bannon et al., 2015) and Nolet et al. (2008) showed that higher Ca levels were associated with higher SM performance over AB in this region.

1.3.2 Experimental design

We used a complete factorial design with three crossed factors: harvest intensity (to affect light), liming (to increase soil fertility), and an AB cleaning treatment (to control competition). Three levels of harvest intensity (control, selection cut, and clear-cut), two levels of liming (no treatment, liming), and two levels of cleaning treatment (no treatment, beech sapling elimination) were tested. Each treatment combination was replicated 4 times, leading to 48 treatment units, which were randomly assigned to a location and were at least 100 m apart (Figure A.1, supplementary material). The study site covered an area of 320 ha though most of the treatment units were concentrated in a 120-ha section. We localized the central point within each treatment unit using a steel pin and used it as the centre of the first plot (of five) in the treatment unit (Figure 1.1). The four other plot centres were located 10 m from the first plot centre and oriented in the four cardinal directions. We used these five plots mainly to describe the tree and sapling strata (see Field measurement section). Moreover, two 4 m^2 subplots were located 2 m north and south of each plot centre to describe the seedling layer (see Field measurement section).



Prism sweep centre point
(factor 2) for basal area (n=5)

Sapling plot
(r =3.09 m, n= 5)

Seedling subplot
(r =1.13 m, n =10)

Beech sapling treatment
(r= 6 m around each centre point)

Liming treatment (r = 10 m around
each centre point leanding to a
r min = 14.14 m from first centre point)

Figure 1.1 Sampling and treatment design used in each treatment unit.

1.3.3 Treatments

Canopy harvesting treatments were implemented in the autumn 2006. Most of the study area was treated using selection cutting (30 % basal area removal distributed over all diameter classes) according to Québec standards for provincial lands (Majcen et al., 1990). Clear-cuts and controls were implemented within this matrix of selection cuts.

Clear-cuts were performed without special care for advance regeneration and varied in size from 0.6 ha (80 m * 80 m) to 1 ha (100 m *100 m). Controls (no canopy harvesting) were 1 ha in area. After harvesting, 1 clear-cut treatment unit was destroyed by road construction, 1 selection cut could not be precisely located, and another selection cut did not end up being harvested and, thus, was considered as another control. These changes left us with 15 clear-cuts, 14 selection cuts and 17 controls (Table 1.1). In May 2007 at the beginning of leaf out, half of the treatment units (i.e., 23) were fertilized with the equivalent of 3 t ha^{-1} of dolomitic lime (29% in calcium and 6% in magnesium), leading to a fertilization of 870 kg ha^{-1} in calcium and 180 kg ha^{-1} in magnesium). As a comparison, Moore and Ouimet (2006) observed positive effect with the addition 1 t ha^{-1} of dolomitic lime. The treatment was equally applied, within a 10 m-radius of each of the five centres in each treatment unit (Figure 1.1), using a modified leaf blower (Stihl BG85, Figure A.2, supplementary material). For half of the treatment units (almost equally distributed according to the canopy harvesting and liming treatments), we eliminated beech saplings within a 6 m-radius of each plot centres (Figure 1.1), using manual cutters for smaller saplings (1-5 cm DBH, diameter at 1.3 m above ground level) and motor-manual brushsaws for bigger saplings (5 to 9 cm in DBH) in June 2007.

1.3.4 Field measurements

Data collection was performed from autumn 2006 (pre-harvest) to late summer 2013, as detailed in Table 1.2. For each treatment unit, a factor 2 (metric) prism sweep was performed at each of the five plot centres in which species of all trees ≥ 9.1 cm in DBH was recorded. In autumn 2011, all sugar maple and beech trees within a 13 m radius around the first plots of each treatment unit (partial cuts and controls) were cored with an increment borer at DBH. This radius was selected to ensure that the sampled trees had potentially been affected by liming (Figure 1.1). The number of SM and AB saplings was recorded by DBH classes (1.1-3 cm; 3.-5 cm; 5.1-7 cm; 7.1-9 cm) at each plot centre, within a 3.09 m radius (30 m^2). In 2013, one sapling of both species and each DBH class (when present) in partial cuts and controls was cut at DBH and a disk was brought back to the laboratory for further radial growth analysis. Sugar maple, beech and other species (mainly yellow birch, ironwood and trembling aspen (*Populus tremuloides Michx.*)) seedlings (< 1.1 cm at DBH) were counted within each 4 m^2 circular subplot centre (1.13 m radius) 4 times during the 8-year period of investigation. Further, the height of the tallest seedling for each species in each plot was recorded in August 2013.

Table 1.1 **Number of treatment units (*n*) and mean pre-harvest basal area in sugar maple (SM) and American beech (AB) by treatment combinations.**

Treatments			n	Pre-harvest basal area (m2*ha^{-1})				
Canopy opening	AB sapling elimination	Liming		SM	AB	Mean elevation (m)	Mean slope (%)	Mean summer radiation (MJ)[1]
Control	no	no	4	9.6	7.8	304.0	5.3	2 303
		yes	4	10.2	6.8	271.8	6.4	2 292
	yes	no	4	11.9	7.6	298.8	7.2	2 263
		yes	5	11.0	7.2	290.2	3.1	2 307
Selection cut	no	no	4	6.9	10.1	272.5	6.5	2 292
		yes	4	6.5	8.5	285.0	7.2	2 288
	yes	no	4	10.7	8.9	295.0	8.3	2 248
		yes	2	6.6	13.4	271.0	7.3	2 270
Clearcut	no	no	3	9.1	8.0	290.7	7.2	2 302
		yes	4	11.7	6.4	265.3	10.6	2 174
	yes	no	4	12.3	6.2	282.0	4.5	2 299
		yes	4	8.8	8.0	286.8	4.4	2 292

[1] Calculated with the function Solar radiation of Arc Toolbox in ArcGIS (v.10.2)

Table 1.2 Chronology of treatments and data collected during the present study.

	Au2006[1]	Sp2007[1]	Au2007[1]	Su2011[1]	Au2011[1]	Su2013[1]
Tree harvesting	x					
Liming		x				
Regeneration treatment		x				
Seedling count	x	x	x			x
Seedling height						x
Sapling count	x	x	x			x
Sapling disks						x
Tree composition	x					
Tree boring					x	
Light measurement				x		
Soil sampling		x				x

[1] Au: Autumn; Sp: Spring; Su: late-Summer

To quantify the light environment created by each canopy opening and beech regeneration treatment, we took hemispherical photographs (at 0.5 m in height) at the centre of each treatment unit at the end of summer 2009. For each treatment unit, 5 soil samples (one at each plot centre) were taken from the B-horizon in spring 2007 prior to liming and in summer 2013, and later composited to estimate average soil conditions.

1.3.5 Laboratory analyses

The ring-widths of 12 years (1998-2009) for the tree cores, and 15 years (1998-2013) for the sapling disks were measured to the nearest 0.01 mm using a 40X magnification scope and a sliding measurement stage (Velmex Inc., Bloomfield, NY, USA), which was coupled to a digital meter. For light measurements, each hemispheric photograph was converted to black and white format and analyzed with GLA (Gap Light Analyzer; Fraser 1999). Finally, soils samples were air dried for several weeks and sieved to pass a 2 mm-mesh screen prior to analysis. Bulk pH of 2:1 (soil:deionized water) slurries was measured with a glass electrode-calomel probe (pHM82, Standard pH Meter; Radiometer Copenhagen, Brønshøj, Denmark). Exchangeable soil cations were extracted with unbuffered 0.1 mol*L^{-1} $BaCl_2$ solution (Hendershot et al. 1993). Cation (Ca, Mg) concentrations were determined by atomic absorption spectrometry (PerkinElmer Inc., Wellesley, MA).

1.3.6 Data analyses

All of our statistical analyses followed the model comparison approach that was based on the Kullback-Leibler information quantity, as presented by Anderson et al. (2000): this approach is different from the classical null hypothesis testing approach as the goal is to identify the best model of a set of models rather than to test an alternative hypothesis vs a null hypothesis. For each response variable (indicator), we compared the performance of a full model to simpler models using the three factors (harvest intensity, liming and cleaning treatment) of our experimental design as predictor variables. This approach allowed us to test various plausible hypotheses regarding the effect of our predictor variables on the response variables in two ways. First, by comparing the corrected Akaike information criterion (AICc) obtained by each model, it is possible to calculate the weight (ω) of a specific model, which can be interpreted as the probability that this model is the best among all tested models. Second, since a predictor variable may appear in more than one model, it is also possible to sum up the weight of the models in which a predictor variable appears. This cumulative weight can be interpreted as the probability that a specific predictor variable be part of the best tested model (in contrast with p values used in null model testing). All analyses were performed in R (version 3.1.0; R Development Core Team 2013) and were run separately for SM and AB because the degrees-of-freedom for testing a four-way interaction (with species as a factor) were too few.

For adult trees, we verified the effect of treatments on mean radial growth between the post-harvest period (2007-2011) and the pre-harvest period (2002-2006) using a mixed–effects model, with treatment unit as the random variable (*lmer* function of package *lme4* in R). For saplings, the response to treatments was evaluated based on the difference in basal area between 2007 and 2013, summed by treatment unit, using the *lm* function in R. We did not use 2006 data for saplings because we were more interested in testing the treatment effects on post-harvest dynamics than in evaluating direct harvesting effects. For the same reason, we used autumn 2007 data for AB (after destructive AB treatment), while we were able to use spring 2007 data for SM as they were not destroyed during AB treatment. For saplings, we also verified the response in mean sapling radial growth between the post-harvest period (2008-2013) and the pre-harvest period (2002-2006) using a mixed model in the same manner as we did for tree growth. For seedlings, we first verified the treatment effects that were based on the difference in the density (stems*ha^{-1}) of seedlings between 2013 and 2006 summed by treatment unit with the *glm.nb* function (*MASS* package in R). Second, we averaged the height of the tallest individual by species for each subplot and evaluated the effect of treatments using a mixed model in the same manner as we did for tree growth. Finally, we compared the capacity of the 3 treatments to predict the species (response variable) that had the tallest seedling in subplots (in 2013) with a multinomial logistic regression using treatment unit as a random variable; this analysis was performed with the *polytomous* package in R.

1.4 Results

1.4.1 Direct effects of treatments on light environment and soil chemistry

Clear-cutting greatly increased light availability compared to controls and, to a lesser extent, to partial cuts (Figure 1.2). Beech sapling elimination also increased light availability, but not as much as clear-cutting. Model comparisons showed that the additive model including canopy opening alone or in combination with the beech elimination treatment had respectively 73% and 27% probability of being the best model to explain light availability when compared to the intercept model (Table A.1). Seven (7) years after treatment, limed treatment units had higher Ca and Mg concentrations and slightly higher pH, while there were no marked differences in soil chemistry before treatment (Figure 1.3). For Ca and Mg, the model using liming alone had more than a 99% probability of being better than the model using the intercept alone while this probability dropped to 75% for pH (Table A.1). Soil parameter values were generally higher, with or without liming, in 2006 than in 2013. We attribute this result to the season of sampling. In 2006, soil samples were taken in the early springbefore leaf emergence, while they were taken in late summer in 2013.

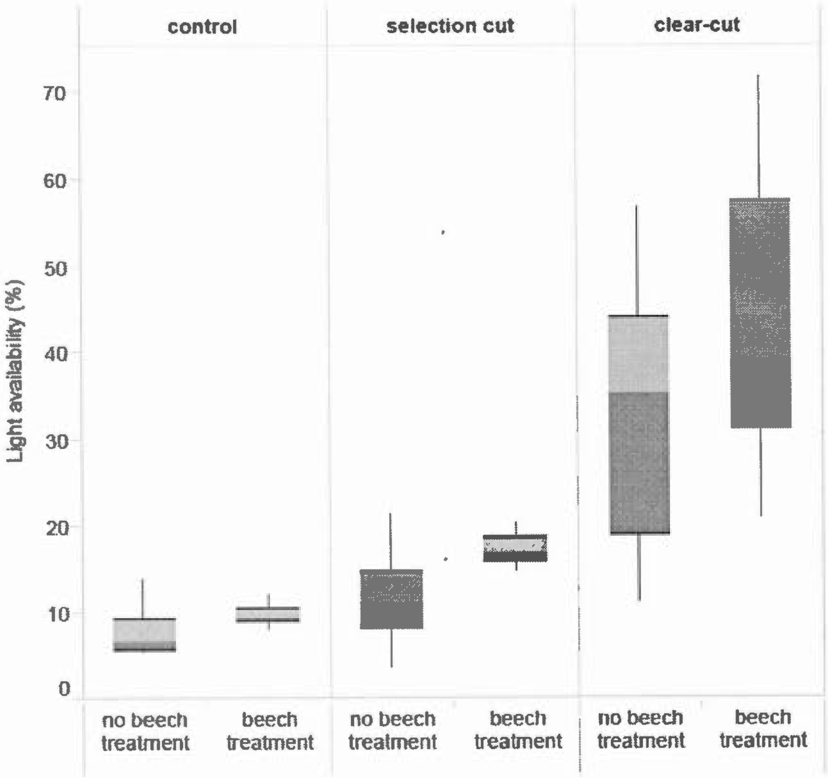


Figure 1.2 Light availability as a function of canopy opening and beech sapling elimination treatments. The limits of the box are the 25 and 75 percentiles, the separating line between the two shades of grey is the median, the lower and upper limits of the whiskers are the 10th and 90th percentiles, and points are beyond 1.5 x the interquantile range (25th-75th percentiles).

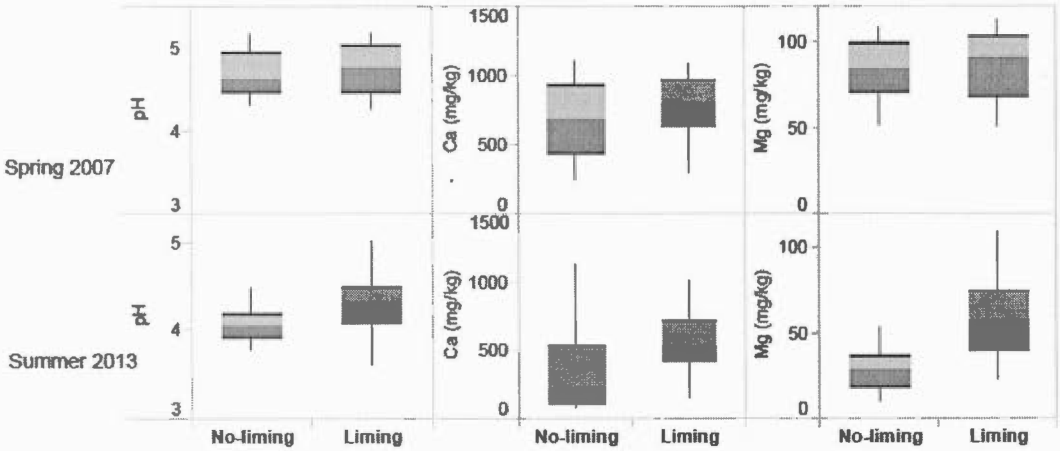


Figure 1.3 **Effect of liming on Ca and Mg concentrations and on pH. Details of the box plots are included in Figure 1.2.**

1.4.2 Mature tree radial growth

Mature tree radial growth of both species increased from pre-treatment (2001-2006) to post-treatment period (2007-2011). Both species reacted positively to selection cutting with canopy opening (CO) respectively having 97% and 75% for SM and AB of being the best model that was tested (as indicated by ω, Table 1.3). Since ω is higher for SM than for AB, it means that the effect of the canopy opening treatment is statistically stronger for SM than for AB. However, since the intercept model is higher than 10 % (15%) for AB, it should not be completely rejected, meaning that there is still a reasonably high probability that none of our treatments (canopy opening, liming and beech treatments) had an effect on AB tree radial growth (Figure 1.4, Table 1.3). While SM growth remained stable in controls between the two periods, AB growth decreased. We attribute this decrease in tree growth to the sudden introduction of beech bark disease (nectria fungal infection caused by feeding injury from the exotic beech scale insect *Cryptococcus fagisuga,* e.g. Houston, 1975) into the area.

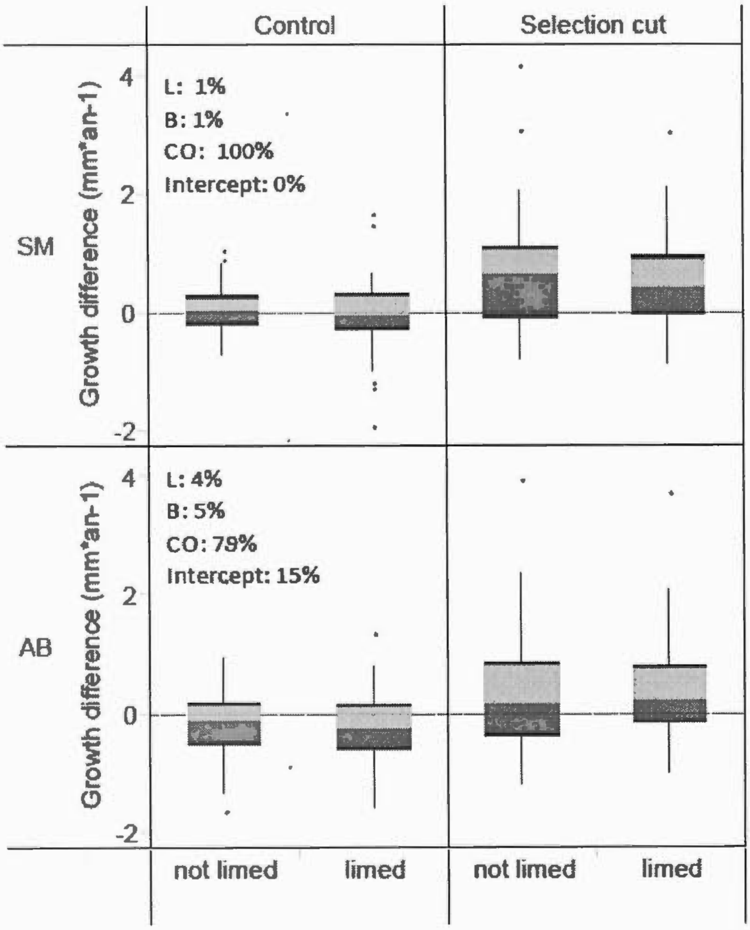


Figure 1.4 Mature tree radial growth change between pre and post treatment periods for sugar maple (SM) and American beech (AB) according to the canopy opening and liming treatments. Percentages related to L, B, CO represent their respective cumulative probabilities to be included in the best model (see Methodology and Table 1.3 for details). The percentage associated with the intercept is provided for comparison. Details of the box plots are included in Figure 1.2.

1.4.3 Sapling basal area and radial growth

Basal area of sugar maple saplings (BA_{SM}) decreased immediately following treatments because of the negative effects imposed by harvesting operations -for both selection cut and clear-cut treatments - on sapling understory cover (Figure A.3). Post-treatment (2007 to 2013), none of the treatment had a clear effect on SM and AB sapling basal area (Table 1.3, Figure A.3). As was the case with mature tree radial growth, sapling growth of both species increased after treatments (Figure 1.5). Again, it appeared that only opening the canopy (selection cut) had a positive effect on radial growth (ω = 92 % for SM and 93 % for AB) and that liming had no effect ($\omega < 1\%$, Table 1.3), even though growth variation among saplings appeared lower with liming. Further, the effect of canopy opening lasted longer for AB than for SM, given that six years after treatment AB sapling growth was still greater than its pre-treatment level, while SM sapling growth returned to its pre-treatment level (results not shown).

Table 1.3 Model comparison for mature tree growth, sapling basal area, sapling radial growth, seedling density and seedling height and for each species

a) Sugar maple

		Tree growth		Sapling basal area		Sapling growth		Seedling density		Seedling height	
Model	k	Δ-AICc	Weight (ω)	Δ-AICc	Weight (ω)	Δ-AICc	Weight (ω)	Δ-AICc	Weight (ω)	Δ-AICc	Weight (ω)
L*B*CO	13	25.1	0.0%	14.7	0.0%	26.6	0.0%	14.7	0.0%	0.0	100.0%
L*B	5	22.9	0.0%	0.0	39.9%	19.0	0.0%	5.6	4.0%	81.2	0.0%
L*CO	7	8.8	1.2%	9.0	0.4%	7.0	2.7%	11.1	0.3%	39.9	0.0%
B*CO	7	8.6	1.3%	5.9	2.0%	9.9	0.7%	0.0	64.3%	40.5	0.0%
L	3	16.5	0.0%	3.8	5.9%	10.2	0.6%	5.5	4.1%	92.0	0.0%
B	3	16.7	0.0%	1.2	22.0%	11.0	0.4%	2.5	18.5%	92.0	0.0%
CO	4	0.0	97.2%	2.4	12.1%	0.0	91.6%	5.8	3.6%	55.6	0.0%
Intercept	2	12.3	0.2%	1.6	17.6%	6.2	4.1%	5.0	5.2%	96.9	0.0%

b) American beech

		Tree growth		Sapling basal area		Sapling growth		Seedling density		Seedling height	
Model	k	Δ-AICc	Weight (ω)	Δ-AICc	Weight (ω)	Δ-AICc	Weight (ω)	Δ-AICc	Weight (ω)	Δ-AICc	Weight (ω)
L*B*CO	13	20.3	0.0%	24.2	0.0%	22.6	0.0%	21.5	0.0%	0.0	100.0%
L*B	5	13.3	0.1%	4.3	3.4%	26.4	0.0%	8.4	1.0%	56.0	0.0%
L*CO	7	7.2	2.0%	5.4	1.9%	8.3	1.4%	5.0	5.5%	34.9	0.0%
B*CO	7	6.8	2.5%	7.2	0.8%	5.5	5.9%	5.7	3.9%	32.0	0.0%
L	3	6.9	2.3%	0.5	22.5%	20.9	0.0%	3.8	9.8%	67.8	0.0%
B	3	6.6	2.8%	1.3	15.3%	18.7	0.0%	5.9	3.4%	65.8	0.0%
CO	4	0.0	74.8%	0.2	26.8%	0.0	92.7%	0.0	67.0%	51.3	0.0%
Intercept	2	3.2	15.4%	0.0	29.2%	16.5	0.0%	3.9	9.4%	72.2	0.0%

L: Liming; B: Beech sapling elimination treatment; CO: Canopy opening treatment; k: number of parameters in the model. Δ-AICc: Difference in corrected Akaike information criteria compared with the best model; w: model weight.

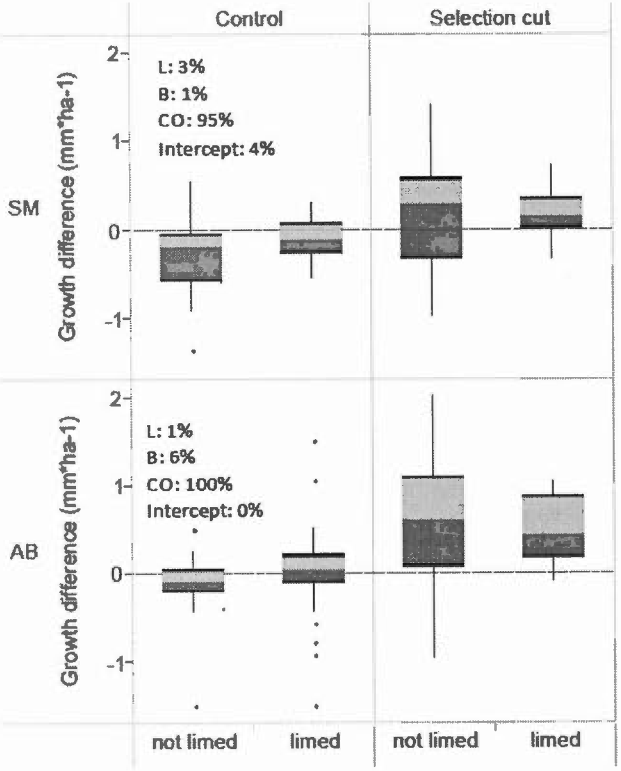


Figure 1.5 Sapling radial growth change between pre- and post-treatment periods for sugar maple (SM) and American beech (AB) according to the canopy opening and liming treatments. Percentages related to L, B, CO represent the cumulative probabilities that liming, sapling beech elimination, and canopy opening treatments would be respectively included in the best model that was tested for a species (see Methods and Table 1.3 for details). The percentage associated with the intercept is provided for comparison. Details of the box plots are included in Figure 1.2.

1.4.4 Seedling abundance and tallest height

The interaction between the beech control treatment and the canopy opening treatment provided the best model ($\omega = 64\ \%$, Table 1.3) for explaining the development of sugar maple seedling densities (D_{SM}) from 2006 to 2013 (Figure 1.6). With a $\omega = 19\ \%$, the beech control treatment alone cannot be discarded, but liming and the canopy opening treatments, both with $\omega < 4\ \%$, cannot be considered as appropriate models. More precisely, a clear increase in D_{SM} was observed when the AB control treatment was imposed, combined with no openings in the canopy. Otherwise, D_{SM} was quite stable. The best model for explaining AB density (D_{AB}) development between 2006-2013 was clearly the one that included the canopy opening treatment alone ($\omega = 67\ \%$). No other model performed better than having a 10 % probability of being the best model. Regardless of liming or beech control treatments, selection cuts led to an increase in D_{AB} (Figure 1.6), while D_{AB} did not change much for other canopy opening treatments.

For the tallest seedling indicator, the interaction between canopy opening, liming and beech elimination treatments was the best model ($\omega = 100\ \%$, Table 1.3) for both species. The canopy opening treatment, as shown by corrected Akaike information criteria (AICc) (in Table 1.3 and Figure 1.7), was the treatment that had the most important effect on dominant seedling height. In the controls, AB was clearly the species with the dominant seedlings, even though dominant AB seedling height was lower when there was an AB sapling elimination treatment. In selection cuts, AB was still the dominant species, even though dominant seedling height of SM was greater than that measured in the controls.

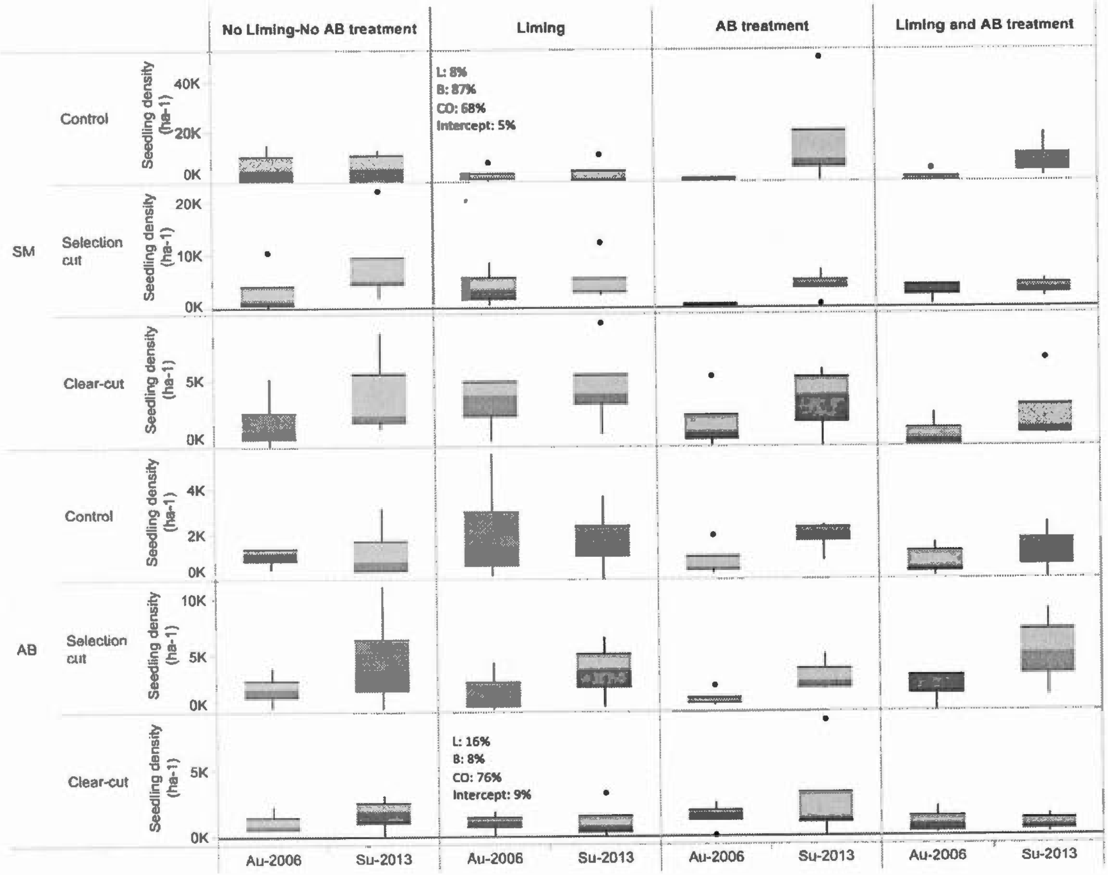


Figure 1.6 Difference in seedling density before and after treatment according to the various treatments for sugar maple (SM) and American beech (AB). Au: Autumn; Su: late-summer. Percentages related to L, B, CO represent the cumulative probabilities that liming, sapling beech elimination, and canopy opening treatments would be respectively included in the best model that was tested for a species (see Methods and Table 1.3 for details). The percentage associated with the intercept is provided for comparison. Details of the box plots are included in Figure 1.2.

In clear-cuts, the height of dominant SM seedlings is very similar to that of AB dominant seedlings. The effects of liming and beech control treatments appeared to be more subtle. For SM, the liming treatment seemed to have a positive effect in clear-cuts when there was no AB elimination treatment; it also had a positive effect on SM height when AB sapling elimination was coupled with selection cutting.

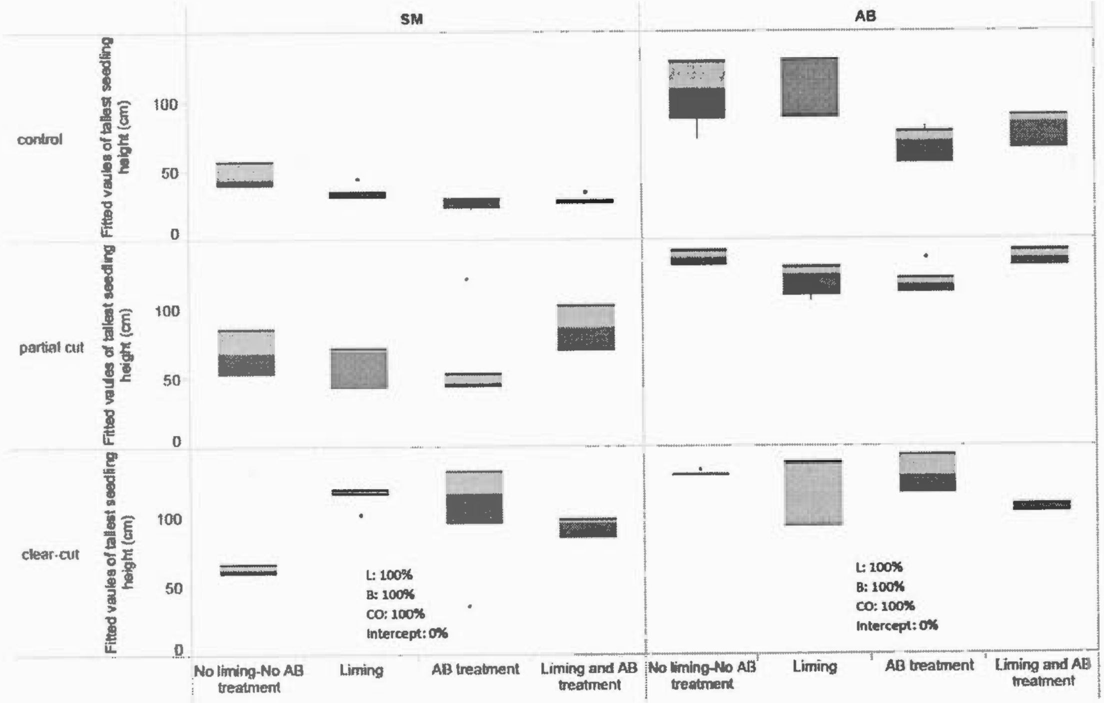


Figure 1.7 Mean height of the tallest seedling in each subplot for the various treatments for sugar maple (SM) and American beech (AB). The fitted values refer to the predicted values at the plot level, after taking into account the random effect. Percentages related to L, B, CO represent the cumulative probabilities that liming, sapling beech elimination, and canopy opening treatments would be respectively included in the best model that was tested for a species (see Methods and Table 1.3 for details). The percentage associated with the intercept is provided for comparison. Details of the box plots are included in Figure 1.2.

Finally, seven years after treatment AB represented the dominant species in 60 % of the subplots within the controls and selection cuts (Figure 1.8); however, this percentage dropped to 25 % within clear-cuts in favour of SM (about 40 %) and other species (about 35 %). The multinomial logistic regression confirmed that the canopy opening treatment had the most substantial effect among treatments since it predicts the most efficiently (ω = 95 %, Table 1.4) the species with the tallest seedling.

Table 1.4 Model comparison for the multinomial logistic regressions used to predict the species with the dominant seedling at the subplot level.

Model	k	Δ–AIXχ	Weight (ω)
L*B*CO	13	860.9	0.0%
L*B	5	980.0	0.0%
L*CO	7	917.0	0.2%
B*CO	7	840.9	5.2%
L	3	68.6	0.0%
B	3	69.4	0.0%
CO	4	0.0	94.6%

See Table 1.3 for abbreviations.

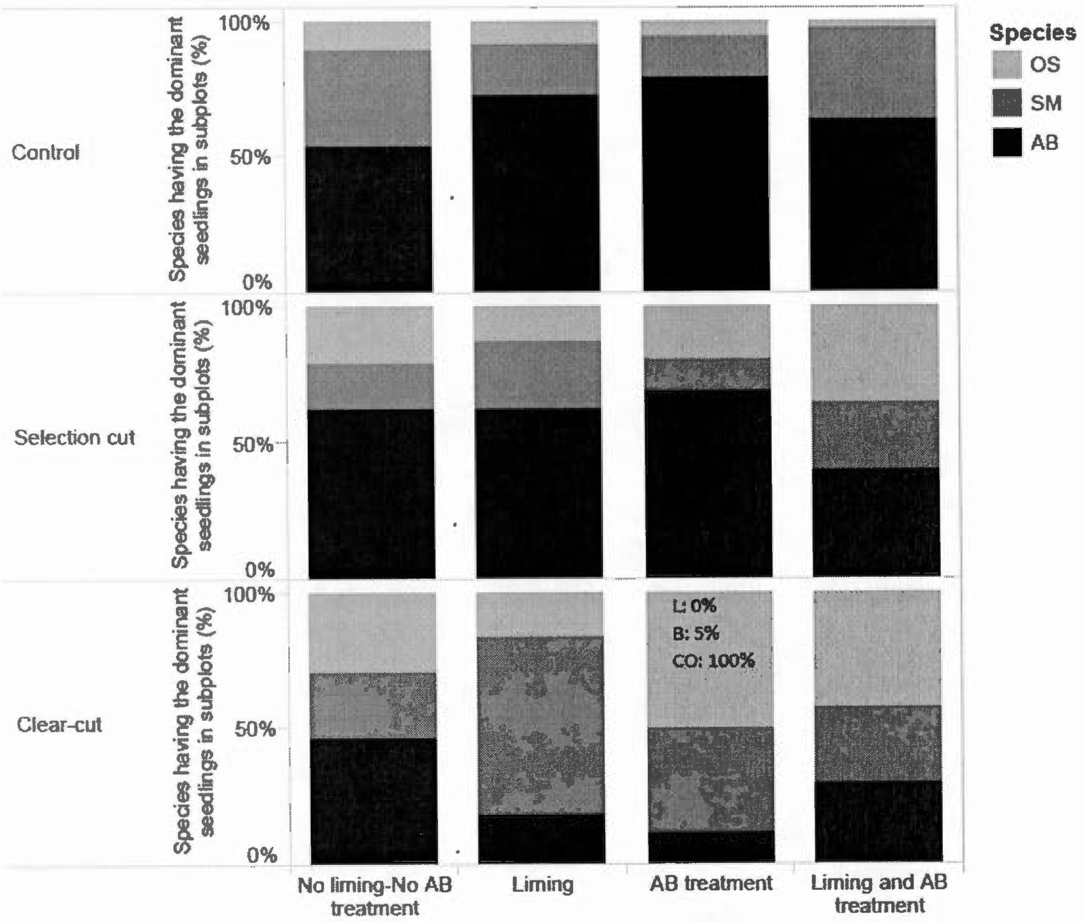


Figure 1.8 Percentage of each species having the dominant individual seedling in subplots according to the various treatments. SM: sugar maple; AB: American beech OS: Other species. Percentages related to L, B, CO represent the cumulative probabilities that liming, sapling beech elimination, and canopy opening treatments would be respectively included in the best model that was tested for a species (see Methods and Table 1.4 for details). n = 85, 70 and 75 respectively for controls, selection cuts and clear-cuts.

1.5 Discussion

1.5.1 The light-soil interaction hypothesis

Globally, our results agreed with the first part of the light-soil interaction hypothesis (Nolet et al., 2008) which states that SM performance improves relative to that of AB as light availability increases. This was first observed in the situation where the removal of AB saplings greatly promoted SM seedling abundance. Second, SM was found to be more often the tallest seedling in clear-cuts compared to partial cuts and controls. However, our results did not generally agree with the second part of the light-soil hypothesis which states that SM response to light availability should be more pronounced as soil fertility increases. We found almost no effect of liming on SM.

It is on control sites (no canopy harvesting) that the removal of AB saplings greatly promoted SM seedling abundance, without favouring AB seedling abundance. It should be noted that the elimination of AB saplings did not have this effect in selection cuts. Our field observations suggest that selection cuts favoured the development of the shrub layer (mainly stripped maple -*Acer pensylvanicum* L.- and beech saplings), by imposing sudden and abundant light inputs (Figure 1.2), which in turn limited SM seedling recruitment. The negative effect of competing shrubs in the understory has been observed in many forested ecosystems although the competing species vary (Hill and Silander, 2001). Invasion by dense beech thickets has also been observed following the arrival of the beech bark disease (Cale et al., 2012). In our study area, the understory is often invaded by beech even before the beech bark disease occurs (Nolet et al 2008). In constrast in clear-cuts, the shrub layer is eliminated, which favours SM seedling growth and survival.

It is also possible that our results at the seedling stage have been influenced by mast seed years. It seems that 2007 was a good seed year for SM as shown by seedling counts (see supplementary material, Figure A.4). After 2007, SM seedling density consistently decreased until 2013. Consequently, our results could be linked to the synchronisation of our treatments with the high 2007 SM seed production. AB seedling density also increased in the spring 2007 but we cannot attribute it directly to mass seed production since it is also possible that harvesting treatments triggered root sprouting.

The regeneration success that we observed may also be lower in regions with high levels of deer browsing as browsing has been identified as a factor explaining SM regeneration (Sage et al., 2003). In our study area, our group as well as Roy and Doyon (2012) observed only very limited effect of deer grazing on SM regeneration.

Our results with the tallest seedling indicator are also consistent with the light-soil interaction hypothesis. While AB represented the species with the tallest seedling in 60 % of the subplots within the controls and selection cuts, this percentage dropped to 25 % in clear-cuts (except for the combined no-liming & no-AB treatment, Figure 1.8). The results at the seedling stage thus suggest that clear-cutting, which was most likely due to an increase in light availability (see supplementary material), decreases AB height dominance over SM in a manner that could not be achieved through selection cuts.

The second part of light-soil hypothesis stated that SM response to light availability should be more pronounced as soil fertility increases. Our results are in agreement with this only for one indicator, the tallest seedling, and only in a few situations. First, in treatment units where selection cuts and AB sapling elimination were coupled, liming had a positive effect on the average height of the tallest SM seedling. This effect of liming was more obvious in clear-cuts, where liming alone led to SM seedling heights as great as those observed in treatment units with the AB sapling elimination treatment. It remains possible that we did not observe liming effects on dominant seedlings in controls and selection cuts because logging operations were not severe enough (or absent) to eliminate AB advance seedling regeneration. It may then be hard for SM, even with a possible boost from liming (e.g., like the response that was observed for partial cut & AB treatment, Figure 1.7), to catch up with AB seedlings that were already much taller.

Overall, our results indicate that the predictive power of the light-soil hypothesis is limited in our study system as there is only minimal evidence (i.e. the seedling stage only) to support the second component of the L-S hypothesis. Moreover, many results were unexpected, such as the effect of the AB sapling elimination treatment, which promoted SM seedling recruitment only in controls. As already mentioned, earlier studies focusing on gap dynamics showed that larger and more frequent openings favour SM at the expense of AB regeneration (Canham, 1988; Poulson and Platt, 1996). Hence, it is contradictory that larger openings - created by selection cuts in this study, by a severe ice-storm (Beaudet et al., 2007) or by shelterwood harvesting (Nelson and Wagner, 2014) - do not allow SM to outperform AB. We believe this contradiction could be explained by considering the regeneration status of stands in which the various measurements were made. When AB has already invaded the sapling layer, as was the case in many of our stands, it seems very unlikely that a significant number of SM seedlings (or rare SM saplings) would reach the canopy, since AB saplings (that already have a clear height advantage) rapidly benefit from any canopy opening. The invasion of the sapling layer by AB prior to the beech bark disease as observed in many regions in eastern North America, however, is still poorly understood (Gravel et al., 2011).

1.5.2 Liming and silvicultural implications

Liming has been proposed as a solution for improving sugar maple establishment and growth in maple stands of low soil fertility (Moore et al., 2012). Our results do not support such an idea even if our study was conducted on soils with poor Ca and Mg levels (Bannon et al., 2015). Indeed, liming with 3 tonnes per ha of dolomite lime had a very limited effect on sapling and tree growth and seedling establishment of sugar maple and American beech, even though its effects on soil chemistry were still evident 6 years after treatment (Figure 1.3). Such results are not surprising for beech since similar responses have been reported previously (Long et al. 2011). The lack of a clear significant effect for sugar maple is more surprising, since many studies have reported, for different stem development stages, a positive response to calcium fertilization (Juice et al., 2006; Long et al., 2011).

We do not expect the weak response of sugar maple to liming that was observed in this study was due to the level of lime that was used, since this quantity lies within the maximum range where Vadeboncoeur (2010) had reported a positive effect in his meta-analysis. Instead, we propose that the repeated stresses that have been experienced by sugar maple trees in recent decades could explain this result (Long et al 2009). Obviously, more research is needed to understand the type and level of fertilization needed and on the generalizability of the results. Still, if we are unable to provide a clear explanation, in a research context, as to why the effects of liming were so weak, foresters are even less likely to identify stands that are suited for liming in an operational context. Thus, based on 1) the uncertainty of liming effects on SM performance, 2) the cost of purchasing and spreading lime, 3) the potential environmental impacts of its additions on soil and forest ecosystems (e.g., Auclerc et al. 2012), and especially, 4) the greater efficiency of other silvicultural treatments in promoting SM over AB, we do not advocate the extensive use of liming.

A possible silvicultural treatment to promote SM over AB, although drastic, is to combine a clear-cut with the elimination of the AB sapling layer. Such a treatment would not completely eliminate AB from stands, but would allow SM and other species to establish and develop on cutovers. Such a clear-cut treatment is unlikely to be socially acceptable on a large scale basis, and they may have detrimental effects on stream water quality (Wang et al. 2006) and avian communities that rely on closed mature forests (Doyon et al., 2005). Therefore, it should be used sparingly and preferably when there is a presence of SM seedling advance regeneration.

A second silvicultural treatment, which seems more promising, is inspired by the abundant SM regeneration that is observed in controls, combined with the AB sapling elimination treatment. For stands where AB saplings dominate the understory, we propose eliminating those saplings a few years before a selection cut is applied. Once SM regeneration is properly established (e.g., 5 years), the selection cut could then be implemented; this treatment sequence, which is similar to what is sometimes applied in shelterwood cuts, would require further work as we did not directly test it.

Moreover, as the timing of the AB sapling elimination treatment and selection cut may be constrained by operational logistics (e.g., in terms of planning), another solution would then be to combine sapling beech suppression with low intensity harvesting (Nolet et al., 2014) to prevent shrub layer expansion. Based on our results, the simultaneous combination of a traditional selection cut with AB sapling elimination would not favour strong SM regeneration establishment, as it promotes development of the pre-existing shrub layer and AB advance seedling regeneration.

Given differences in fertility, competing shrubs, mast seed years, disturbance and meteorological events, we do not claim that our results and proposed silvicultural treatments will apply to all SM-AB dominated ecosystems. In fact, our results rather advocate for solutions adapted to local situations than a one-size (i.e. liming)-fits-all approach.

1.6 Conclusion

A novel aspect of this study is the use of liming in conjunction with canopy opening and beech understory removal. This allowed us to test for the first time the interactive effects of these three factors on sugar maple-American beech dynamics at the seedling, sapling and adult tree stages. Contrary to many previous studies, we found that liming did not significantly improve the growth of sugar maple even when it was associated with the removal of the understory beech layer and the opening of the overstory canopy. Based on these results, we cannot recommend, for sites having similar environmental conditions as our study region, the use of liming in our forests to promote sugar maple growth over beech. Instead, we believe that treatments involving the complete or partial removal of the beech understory are more likely to promote understory sugar maple growth and establishment.

1.7 Acknowledgements

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CHAPITRE II

EXTREME EVENTS AND SUBTLE ECOLOGICAL EFFECTS: LESSONS FROM A SUGAR MAPLE-AMERICAN BEECH CASE[2]

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[2] Ce chapitre vise à être publié dans la revue PNAS. Dans cette revue, la méthodologie doit apparaître à la fin. Aussi, on retrouve souvent de courts éléments de la méthodologie dans l'Introduction, comme je le fais ici. Les sections résultats et discussions sont souvent regroupées et il n'y a généralement pas de section conclusion. Les articles y sont relativement courts aussi (environ 3500 mots). Dan Kneeshaw est l'autre co-auteur pour cet article.

2.1 Abstract

Increasing extreme events related to global changes are expected to affect the dynamics of forest ecosystems. If the disruptive stressors (e.g. insects, drought) affect tree vigor without causing mortality, the ecological effects may be subtle making subsequent ecosystem dynamics more difficult to predict than in the case of disturbances causing death. We studied a forest ecosystem, dominated by sugar maple and American beech, to i) verify whether a change occurred (gradual or abrupt, recovered or not) - in the growth dynamics between the two species over a 60-year period, ii) identify the likely causes of this change and iii) investigate whether such change could trigger other long-time ecological consequences. We found that sugar maple growth was negatively affected by an extreme event (or a few events) between 1986-1989 while beech was not affected. Twenty-years after the 1986-1989 growth drop, sugar maple i) has a slower growth than American beech although it was similar before, ii) does not respond to monthly climatic variations as it did before the growth drop and iii) had lower resilience when faced with a new stressing event. Overall, our study, besides showing that extreme events with subtle effect may change the dynamics on an ecosystem, also highlights that subtle effects can last for long periods and are therefore more likely to interact with other extreme events, stresses or disturbances and accelerate ecosystem misadaptations to climate.

2.2 Significance[3]

We report how an extreme climate event triggered subtle changes in tree species dynamics, leading to a shift in the species dominance. The exact nature of the event (thaw-freeze, drought, insect) is complex but its effects, though subtle, are obvious. Twenty-years after a severe growth drop, sugar maple i) continues to exhibit a slower

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[3] Cette section, requise par PNAS, ne doit pas dépasser 120 mots.

growth than American beech while it was quite similar before, ii) does not respond to monthly climatic variations as it did before the growth drop and iii) showed low resilience in the face of a new stressing event. Altogether, this study shows that extreme events, anticipated to occur more frequently with climate change, may through subtle effects on species dynamics accelerate the emergence of ecosystems maladapted to their environment.

2.3 Introduction

Global changes, changes in natural disturbance regimes (Kurz et al., 2008), increases in extreme climatic events (Bell et al., 2004) and the arrival of new pathogens (Ricciardi, 2007) are expected to affect forest ecosystem dynamics in a variety of ways. When events kill trees suddenly (e.g. fire or wind), subsequent forest dynamics are fairly predictable and can be relatively easy to model (Foster, 1988; Kruger and Reich, 1997). In contrast, if the disruptive agents (e.g. insects, drought) affect tree vigor without necessarily killing them, the ecological effects may be more subtle. Subsequent ecosystem dynamics are then more difficult to predict because many interacting plant physiological processes are involved (McDowell et al., 2011; Rosenzweig et al., 2001). Incidentally, researchers have recently become interested in in pervasive small-scale mortality events, such as increased drought-induced mortality, that when scaled over large areas and long time-frames affect a large number of trees (e.g. Allen et al., 2010; Peng et al., 2011). Moreover, these subtle effects may last for long periods of time depending on the tree vigor at the moment a stress occurs (Camarero et al., 2015; Mamet et al., 2015) or if multiple stressors are implicated (Denny et al., 2009; Gutschick and BassiriRad, 2003). In a context where we wish to predict the effects of climate change and adapt to it (Millar et al., 2007; West et al., 2009), it is essential to understand how species and individuals recover following such non-destructive disruptive events.

The sugar maple (*Acer saccharum* Marsh.)-American beech (*Fagus grandifolia* Ehrh.) ecosystem is particularly interesting for such a question because it is generally agreed that these two long-lived and late-successional species co-exist – i.e. none seems to supplant the other (Poulson and Platt, 1996). Thus, following non-destructive disruptive events, we should be able to detect whether there is a change in the dynamics between the two species and possible recovery. Moreover, there is an extensive literature on the decline in the growth of sugar maple, associated either to acid rain (Juice et al., 2006), drought events (Allen et al., 1992; Gavin et al., 2008), thaw-freeze events (Payette et al., 1996) or insects (Bauce and Allen, 1991; Hartmann and Messier, 2008), which suggests that the dynamics between the two species could have changed in the last decades in favor of beech. In addition, some studies (Beaudet et al., 1999; Gravel et al., 2011) have already identified a change in the dynamics between the two species at the regeneration stage.

Thus, in this article, we wish to i) verify whether a change occurred (gradual or abrupt, recovered or not) - in the growth and subsequent species dynamics between two co-existing late-successional species, viz. sugar maple and American beech, ii) identify the likely causes of this change and iii) to investigate whether such change could trigger other long-time ecological consequences. This last question is especially critical to appraise the reliability of forest models that aim to predict the effects of global change on forest ecosystems.

To answer these questions, we measured the radial growth of more than 150 individuals of both species and of various sizes (10-40 cm at DBH- diameter at beast height) over a 60-year period. The database used has the particularity that individuals were sampled in pairs (one individual per species of similar size) to minimize the effects of the growing environment - in terms of light and soil conditions - when comparing both species growth.

2.4 Results and discussion

2.4.1 Growth decline

Radial growth of the two climax species, sugar maple and beech, was very similar from 1950 to 1985 (Figure 2.1A) except for a few years around 1955. From 1975 to 1982, there is a growth drop for both species, but because it is observed for both species, it is difficult to disentangle whether the growth drop is due to a stress that affected both species or simply to self-thinning or tree age. Afterwards, there is an initial sharp decline in the growth of maple in 1986, both in absolute terms and relative to beech. A second drop is observed in 1988 followed by a weak recovery in 1990. Between 1990 and 2005, the growth of sugar maple never recovered to beech's growth rate (Figure 2.1A, 2.1B). These findings apply to all sampled diameter size classes, but growth drops in absolute values are much more pronounced in bigger stems (Figure 2.1C) as observed by Mérian and Lebourgeois (2011) for tolerant species affected by drought. This more severe growth drop for bigger stems cannot be attributed to a size-effect or a natural stand dynamics effects as it is observed across size classes (Figure 2.1C) and an additional dataset (Figure B.1) shows that 40-cm DBH sugar maples from the same sites had a 2.3-mm*yr^{-1} radial growth around 1975 whereas similar size SM only grow radially at 1-mm *yr^{-1} nowadays. The abrupt nature of the sugar maple growth decline suggests a cause related to an event (or series of events) elf-thinning or tree agegrowth drop can be observed in all sites across the landscape suggests that the event is weather related or due to a regional disturbance rather than a localized disturbance. After this period of recovery, a further drop in the growth of maple is observed in 2006 and 2007.

2.4.2 Possible causes

Numerous stress events occurred during the studied period, including forest tent caterpillar outbreaks, droughts and thaw-freeze events (Figure 2.1A). The 1986-1989 sugar maple growth drop seems first associated with the major thaw-freeze event observed in January 1986 and later exacerbated by a drought event in 1988 and possible forest tent caterpillar defoliation. As explained by Auclair (1992), after embolisms induced by thaw-freeze events, trees are hypersensitive to drought and more vulnerable to attack by insects. It is worth noting that many authors have reported growth drops for sugar maple in 1986 and/or 1989 across its range (Bishop et al., 2015; Duchesne et al., 2002; Gavin et al., 2008; Hartmann and Messier, 2008; Payette et al., 1996) but without consensus about the causes. Moreover, the reasons behind the contrasting susceptibility between both species in the 1986-1989 period remain obscure even though some hypotheses can be put forward. For example, the strong xylem refilling capacity of sugar maple to recover from winter embolism (Hacke and Sperry, 2001) could be activated too quickly in the case of an intense thaw-freeze event. This could consequently trigger the creation of irreversible emboloisms. It is also possible that beech is better adapted to water stress because of an efficient stomacal control of xylem embolism (Lemoine et al., 2002) or because its smooth and rather homogeneous bark favors stem flow (Frost and Levia, 2014). Despite having indentified thaw-freeze, drought and forest tent caterpillar events as possible causes for the 1986-1989 growth drop, similar events did not cause such sudden and sustained growth decreases for sugar maple during the study period (Figure 2.1A). Obiously, an uncommon perturbation occurred during the 1986-1989 growth drop, but historical data are not precise enough to determine whether this unusual event was related to the intensity of one of the stressors mentionned above or the timing of their co-occurrence (e.g. thaw-freeze event followed by a drought). Although it seems improbable, it is also possible that an yet unidentified stressor may be the cause of the 1986-1989 growth drop. Nevertheless, whatever the exact causes of the 1986-1989 sugar maple growth drop, it appears that the sequels caused by the injuries – e.g. to the xylem - were irreversible (Bréda et al., 2006) since sugar maple growth has still not recovered. More research is obviously needed to understand the causes of the 1986-1989 sugar maple growth drop and the subsequent general decline; this present study opens the door to the testing of new hypotheses (e.g. importance of thaw-freeze events on long-term tree species growth).

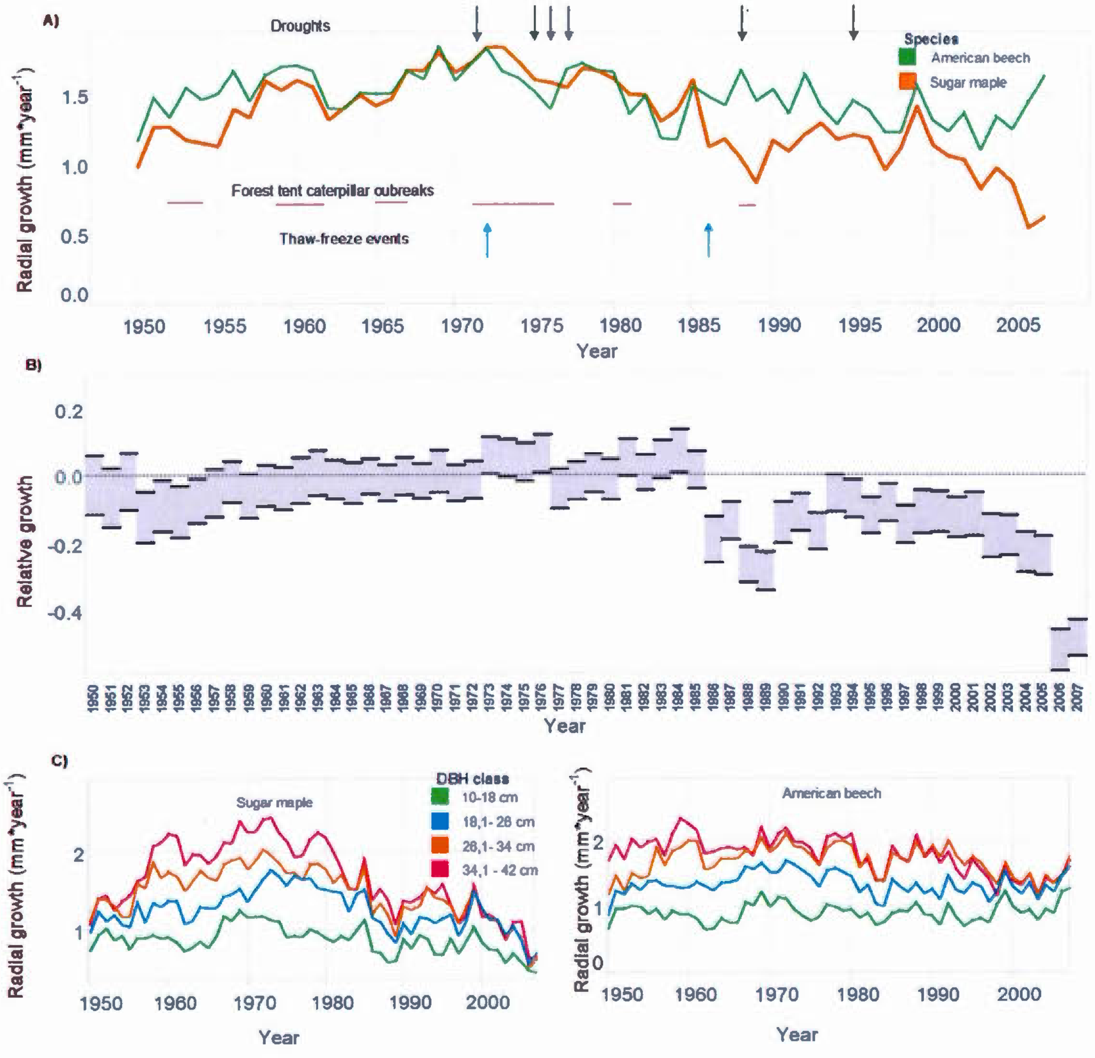

Figure 2.1 **Radial growth comparison between sugar maple and American beech over a 60-year period. A): absolute values B) relative values, a negative**

value signifies a lower growth for sugar maple; the grey boxes indicate confidence intervals at 95%. C) Mean sugar maple and American beech radial growth by DBH class. Black and blue arrows (panel A) respectively indicate drought and thaw-freeze events as indicated by daily meteorological data (see methods and supplementary information). Red lines (panel A) show documented forest tent caterpillar outbreaks (see methods).

2.4.3 Consequences of the 1986-1989 growth drop

Prior to 1986, the radial growth of sugar maple and beech followed each other closely (Figure 2.1A). However, after 1989, their radial growth appears independent from each other. This result, coupled with the inability of sugar maple's growth to recover to the same level as beech after 1989 (Figure 2.1B), clearly reveals a change in the dynamics between the two species. Gravel et al. (2011) also argued for such change in the dynamics between the two species but only at the regeneration stage and without providing explanations. If the stressors that led to the 1986-1989 growth drop also had an impact on the survival of already established seedlings and saplings of sugar maple, it could also explain the relatively low sugar maple regeneration in the ~1980 period observed by Gravel et al. (2011). Data from an additional dataset support this hypothesis as we observe a gap in the regeneration of sugar maple between the years 1978-1986 (Figure B.2, supplementary information). Thus, the 1986-1989 events may not have only changed the growth dynamics relationship between maple and beech for mature stems, but also population dynamics at the regeneration stage i.e. increased sugar maple seedling mortality. Beech, regardless of the stage considered, was less susceptible than sugar maple to the stress that occurred during the 1986-1989 period.

We found surprising the weak association between the two species growth indices after 1989 surprising (Figure 2.1 and B.2) and investigated it. We found that before 1986 (1950-1986) and in accordance with Tardif et al., (2001), there was a clear relationship between climatic variables and sugar maple growth as total rainfall in June and July and the temperature in June explained nearly 38% (adjusted R^2) of the variance of the growth index of sugar maple. For the period 1990-2005, the adjusted R^2 drops to 0 (Figure 2.2). A resampling analysis (see methodology) ensured us that this result was not due to a difference in the number of years between the two periods as the confidence interval for the adjusted R^2 from the resampling analysis was between 0.39 and 0.41. For beech, the relationship with climatic variables was already weaker before 1986 – and probably fortuitos in some cases (Table B.1) and remained low after 1989. Morevover, none of the mulpiple regression analyses explained further growth variation. It thus appears that the association between the growth of sugar maple and climatic variables was decoupled after 1989, as sugar maple stems capacity to take advantage of most favorable climatic conditions likely decreased thus reducing its ability to use these favorable periods as a competitive advantage over beech.

The latest drop in sugar maple growth observed in 2006-2007 (for which no precise cause could be identified) also highlights the potentially long lasting effects of the 1986-1989 stressors. When the relationship between the sugar maple growth drop in 2006-2007 is compared with the one in 1986-1989 (Figure 2.3), we observe that the trees that were the most affected in 1986-1989 are those that are the most vulnerable in 2006-2007. This is especially true for bigger stems (Figure 2.3), indicating that growth recovery is more difficult for bigger (and older) stems. As a result of this lack of recovery, the difference in growth rates between sugar maple and beech tends to shift to the benefit of beech

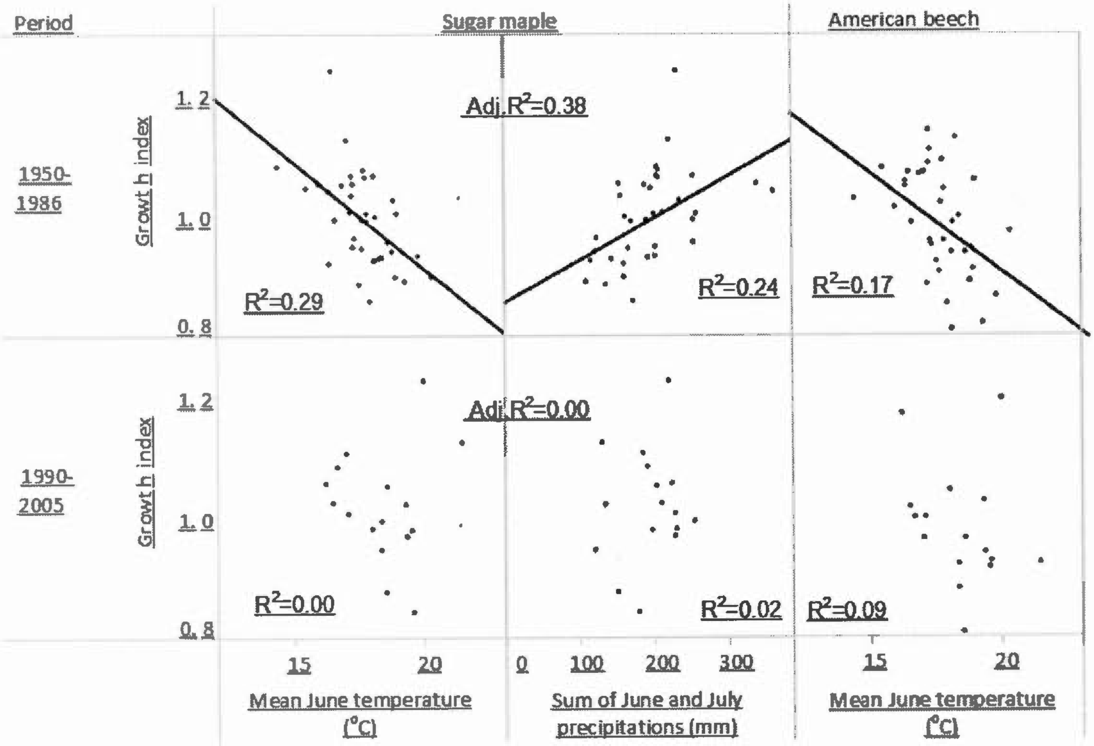

Figure 2.2 Sugar maple and American beech detrended growth indices as a function of mean June temperature and June-July precipitation. R^2 are provided for simple regressions while adjusted R^2 are provided for multiple regressions. None of the multiple regression analyses for American beech are shown as they did not explain any further variation in growth.Trend lines show significant ($p < 0.05$) simple linear relationships. Climate variables are presented in Figure B.4

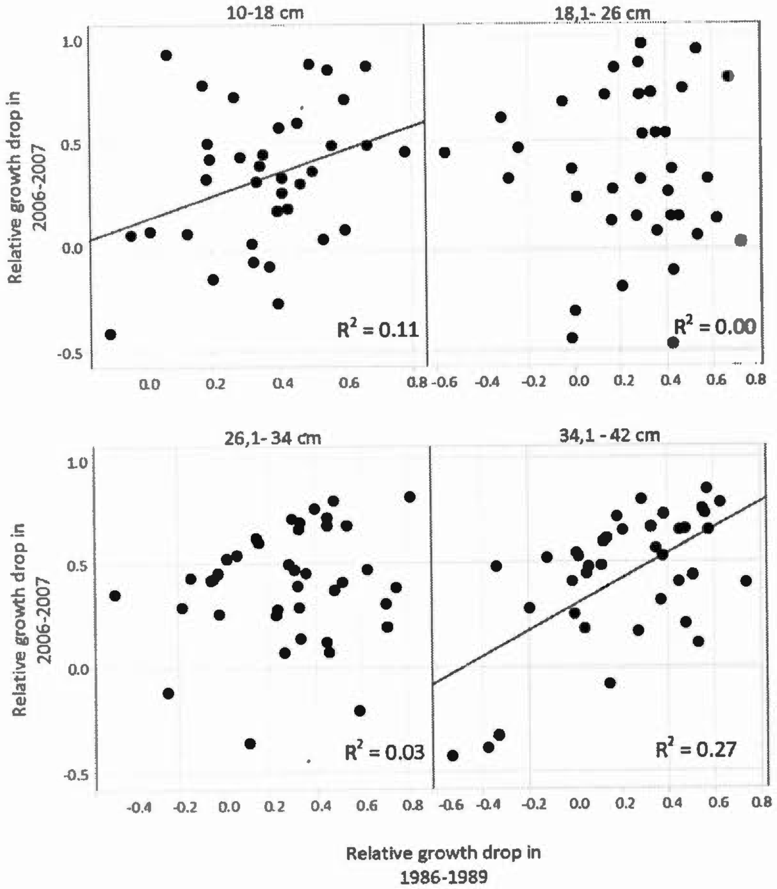

Figure 2.3 Relative radial sugar maple growth drop in 2006-2007 as a function of the relative diameter growth drop in 1986-1989 by DBH classes. Trend lines show significant ($p < 0.05$) simple linear relationships. See methods for details on relative growth radial calculations.

2.4.4 General discussion

Usually when we refer to extreme events related to climate change, we think of extreme short-term effects. In forest ecosystems, major droughts (Amoroso et al., 2015; Breshears et al., 2005) or icestorms (Hooper et al., 2001) (extreme climatic events) that cause sudden tree death whether punctually as large numbers of trees or as increased rates of mortality whose effects are thus observed over a number of years (extreme ecological effects) represent examples of this perception (Anderegg et al., 2015; McDowell et al., 2011). The case presented in this study is a reminder that the effects of extreme events are often subtle and difficult to detect (Mamet et al., 2015) - as we could not identify the causes of the 1986-1989 growth drop with certainty and as the drop growth itself required detailed analyses - but may have important long-term consequences. Subtle ecological effects induced by extreme events (hereafter, subtle effects) present several particularities.

First, subtle effects may last and thus have a long-term influence on species dynamics in an ecosystem (Mamet et al., 2015). When an extreme climate event affects an ecosystem that contains long-lived species (as is the case for forest ecosystems), the event may have long-term repercussions if it affects physiological processes in individuals (Gutschick and BassiriRad, 2003; McDowell et al., 2011) - as observed for sugar maple growth - that changes the competitive relationship between species. When individuals of different species (e.g. sugar maple vs American beech) or different life stages within the same species (e.g. Older versus younger sugar maple), are not affected equally, the extreme climatic event will have a marked effect on the dynamics of the ecosystem (Aakala et al., 2011; Mueller et al., 2005).

Second, consideration of subtle effects adds perspective to understanding misadaptation, i.e. current ecosystems may be poorly adapted to future climate conditions (Williams et al., 2007). Since sugar maple growth has not recovered from the 1986-1989 stress and its growth-climate relationship may have shifted since then, this can be interpreted as a warning that this ecosystem is already misadapted to the current climate. In other words, extreme climate events that generate subtle effects may accelerate ecosystem misadaptation to climate to a point where the resilience of the ecosystem is exceeded and from which the system drifts towards another basin of attraction (Walker et al., 2004).

Third, as the subtle effects caused by extreme events can last for long periods, there is a high probability that they will interact with other extreme events, stresses or disturbances to produce compound events (Denny et al., 2013) and decline spirals. This is perceptible for bigger sugar maple for which we observed that the most vulnerable individuals in 2006-2007 are those. thate were themost severely affected during the 1986-1989 period. The consequences of such interactions between different stressors are difficult to predict. For example, for the sugar maple-American beech ecosystem, sugar maple decline co-occurs with the arrival of beech bark disease which kills most mature beech trees. This co-occurrence of stressors that affect bigger stems of both species could lead to the development of dense recalcitrant understory layers (Royo and Carson, 2006), and/or the loss of forests with old-growth attributes that society often wishes to promote (Keeton, 2006). These hypotheses would, ideally, be tested through modelling.

However, our study case also reveals that modelling the subtle effects of extreme climatic events is a challenge. How can we 1) forecast the nature of the extreme events if we are not sure of the nature or compound effect (thaw-freeze, drought or insect outbreak) of the events that triggered past subtle effects?; 2) be certain of the – single or compound – effects of the events since they are very difficult to disentangle (as shown in this study); 3) predict which events will not equally affect species, or even, individuals of a same species (i.e. ontogenic effects); 4) be sure that we understand the relationship between processes (e.g. sugar maple growth after the 1986-1989 period) and climatic variables when they are in constant change. Because of uncertainties related to extreme climatic events (Easterling et al., 2000), we believe that novel ecological modelling approaches should focus 1) on identifying the most important processes to monitor in ecosystems and 2) on assessing the actions to implement to increase ecosystem resilience in the face of climate change.

2.5 Methods

2.5.1 Study area

This study was conducted in the Papineau-Labelle Wildlife Reserve (46°13'48"W, 75°09'55"N) of Quebec, between Lakes Montjoie and Du Sourd, and about 100 km northeast of Canada's capital, Ottawa. The area is located in the eastern portion of Lac du Poisson Blanc landscape unit (Robitaille and Saucier, 1998) of the western sugar maple-yellow birch (*Betula alleghaniensis* Britton) bioclimatic region (Saucier et al., 2011). The landscape contains numerous hills with elevations < 450 m a.s.l. and averaging 300 m in height. Mean annual temperature is 3.7°C, mean annual precipitation is roughly 1100 mm (including 250 mm as snow), and the number of degree days above 0°C is 2716 (Environment Canada, 2014). Surficial geology for the study area is characterized by thin to moderately thin glacial till composed of metamorphic rocks, such as gneiss, topped by sandy Dystric Brunisols (GPPC, 2010). The forest canopy is dominated by sugar maple in association with yellow birch, American beech, American basswood (*Tilia Americana* L.), ironwood (*Ostrya virginiana* Mill. K. Koch), eastern hemlock (*Tsuga canadensis* (L.) Carr.), and balsam fir (*Abies balsamea* L. Mill.).

2.5.2 Tree sampling

Ten (10) sugar maple dominated stands, with no tree harvesting in the last 20 years, were selected in the fall 2007. In each of these stands, we sampled 16 sugar maple and 16 American beech, for a total of 160 pairs of the two species divided into four major classes of DBH 10-18 cm; 18.1 to 26 cm; 26.1 to 34 cm; 34.1 to 42 cm). To minimize the effects of the growing environment - in terms of light and soil conditions - when comparing both species growth, individuals were sampled as part of a pair, one sugar maple and one American beech. We considered individuals as a pair if they met the following criteria:

- To have less than 2 cm DBH difference (in 2007);
- To be part of the same dominance class (oppressed, intermediate, co-dominant or dominant)
- To have, in 2007 similar competition from surrounding trees, measured using a factor 2 (metric) prism sweep;
- To be far enough from each other to avoid direct competition for light;
- To be close enough to each other (e.g. 25 m) to reasonably assume they grew on similar edaphic conditions.

In addition, a minimum 100 m-distance was respected between each pair of trees. For each tree, a core was sampled to the pith of the tree (unless trees were rotten) using an increment borer.

Core samples were mounted, and then sanded using increasingly fine sandpaper grits. The ring-widths, from 1950 to 2007 were measured to the nearest 0.01 mm using a 40X magnification scope and a sliding measurement stage (Velmex Inc., Bloomfield, NY, USA), which was coupled to a digital meter. Quality control of cross-dated series was checked using both graphical and statistical methods provided by the dplr package (Bunn, 2010) in R (version 3.1.0; R Development Core Team 2013) which integrates many of the functionnalities of commonly-used dendrochronological software such as COFECHA (Holmes, 1983).

2.5.3 Data analysis

In order to check for a change in sugar maple and beech growth over time (1950-2007), we first averaged the radial growth of each species for each year. Second, we calculated the difference in radial growth between sugar maple and American beech for each pair of trees and for each year. We then calculated the mean difference (and confidence interval at 95%) between both species for each year. We visually inspected the radial growth patterns of both species for reduced tree ring patterns that could be associated with potential stressors: insects, droughts and thaw-freeze events. As the forest tent caterpillar (FTC) is known to feed on sugar maple, we used the data documented by Cooke and Lorenzetti for the study region (2006) to identify possible FTC outbreaks. Drought and thaw-freeze events were identified using the daily data from the closest weather station (Mont-Laurier, Environment Canada 2014). We considered a drought event to occur when the total amount of precipitation over a 21- continuous day period (form May to August) was 5 mm or less. As a comparison, the mean daily precipitation for the region in summer is 3 mm. Six drought events were identified between 1950 and 2007 (Figure B.5, supplementary information). A winter thaw-freeze event compounds a warm (usually > 0°C) period followed by an abrupt drop in temperature (Bourque et al., 2005; Pockman and Sperry, 1997). To identify the most important thaw-freeze events over the 1950-2007 period, we plotted each individual day (x_i) from January and February of each year according to a) the thaw length, i.e., the number of consecutive warm days (reaching at least 0°C) and b) the temperature drop, i.e., the difference between the maximum temperature of x_i and the minimum temperature of x_{i+1}). From this analysis, we decided to keep the two most obvious thaw-freeze events (Figure B.6, supplementary information).

To evaluate the relationship between climate and species growth, we first calculated a detrended growth index for both species. This detrending process was accomplished in two steps (Mérian and Lebourgeois, 2011), again using the dplr package (Bunn, 2010). First, we fitted a 20-year cubic smoothing spline with a 50% frequency response on each raw measurement series (individuals). Then, for each species, residuals from the fitting procedure were averaged by year using a bi-weighted robust mean to obtain a growth index (Figure B.3, supplementary information). To verify whether the relationship between climatic variable changed after the 1986-1989 growth drop, we first performed simple correlation analyses between monthly temperature, precipitation and water balance (obtained through BioSIM, (Régnière and Saint-Amant, 2008)) and growth indices for both species and for two periods: 1950-1985 and 1990-2005 (i.e. before the event of 2006-2007 for this specific analysis). Climate-growth relationships were performed using both current and previous climatic variables. For further regression analyses, we kept only variables that appeared to have an influence on species growth during the 1950-1985 period (Table B.1). To ensure that the best relationships between climate and growth for the 1950-1985 were not an artefact of a bigger dataset (36 years compared to 16 for the 1990-2005 period), we performed a resampling analysis, in which 1000 samples of 16 random years (between 1950-1985) were generated. Multiple regression analyses were performed on each of the 1000 samples and the confidence intervals of the adjusted R^2 were compared to the R^2 obtained using all years. This analysis of the stationnary – or non-stationnary - effect of climatic variables on growth is inspired from usual stationnary analyses, but it allows to i) to directly test whether there is a change in the climate-growth relationship after a specific event, ii) analyse periods that differ in their length and iii) incorporate a multiple regression in the analysis.

Finally, to verify the presence of a link between the 1986-1989 drop and the one observed in 2006-2007, we calculated for each individual maple its relative drop growth compared to the growth in the years preceding the drop:

Relative growth drop in 1986-1989 (RDG_1) = $(G_{1986\text{-}1989} - G_{1982\text{-}1985})/(G_{1982\text{-}1985})$ (1)

and

Relative growth drop in 2006-2007 $(RDG_2) = (G_{2006\text{-}2007} - G_{2004\text{-}2005})/(G_{2004\text{-}2005})$ (2)

where G is the mean radial growth for the identified period. We then performed a simple regression between RDG_1 and RDG_2. All statistical analyses were performed in R (version 3.1.0; R Development Core Team 2013).

2.6 Acknowledgements

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CHAPITRE III :

COMPARING THE EFFECTS OF EVEN- AND UNEVEN-AGED SILVICULTURE ON ECOLOGICAL DIVERSITY AND PROCESSES: A REVIEW[4]

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[4] Ce chapitre a été écrit dans l'optique d'être publié dans la revue Biological Consevation. Les co-auteurs sont : Dan Kneeshaw, Christian Messier et Martin Béland.

3.1 Abstract

In a the context of increasing modification of forested landscapes due to an ever-rising demand for wood products, conservation areas may fail to maintain terrestrial biodiversity if they are not supported by the surrounding managed forest matrix. Forest managers today must therefore ensure that their practices protect biodiversity and important ecological processes. Worldwide, forests are managed by one of two broad approaches – even- and uneven-aged silviculture. Despite the lack of a thorough literature comparison of the ecological effects of these two approaches, there is an entrenched belief that uneven-aged silviculture is better at protecting biodiversity and key ecological processes. We reviewed more than 70 papers worldwide to compare even- and uneven-aged silviculture regarding their effects on species/structural diversity and functions, all being elements that contribute to forest resilience. Although both approaches affect these elements, we found that uneven-aged silviculture does not systematically favour species/structural diversity and functions compared to even-aged silviculture. Our review thus provides compelling evidence to support the need for a diversity of silvicultural techniques to support diversity and function while earlier argument were proposed primarily on the basis of disturbance regimes or observed distribution.

3.2 Introduction

Forests are used primarily for extracting wood to fulfil human needs but they also provide important habitats to two-thirds of terrestrial organisms (Duraiappah et al., 2005) and thus are of conservation concern. As the human population is projected to reach 8.2 billion people by 2030, the demand for wood products will also inevitably increase (FAO, 2009), intensifying the pressure on non-protected forests to be managed for wood production. In such a context, conservation areas may fail to maintain terrestrial biodiversity if they are not supported by the surrounding managed forest matrix. However, the contribution of the managed forest matrix to biodiversity conservation depends on silvicultural practices that provide suitable habitats and maintains ecological processes (Messier et al., 2013).

In recent decades, there has been rising public pressure against the systematic of even-aged silviculture around the world because of its perceived negative aesthetic and ecological impacts. It has also been shown that the overuse of even-aged techniques has led to changes in forest structure and biodiversity compared to natural systems (Bergeron et al., 2002; Cyr et al., 2009; Paillet et al., 2010). Many authors have proposed alternatives to traditional forestry, ranging from better protection of key elements within managed ecosystems (Franklin et al., 1997), an increased proportion devoted to forest ecosystem conservation (Seymour and Hunter, 1992), and decreased use of even-aged silviculture in favour of uneven-aged silviculture (O'Hara, 2002) (See Panel 1 and Figure 3.1 for a brief description of even- and uneven-aged silviculture). The latter grew due to an influence of European forestry and continuous cover techniques, a desire for increased 'naturalness', and in western North America coastal forests due to the rarity of large-scale natural disturbances. In regions where small-scale natural disturbances, such as partial windthrow or individual tree mortality due to insects or diseases are prevalent, forests would be better reproduced by uneven-aged silviculture (Gillis, 1990). Some authors have in fact called for a gradient of silvicultural techniques from even-aged total cuts to smaller openings to continuous cover forestry (Gauthier, 2009; Schütz, 2002). Moreover, the belief that uneven-aged forest management is a more appropriate tool has spread among various groups, ranging from foresters (e.g., O'Hara and Ramage, 2013) to forest ecologists (e.g., Déchêne and Buddle, 2009) and environmentalists (e.g., Pro Silva, 2012). The IUFRO uneven-aged silviculture group clearly states (IUFRO, 2016) : "A resurgent interest in uneven-aged silviculture is occurring all over the world as it is increasingly seen as a viable alternative to even-aged systems where concerns over aesthetics, resilience to climate change, wildlife management, or maintenance of continuous cover predominate." In Europe for example, recent decades have seen the direct transformation of existing even-aged plantations to mixed, uneven-aged managed forests (Pommerening and Murphy, 2004). Nevertheless, a thorough and unbiased comparison of the existing literature on the effects of these two approaches is lacking with respect to key ecological processes.

Panel 1: Brief description of even- and uneven-aged silviculture

Even-aged silviculture is a set of silvicultural treatments that favour the regrowth of a stand dominated by trees that are mostly of the same age. Uneven-aged silviculture is a set of silvicultural treatments that favour regrowth of at least three age classes (Helms, 1998). The two approaches differ in their implementation spatially and temporally. Even-aged management implies a clear-cut, or a final cut that resets the stand to a regeneration stage so that stems grow surronded by stems with similar ages and sizes. Uneven-aged management implies repeated partial cuts that regenerate the stand more continuously and leave some permanent forest cover so that stems grow surronded by stems with highly varying ages and sizes. Because the amount of timber harvested per unit of surface in one entry is not the same for both approaches, for a same amount of timber harvested, the footprint in the forest that is left by the two systems differs (Figure 3.1).

Figure 3.1 Schematic representation of the difference in the landscape structure between A) even-aged and B) uneven-aged silviculture. In even-aged silviculture, trees in each stand are surrounded by trees with similar ages and heights while in uneven-aged silviculture, trees are surrounded by trees of varying ages and heights. In both cases, smaller trees are expected to replace larger trees once the latter are harvested.

In this article, we question whether the more socially and aesthetically appealing uneven-aged silvicultural approach is better suited than even-aged silviculture to maintaining/promoting biodiversity and key ecological processes as well as promoting ecosystem resilience. To answer this question, we first summarize a literature review of scientific papers that included a comparison between effects of even- and uneven-aged silviculture on diversity of various taxa and measurement of various ecological processes, covering various types of forests from forest biomes around the world. We then explain the management/policy implications of our findings and how they can contribute to the debate – among foresters and conservationists – regarding the best use of even-aged and uneven-aged silviculture.

3.3 Literature review

3.3.1 Approach and rationale

Favoring ecosystem resilience is often seen as a solution to help forests to adapt to global changes (Millar et al., 2007; Thompson et al., 2009). However the literature on the effects of even- and uneven-aged silviculture on forest ecosystem resilience is almost inexistent – and is probably related to the difficulty of measuring resilience (Neubert and Caswell, 1997). In this paper, we refer to resilience as "the capacity of a system to absorb disturbance and reorganize while undergoing change so as to still retain essentially the same function, structure, identity, and feedbacks" (Walker et al., 2004). Moreover, we answer the question "*Resilience of what to what*" (Carpenter et al., 2001) with *of what* being of forest ecosystems (not species or genes) at any scale and with *to what* being any new stressor triggered by global changes. Ecosystem resilience is often related to the complexity of interactions between the various components and processes of an ecosystem (Puettmann et al., 2013). In this sense, each component and process has a role in the resilience of the ecosystem. From this premise, we performed a literature review to compare the effect of even- and uneven-aged silviculture on a large array of ecological indicators. Even though all indicators may not all have the same importance for ecological resilience, we do not judge the merit of the indicators proposed but rather follow the logic that these are indicators that have value both to society and ecologically (Elbakidze et al., 2011; Kneeshaw et al., 2000).

To perform the literature review, we searched for scientific papers (rather than dissertations or technical reports, which are not always in scientific databases) that included a comparison between effects of even- and uneven-aged silviculture on one or many ecological indicators. We used comparisons from all different forest ecosystems where the comparison was available to identify whether the underlying relationships were ecosystem-dependent. We complemented this initial search with meta-analyses and reviews that dealt with the impact of canopy removal intensity on a wide variety of elements of ecological resilience. Our search was performed using three different scientific databases: Web of Science, Scopus, and Google scholar. Because many words other than "even-aged" and "uneven-aged silviculture" may be used to refer to these systems (e.g., clear-cut, selection cut) and because keywords did not always indicate a comparison between the two silvicultural approaches of interest, we could not use an "automated" search. Instead, we carefully evaluated several hundred abstracts that contained "even-aged," "uneven-aged," "selection cut" or "clear-cut," and verified whether there was an even/uneven-aged ecological comparison. Some studies were likely missed since forest ecologists do not always use forestry terms to define the silvicultural treatment under study. We provide an example of results of the review for tree species (Table 3.1), while the results for other elements of resilience are provided as supplementary information (Tables C.1-C.9). When summarizing a paper, we attempted to be true to the interpretations that the authors made of their own results regarding the compared effects of even- and uneven-aged silviculture. Figure 3.2 shows the geographical distribution of the 70-plus studies found in our literature review. Despite our goal of being geographically representative, published studies are primarily concentrated in the Northern Hemisphere and mostly in the Americas. Although the studies were conducted in forests of varying species composition, most were conducted in forests that were dominated by deciduous forest species.

Table 3.1 Literature comparing even- and uneven-aged silviculture for tree species diversity

Elements studied	Effect	Time/spatial scale consideration	Biome	Reference
Diversity (Shannon)	EAS>UAS>UC	40 years after treatment/No	Temperate Deciduous Forests	Niese and Strong (1992)
Richness	EAS=UC >UAS	~ 10 yrs post-treatment/No	Temperate Deciduous Forests	Doyon et al. (2005)
Regeneration richness	EA=UC=UAS	1 year post-treatment/No	Temperate Deciduous Forests	Messina and Schoenholtz (1997)
Regeneration Richness	EAS=UAS>UC	11 years post-treatment/Yes	Tropical Moist Forests	Parrotta et al. (2002)
Diversity (Shannon) Richness-plot Richness-site	UAS=EAS=UC UAS>EAS;UAS=UC UAS=EAS=UC	4 years post-treatment/No	Temperate Deciduous Forests	Elliott and Knoepp (2005)
Richness	UAS>EAS=UC	Undefined/No	Mediterranean Forests	Torras and Saura (2008)

Legend: **EAS**: Even-aged silviculture; **UAS**: Uneven-aged silviculture; **UC**: Uncut. The column **Effect** refers to what is generally preferable in terms of ecosystem resilience. For example, UC>UAS>EAS means that for this indicator uncut stands performs better than uneven-aged silviculture, which in turn performs better than even-aged silviculture. The column **Time/spatial scale consideration** provides information about the time since harvesting or the various stages studied for EAS. Also, as most papers have focused on stand-scale effects, this column gives information ("/Yes "or "/No") whether the authors included a landscape consideration in their analysis or discussion. For **Biomes**, see Figure 1.

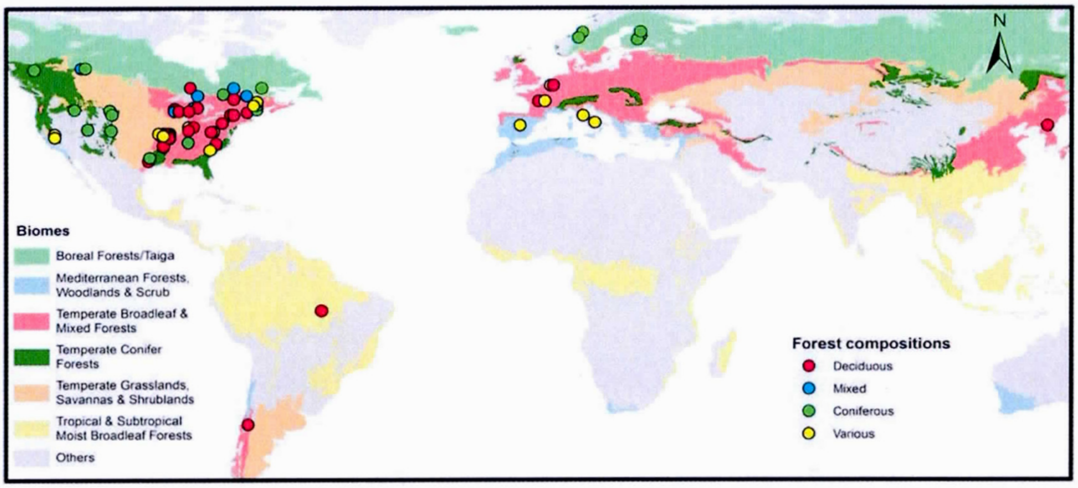

Figure 3.2 **Approximate location and species composition of the reviewed studies in relation to forest biomes. The term "various" means that studies were conducted in more than one forest composition.**

3.3.2 Generalities

The following sections provides, for each taxa (or group) and process, a short summary of our findings. This summuray first aimed at assessing whether an approach (even- or uneven-aged silviculture) clearly outperforms the other one for a given taxa or process. Second, it aimed at identifying general factors that must be considered when comparing even- and uneven-aged silviculture and also short-comings that should be avoided in the comparison of the approaches. Hence, it was not our intention to try to explain contadicting results among studies.

3.3.3 Flora

We identified a surprisingly limited number of studies comparing effects of even-/uneven-aged silviculture on tree species diversity and composition (Table 3.1). From the limited number of studies found in our literature review, even-aged silviculture tends to favour species richness compared to uneven-aged silviculture at the stand level, which could be considered positive for forest resilience as it contributes to spread the risk in case of a major stress or perturbation (Millar et al., 2007). Niese and Strong (1992) consider that uneven-aged silviculture may lead to dominance or monocultures of late-successional species. Even-aged silviculture often triggers larger changes in species composition than does uneven-aged silviculture (e.g., Parrotta et al., 2002), but this does not necessarily mean a loss of resilience if the new species composition continues to provide important ecosystem services (i.e., Holling's re-organization phase; Drever et al., 2006). However, in terms of maintaining some key functional traits, the loss of species is a concern if the rotations that are used for even-aged silviculture are too short for the recruitment of late-successional species. It can also lead to state shifts at the landscape or regional scale if the matrix shifts from one that is dominated by late-successional to early successional species (Gauthier et al., 2009).

Understory (shrubs and herbs) species diversity has been studied much more than tree species diversity in comparisons of even-/uneven-aged silviculture (Table C.1). From the literature review, it does not appear that either type of forest management negatively affects understory species richness and diversity in the longer-term. However, even-aged silviculture may have a strong impact on understory plant species composition in the short-term (e.g., Haeussler et al., 2007). This short-term impact is apparently influenced by the level of soil disturbance incurred during harvesting operations (Kern et al., 2006). Over the longer term and using a meta-analysis, Duguid and Ashton (2013) showed that the effect of even-aged silviculture on richness depended upon the development stage, with the lowest diversity found at the understory re-initiation stage (about 30-50 years after harvest). These results highlight the importance of studying various stand development stages after even-aged silviculture when making comparisons with uneven-aged silviculture as differences between the two systems may vary, depending on the even-aged development stage to which the comparison is made. A few studies reported that uneven-aged silviculture could trigger the development of a dense shrub layer (Decocq et al., 2013), a phenomenon observed worldwide that strongly influences understory forest dynamics (Royo and Carson, 2006).

For structural elements, it is difficult to draw clear conclusions regarding major long-term differences found between even- and uneven-aged silviculture (Table C.2), since results depend upon the ecosystem being studied, the manner in which treatments were implemented, and the manner in which data were collected (e.g., minimum diameter of down woody debris). Yet it is clear from our review that an overall loss of structural diversity occurs in managed forests for both even- and uneven-aged systems. This supports the idea that there is a need for un-managed stands in landscapes to promote forest resilience.

Very few studies have compared mycorrhizae, lichens, bryophytes, fungi and bacterial communities between even- and uneven-aged silvicultural systems (Table C.3). While microbial communities do not seem to respond strongly to forest management, one study by Kropp and Albee (1996) reported a marked decrease in ectomycorrhizal fungi richness in relation to harvesting intensity in lodgepole pine forests in Utah, with a total of 33, 24 and 5 species identified respectively for control, partial cut and clear-cut stands. These elements of the forest ecosystem definitely require deeper attention, especially mycorrhizae because of their fundamental importance in the functioning of forest ecosystems (Simard, 2009).

3.3.4 Fauna

For both mammals (Table C.4) and birds (Table C.5), population responses to even-uneven-aged silviculture are species-specific and not generalizable across all taxa indicating no consistent pervasive effect of either management type. However, birds (e.g., Morris et al., 2013) are more strongly associated with distinct forest development stages and forest structures than are mammals. It is also clear from the review that uneven-aged silviculture that is practiced uniformly across a landscape reduces avian diversity, while this trend is not as clear for mammals. For both taxonomic groups, time since treatment is important. For example, Thornton et al. (2012), in coniferous forests in Idaho, showed that in the short-term, both clear-cuts and partial cuts negatively affected snowshoe hare (*Lepus americanus*). However, older clear-cuts (15- to 40-years-old) were the best habitat for this species. In oak forests of Missouri, Morris et al. (2013) , observed that some early negative effects of both even- and uneven-aged silviculture on some bird populations were still apparent 14 years after harvest, while they did not last for others. At the landscape level, Becker et al. (2011) showed that the abundance of all avian guilds increased with forest harvesting in West Virginia until a guild-specific harvest threshold (proportion of the landscape under forest management) was attained. Once this threshold was exceeded, forest-interior and interior-edge guilds were disadvantaged, and primarily by clear-cuts. Hence, in terms of resilience of mammals and birds, neither the even- nor the uneven-aged approach outperforms the other.

Although responses of amphibians and reptiles (hereafter, referred to as "herps") are also species-specific, any kind of forest management, i.e., uneven-aged or even-aged, appears to be more detrimental to herps than to birds or mammals (Table C.6). In fact, positive responses of herp species to any kind of logging are rarely observed, especially towards clear-cuts at the stand scale. Tilghman et al. (2012), in their meta-analysis, observed that populations generally recovered as the forest regenerated, while Homyack and Haas (2009) observed no recovery 13 years after harvesting by even- or uneven-aged silviculture. Considering the multitude of entries on uneven-aged compared to even-aged selection silviculture, the latter authors were not convinced regarding environmental benefits of selection cuts at the landscape level.

According to our review, invertebrates (Table C.7) are not very sensitive to the silvicultural system being used (even- or uneven-aged, e.g., Johnston and Holberton, 2009). However, several authors highlighted the importance of unmanaged forests in the landscape (du Bus de Warnaffe and Lebrun, 2004; Summerville, 2011). In Michigan and Wisconsin, Latty et al. (2006) showed that beetle communities in stands that were recently managed using uneven-aged silviculture and others that were managed in the past with even-aged silviculture were very different from those of old-growth forests, even if there were few species that were strictly associated with the different types of disturbance history.. The authors estimated that at the landscape scale, insect species that preferred old-growth forests have declined to a large extent. As with herps, both silvicultural approaches have negative effects.

3.3.5 Carbon and nutrients

From our review of the available literature, we cannot conclude that one silvicultural system outperforms the other in terms of its ability to sequester carbon (Table C.8). First, many studies were conducted at a single moment in stand development and most very shortly after treatment (e.g., Lee et al., 2002; Laporte et al., 2003). The most complete studies, based upon simulations (Pukkala et al., 2011; Moore et al., 2012; Nunery and Keaton; 2012) or long-term measurements (Nilsen and Strand, 2013), provide equivocal results in terms of the best silviculture approach to sequestering or store carbon. These contradictions may be due to the complexity of the calculations, as acknowledged by Moore et al. (2012), who emphasized that the accuracy of their results depended upon several factors, including the forest products that were generated. Nunery and Keeton (2012) even showed that variations in the use of even-aged silviculture that included various intensities of structural retention stronly influence carbon storage.

The effects of even- versus uneven-aged silviculture on soil processes and functions are two-fold (Table C.9). First, it appears that the effects of both silvicultural approaches on the soil are limited (soil chemistry or density; e.g., Elliott and Knoepp, 2005). If we examine soil water or stream water, strong effects are observed. Siemion et al. (2011), in New York State, showed that above a certain harvesting intensity (about 40 % of the watershed), nitrate and calcium concentrations in soil water increased linearly with harvesting intensity. Above this threshold -- most likely to be encountered in even-aged silviculture -- concentrations increased more rapidly than harvesting intensity. Wang et al. (2006), also in New York, observed a roughly linear relationship between harvesting intensity and changes in aluminum, calcium and magnesium concentrations in stream water. Changes in concentrations for nitrate (about 5 X) and potassium (about 100 X) were not linear but increased exponentially after clear-cutting. Stream water chemistry returned to near-pre-harvest conditions about one year after harvest, except for nitrate concentrations. Although they occur for only a very limited time, these increased inputs in nutrients are liable to shift ecosystem states (watercourses in this case; e.g. (Rask et al., 1998)).

3.4 Discussion

Given the array of ecosystems and ecological indicators to be considered, a first general observation of our study is the surprising limited number of studies that compare, in terms of their ecological effects, the two largest categories of silvicultural approaches- even- and uneven-aged. Based on this literature review and on the premise that the ecological indicators examined contribute to forest ecosystem resilience, we conclude that views suggesting that uneven-aged silviculture is better suited than even-aged silviculture for promoting forest resilience in a global change context - as well as the shift in practices in Europe (Pommerening and Murphy, 2004)- is not substantiated by sound scientific results. Specifically, this literature review shows that even-aged silviculture does not necessarily modify biodiversity and forest ecosystem functioning more than does uneven-aged silviculture (Table 3.1, and Tables C.1 to .9). In fact, the ecological effects of even-aged silviculture at the stand scale are rarely as large as the changes in the appearance of a forest stand that occur just after clear-cutting would suggest. This conclusion applies primarily to even-aged silviculture that is based on natural regeneration. For most studies that were reviewed, clear-cutting was not followed by tree planting. Since tree planting generally implies site preparation and control of vegetation competition (Lindenmayer et al., 2012), it is likely that it has a more pronounced ecological effect than does natural regeneration-based, even-aged silviculture. Despite our initial intention to cover a wide variety of forest ecosystems, only a few studies could be found in some forest biomes (e.g., tropical rainforest) or in some regions of the globe (e.g., Asia). Therefore, current evidence does not permit our conclusion to be generalized to all forest biomes and regions of the globe. Moreover, as we analysed only papers that compared even-and uneven-aged silviculture, it is possible that key ecological processes have not been analysed in our comparison. Our study then should be useful for researchers to eveluate whether their specific domain of research has been well covered in the literature in regards of even- and uneven-aged silviculture.

The absence of clear and unambiguous differences in short-term ecological effects between even-aged and uneven-aged silviculture at the stand scale cannot be easily transposed to the landscape scale for two different reasons. First, the lack of differences at the stand scale may not be the same if only one of the two approaches was applied systematically across a landscape. In our review, the proportion of the landscape that was managed by each system was generally not specified. Second, comparisons between even- and uneven-aged silviculture should not ignore the area that is affected by uneven-aged silviculture is much larger (e.g., 4-5 times), given the same quantity of wood being harvested annually (assuming similar productivity between the two systems).

As a conceptual example, consider that the ecological short-term impact (for a hypothetical taxon or process) is respectively 10 for even-aged and 8 for uneven-aged silviculture at the stand scale (Figure 3a) for each hectare that is harvested. It could be the impact on the size of a population of an amphibian species for example. If the area affected by harvesting is 4 times larger for uneven-aged silviculture than for even-aged silviculture, it means that the overall short-term ecological impact reported at the landscape level would be much larger for uneven-aged silviculture (Figure 3a). Furthermore, recovery (time to return to a pre-harvest condition or any desired condition) may be longer (e.g., Haeussler et al., 2007) for even-aged than for uneven-aged silviculture since the volume of wood harvested is larger in even-aged silviculture (Figure 3b). Given the same ratio of short term stand-scale impact, even if recovery rates at the stand level were 2 to 4 times longer for even-aged silviculture, the ecological impact of uneven-aged silviculture would be larger than with even-aged silviculture over most of the 80-year rotation (Figure 3c) because its impact is spread over four times the area, each year. The comparison of the relative impacts of both systems could consider the area under the curve for a given period of time starting from the present condition of the forest landscape.

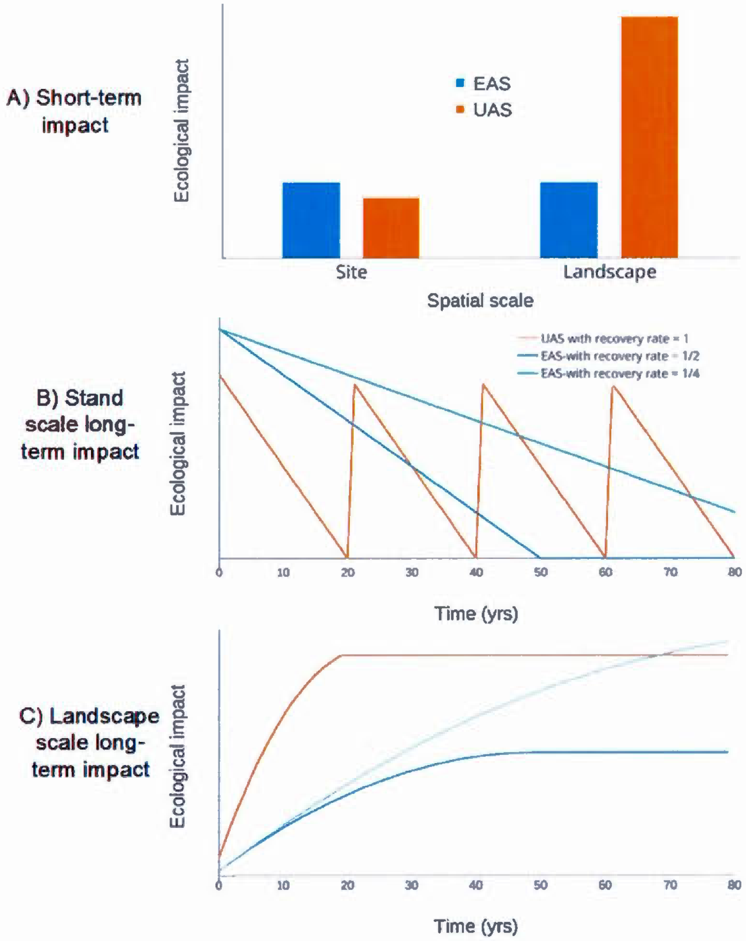

Figure 3.3 Simulated landscape scale ecological long-term impact of EAS and UAS (C) based on hypothetical short-term impacts of UAS as 80% of that of EAS hypothetical short-term impacts (A) and recovery rates (B). A) shows that short-term impacts (hypothetical variable) differ strongly at the landscape level between EAS and UAS because more surface is affected by forestry operations to harvest the same wood volume each year when UAS is used. B) Recovery rates: for UAS the theoretical recovery rate shown is such that at the end of a 20-year cutting cycle, the hypothetical variable recovered to its pre-harvest state; for EAS, two recovery rates are provided: ½ and ¼ the recovery rates of UAS.

This simple example highlights the complexity of comparing even- and uneven-aged silviculture as i) the scaling up from the stand to the landscape scale is often much more complex than a simple multiplication (e.g bird populations that are affected by the spatial assemblage of forest stands, Becker et al. (2011)) and ii) as recovery rates (e.g. Wang et al. 2006), which require long-term assessments, are often not known.

Given the importance of spatial and time scales in the even- vs uneven-aged silviculture comparison, it is very surprising that most of the studies we reviewed did not consider spatial scales in their comparison and that most comparisons were drawn at only one moment in time (Tables 3.1 and Table C.1 to C.9), ignoring that most ecosystems recover after harvesting. A fair comparison would be to contrast average or changing effects of even-aged and uneven-aged harvesting over one full even-aged stand rotation (say, 80-100 years) and for an equivalent time for uneven-aged stands over many cutting cycles (e.g., 4 or 5). Studies on the ecological comparison of even- and uneven-aged silviculture should embrace its inherent complexity rather than ignoring it and focus on the ecological indicators that appear the most important for forest resilience in a given region.

3.4.1 Management implications

While our review showed that even-aged silviculture does not necessarily have larger ecological effects than uneven-aged silviculture following harvesting, we found little evidence regarding the cumulative effects of implementing either systems over a whole landscape. Our review revealed strengths and weaknesses, in terms of ecological impacts, for both even-aged and uneven-aged silviculture. For example, even-aged silviculture appears to be better suited than uneven-aged silviculture for promoting tree and plant species (alpha) diversity, at least at the stand scale. Of course, more diversity is not always better as the nature of the diversity should be considered especially if generalist or non-forest species increase. The various stand development stages that are created by even-aged silviculture at the landscape scale scale (gamma diversity) also contribute to bird and mammal species diversity. However, there are also some ecological effects, which are of concern when clear-cutting/even-aged silviculture is used. This is true for some structural elements (Rüger et al., 2007), mycorrhizal fungi (Kropp and Albee, 1996), lichens and bryophytes (Paillet et al., 2010), some amphibian species (Tilghman et al., 2012), soil integrity (Spinelli et al., 2010), and surficial water runoff (Wang et al., 2006). These ecosystem elements are more fragile and seem better maintained by uneven-aged silviculture. We thus argue that both even-aged and uneven-aged silviculture can have negative effects, which are scale- and organism-dependent. Moreover, variations in even- and uneven-aged silviculture should be implemented (e.g. Nunery and Keeton, 2012) to mitigate these negative effects by creating and conserving a larger gradient of habitat types (Panel 2).

Panel 2: Possible variations in the implementation of even-aged and uneven-aged silviculture

Even-aged and uneven-aged silviculture are not strict concepts and both include several silvicultural systems (Matthews, 1989). Moreover, variations in their implementation can be used to mitigate their respective negative effects.

Clear-cutting (and therefore, even-aged silviculture) is of concern for some of the contributors to resilience that were evaluated. The protection of soils, which has been widely applied to mitigate soil erosion and rutting, is a good example of an improved silvicultural implementation. In addition, the more recent introduction of variable retention treatments that maintain some elements of biodiversity and structure is an important step towards a silviculture of resilience (Franklin et al., 1997; Lindenmayer et al., 2012)

Likewise, specific treatments can also be implemented in uneven-aged silviculture to promote tree species diversity. For example, it may be appropriate to create larger gaps (e.g., greater than 20 m radius) to promote recruitment of less tolerant species in selection cuts (Lorenzetti et al., 2008). In contrast, to avoid invasion in the shrub layer after partial cuts (Angers et al., 2005; Decocq et al., 2013; Zhou et al., 2013), reduction of harvesting intensity (proportion of the stand harvested) has been suggested at each cutting cycle (Nolet et al., 2014).

Moreover, all silvicultural systems can be applied in various spatial configurations (Matthews, 1989). A significant portion of the differences that are observed between even- and uneven-aged silviculture may be due to comparing large clear-cuts to single-tree selection cuts.

By challenging the preconceived notion that uneven-aged silviculture is necessarily better than even-aged silviculture in terms of its lower negative impacts on biodiversity and many ecosystem functions, this review provides collective support for diversification of silvicultural techniques that has previously been suggested from indirect reasoning (Duguid & Ashton 2013; Gauthier et al 2009). Hence, it opens the door to greater flexibility in the use of the two silviculture approaches for promoting forest resilience. However, the implications of this greater flexibility differs according to the proportion of even-uneven-aged currently used in forest ecosystems. For example, in temperate forests of north-eastern America, uneven-aged silviculture is currently preferred to even-aged silviculture (Nolet et al., 2014) in part because it appears closer to the natural disturbance regime (Seymour et al., 2002). For these forests, an increase in the use of even-aged management would probably favour resilience through an increase in both alpha and gamma diversity. In other ecosystems such as the Canadian boreal forest, the use of even-aged silviculture dominates and the use of uneven-aged silviculture is still very limited (Bose et al., 2013). For these predominantly even-aged managed ecosystems, in contrast to north-eastern temperate forests, this greater flexibility in approaches would then suggest an increase in the use of uneven-aged silviculture as suggested by Bergeron et al., (1999) based uniquely on disturbance dynamics rather than an analysis of real effects on biodiversity.

The proportion of even-/uneven-aged silvicuture to use in a landscape should however be specific to its ecological, economic and social situation as there is no one-size-fits-all solution. We provide (Table 4) a series of questions for decision-makers to assist them in evaluating the extent to which one approach should be favoured over another in a given region. We argue that during the forest management planning process, forest managers should identify contributors to ecosystem resilience, which are related to the most important risks to their forests. They should then optimize the planning of silvicultural treatments that would attain targets related to these contributors. In other words, even-/uneven-aged systems should be used as a means of achieving goals rather than as an end in themselves. The integral protection of a proportion of the landscape from timber harvesting should also be part of a diversity conservation strategy, since many studies in our review showed that uneven-aged silviculture was neither better nor worse than even-aged silviculture; significant differences emerged between managed forest and unmanaged forests, viz., some ecosystem elements and functions cannot tolerate any form of timber harvesting.

Tableau 3.2 Questions for guiding the use of even- and uneven-aged silviculture in a given region

In favor of uneven-aged if answered positively	In favor of even-aged if answered positively
• Does even-aged management imply artificial regeneration and site preparation? • Are there invading/exotic species that may be favored by even-aged management? • Are soils sensitive to erosion? • Are there species sensitive to large openings? • Is even-aged management highly dominant in the landscape?	• Does a dense shrub layer often develop following partial cuts? • Are variable retention guidelines after even-aged management well integrated in day-to-day timber harvesting? • Are there species sensitive to road construction/maintenance? • Are there desired species requiring large openings? • Is uneven-aged management highly dominant in the landscape?

3.5 Conclusion

Based on an exhaustive literature review comparing the effects of even- vs uneven-aged silvicultural systems on many ecological factors, we conclude that current views suggesting that uneven-aged silviculture is better suited than even-aged silviculture for promoting forest resilience cannot be substantiated. This finding provides the scientific support to forest and conservation managers for diversifying and optimizing their practices to promote forest resilience as biodiversity is being threatened by many different co-occurring changes and stressors. Historically, even- and uneven-aged silviculture had their promoters for economic, social or ecological reasons. While the dichotomy between even-aged and uneven-aged silviculture may still be important economically and also in terms of social acceptability (although not reviewed in the present paper), we argue that one approach cannot be promoted over the other based solely on ecological grounds.

Our review also reveals that studies that compared even- and uneven-aged silviculture on a large array of ecological indicators and on adequate time and spatial scales are rare. Given the role of forest management in biodiversity conservation, we advocate the implementation – in all forest biomes - of long-term studies comparing even- and uneven-aged silviculture using ecological indicators that cover various spatial scales.

3.6 Acknowledgements

The authors are very grateful to William F.J. Parsons for English editing.

CHAPITRE IV

CONCLUSION GÉNÉRALE

Une série de liens peuvent être tissés entre certains résultats obtenus à travers les différents chapitres (Figure 4.1). D'abord, dans le premier chapitre, nous avancions déjà l'hypothèse que l'absence de réaction de l'érable à sucre au chaulage (1.1) soit due au fait que les tiges d'érable à sucre auraient subi des stress qui les auraient rendues physiologiquement incapables de répondre positivement à une fertilisation. Cette hypothèse est soutenue (Lien 1) par nos résultats du chapitre 2 qui démontrent que les érables de la région à l'étude ont subi des stress importants au cours des périodes 1986-1989 et 2006-2007 (2.1).

Nos résultats, toujours au chapitre 1, montrent que la dominance de l'érable à sucre et du hêtre diminue avec les coupes totales (1.2). Ce résultat est en concordance (Lien 2) avec ce que nous avons observé dans notre revue de littérature (3.1). Cette diversité en essences forestières contribue par la suite à augmenter la diversité d'autres taxas (Lien 3). Dans les deux premiers chapitres, on remarque que les facteurs écologiques ont un effet différent chez l'érable à sucre selon la taille des individus considérés. Étant donné que dans le premier chapitre, ce sont surtout les semis qui sont favorisés par les coupes totales et que dans le deuxième chapitre, ce sont les plus grosses tiges qui sont les plus affectés par les événements extrêmes (L4), il est logique, dans un contexte de résilience face aux changements climatiques, d'envisager utiliser l'aménagement équienne pour une proportion des érablières à hêtre de la région (L5). Cette idée est supportée par le fait que les tiges ayant subi des stress importants semblent plus fragiles aux stress subséquents et que baser l'avenir des peuplements forestiers sur ces tiges est pour le moins risqué.

Ainsi, les résultats de la présente thèse, pris dans leur ensemble, supportent l'idée d'utiliser l'aménagement équienne dans les érablières à hêtre de la région à l'étude. Toutefois, il serait décevant que la thèse soit perçue comme un plaidoyer en faveur d'un aménagement forestier basé uniquement, ou même principalement, sur l'aménagement équienne. Tel que mentionné dans le chapitre 3, une diversité de traitements sylvicoles doivent être envisagés pour faire face aux nombreuses surprises que nous réservent les changements climatiques.

D'une façon plus générale, les chapitres de ma thèse pris dans leur ensemble montrent que la recherche en écologie forestière, d'une part, et que la recherche en sylviculture, d'autre part, ont avantage à être intimement liées, et ce, principalement dans un contexte de changement global. L'ère dans laquelle où on pouvait espérer prédire de façon précise et sans risque de se tromper les effets de l'application de « recettes » sylvicoles est révolue dans le contexte actuel d'incertitudes et de changements perpétuels : la sylviculture et les forestiers doivent se nourrir de la recherche en écologie forestière afin d'élaborer des traitements sylvicoles adaptés à cette nouvelle réalité.

D'autre part, avec des bouleversements climatiques d'une rapidité sans précédent, il est loin d'être assuré que les écosystèmes forestiers pourront s'adapter comme ils ont pu le faire lors de changements climatiques précédents. Ainsi, bien que la maxime « Nature knows best » soit probablement encore vraie, on pourrait rajouter que la Nature en sait moins qu'elle en savait. Devant un tel état de fait, les sylviculteurs, qui pratiquent en quelque sorte la science de l'intervention en forêt, pourraient être tentés de pousser davantage cet interventionnisme. Or, les quelques pratiques sylvicoles étudiées dans ma thèse – le chaulage, le dégagement du hêtre sous-couvert et la coupe totale – montrent que les traitements sylvicoles appliqués pour solutionner une problématique donnée, peuvent avoir des effets mitigés. Par exemple, le chaulage semble très peu intéressant dans la région à l'étude; l'utiliser constitue un mauvais investissement. Même si les deux autres traitements ont des effets en général positifs, on observe une grande variabilité dans leur efficacité, spécialement dans le cas de la coupe totale. En somme, l'interventionnisme sylvicole n'est pas gage de succès, en plus d'être coûteux.

Ainsi, dans un contexte de changement globaux, je propose une que l'on révise notre approche par rapport à l'intervention sylvicole et que l'on considère, en particulier, que l'abstention sylvicole est aussi une option valable. Je propose que l'on révise l'approche interventionnisme en se basant sur quatre principes (Figure 4.2). D'abord, le fait d'intervenir ou non de façon sylvicole devrait être basé sur **l'humilité**, c'est-à-dire que l'on reconnaît que dans un contexte d'incertitude lié aux changements globaux (voir chapitre 2), qu'il est impossible de connaître l'effet exact des traitements sylvicoles appliqués. L'adage du meilleur traitement au meilleur endroit au meilleur moment ne tient plus; divers traitements peuvent être appliqués face à une même situation, dont l'abstention. On a vu par exemple au chapitre 1, que l'absence de récolte marchande, couplée à une élimination des gaules de hêtre, était ce qui avait de plus bénéfique pour la régénération de l'érable à sucre.

Le deuxième principe est celui de la **flexibilité** qui reconnaît que les sylviculteurs seront de plus en plus confrontés à des situations qui leur étaient inconnues : ils n'auront vraisemblablement ni les moyens ni les connaissances pour appliquer les correctifs pour atteindre les objectifs qu'ils s'étaient fixés (i.e. en rendement ou en composition en essences). Devant une telle situation, le sylviculteur ne doit pas tenter, à tout prix, de rectifier une situation au préalable non-désirée, mais plutôt tenter de tirer bénéfice de la situation qui se présente. Encore une fois, l'abstention sylvicole demeure une option. L'humilité et la flexibilité, utilisées conjointement, mèneront à une plus grande complexité (Messier et al, 2013).

Le troisième principe est celui de **l'acquisition de connaissances**. D'une part, par ce principe, le statu quo sylvicole est remis en question. Ainsi, par exemple, les coupes de jardinage, tel qu'utilisées dans les érablières du Québec, favorisent très souvent le hêtre. Cette pratique sylvicole devrait être revue et l'aménagement équienne envisagé (chapitres 1 et 3). D'autre part, il existe une tendance dans le domaine forestier à croire qu'il est plus important d'agir que de comprendre. En ayant une meilleure compréhension des changements dans le dynamisme des écosystèmes (ex. : chapitre 2), on sera plus à même d'identifier des pratiques sylvicoles adaptées, mais surtout d'éviter de faire des actions qui risquent d'aggraver certaines situations. Si une partie des ressources destinées auparavant à l'intervention sylvicole est plutôt destinée à l'acquisition connaissance (et au monitoring), on encourage indirectement l'abstention sylvicole. On pourrait résumer ce principe par : « faire moins mais mieux ».

Les changements globaux placeront les sylviculteurs devant toutes sortes de défis et surprises. Il sera de toute évidence impossible économiquement d'intervenir partout. Le quatrième principe, la **catégorisation**, vise à classifier les écosystèmes d'un territoire (un peu comme dans la Triade) en fonction de l'intensité des problématiques d'adaptation aux changements climatiques en 3 catégories : a) écosystèmes qui ne demandent pas d'intervention particulière (ex. : écosystèmes pour lesquels on n'observe pas ou peu de problématiques liées aux changements globaux) b) écosystèmes sous surveillance (l'érablière à hêtre pourrait être un exemple) et c) écosystèmes fortement atteint nécessitant une intervention pour maintenir les fonctions désirées (ex. : peuplements de frênes). En confrontant cette catégorisation avec l'importance des écosystèmes (en termes de superificie et de biens et services offerts) sur le territoire, l'aménagiste sera plus à même d'identifier les écosystèmes prioritaires sur lesquels intervenir.

Je crois que ces principes, utilisés conjointement, peuvent aider les aménagistes et les sylviculteurs à mesurer leur niveau d'intervention dans leur désir de promouvoir l'adaptation des forêts aux changements climatiques. Je crois aussi que l'étude de cette mesure de l'intervention humaine dans les écocsystèmes face aux changements globaux constitue une avenue de recherche à la fois importante pour la société et prometteuse du point de vue scientifique. Cette avenue de recherche, que l'on pourrait nommer « du combien » se distingue de celle du « comment » (ex. Millar et al., 2007; West et al., 2009) et en est en fait la suite logique.

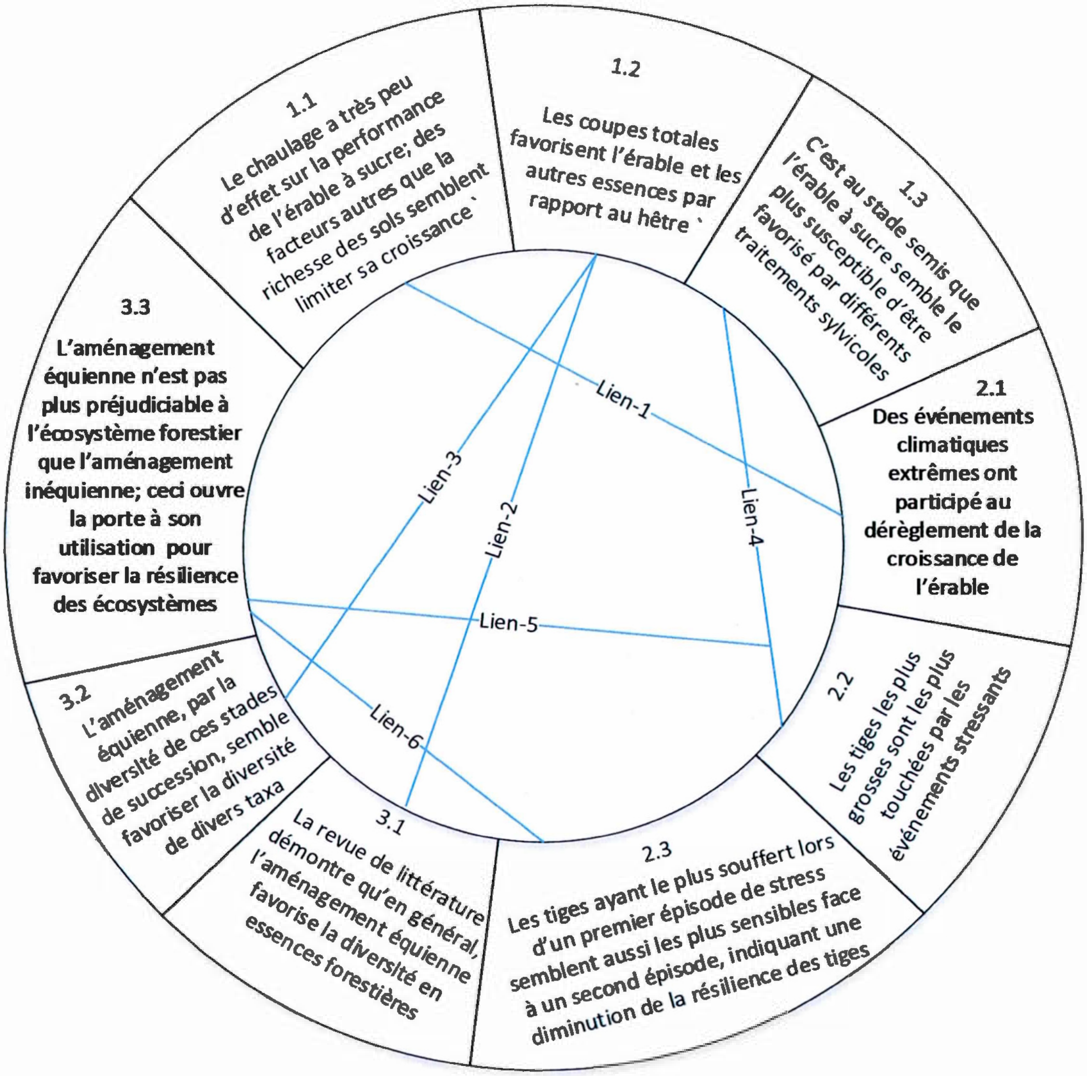

Figure 4.1 **Liens entre les chapitres de la thèse à travers certains résultats importants.**

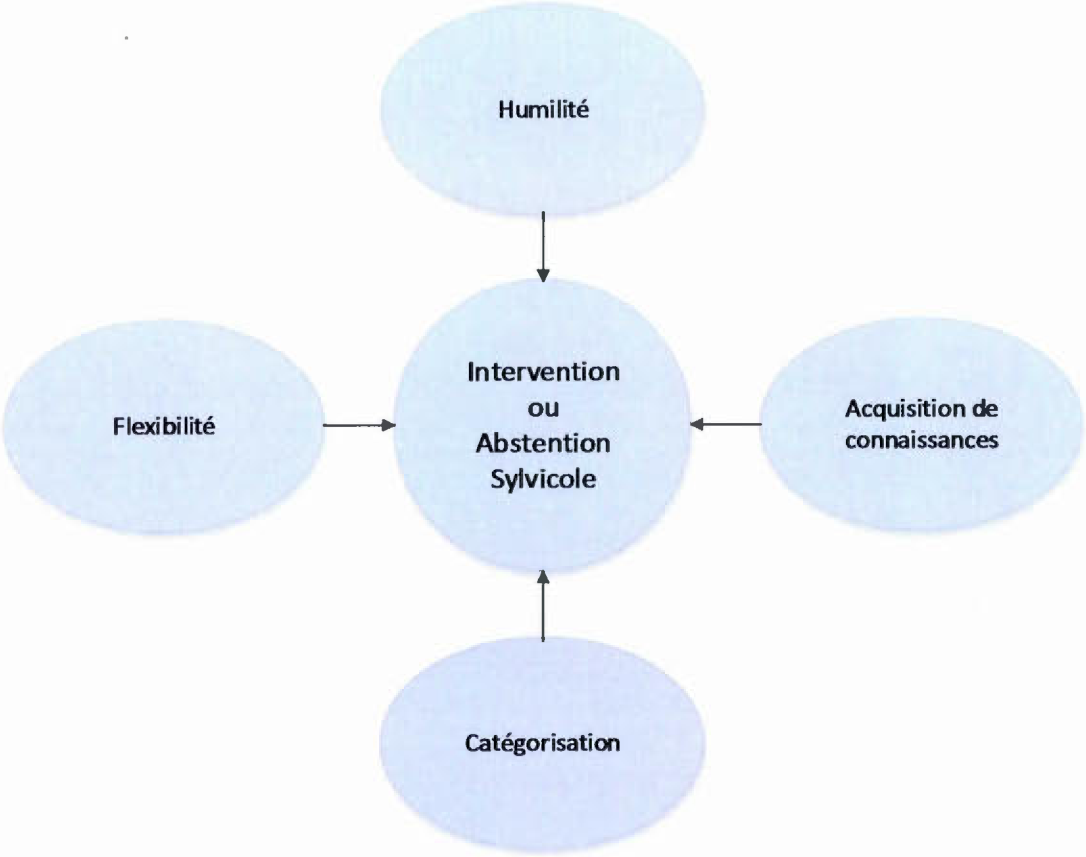

Figure 4.2 L'intervention ou l'abstention sylvicole face aux changements globaux régentée selon quatre principes.

APPENDICE A

SUPPLEMENTARY MATERIAL TO CHAPTER I

Study site

Figure A.1 Study site and treatment units localisation.

Statistical results from model comparisons for light, Ca, Mg and pH

Table A.1 Model comparison for light, Ca, Mg and pH.

Parameter	Model	k	Δ-AICc	Weight (ω)
Light	CO	4	0.00	73%
	CO+B	6	2.00	27%
	Intercept	2	20.66	0%
Ca	L	3	12.10	100%
	Intercept	2	0.00	0%
Mg	L	3	0.00	99%
	Intercept	2	10.21	1%
pH	L	3	0.00	75%
	Intercept	2	2.20	25%

See Table 1.3 for abbreviations.

Modified leaf blower

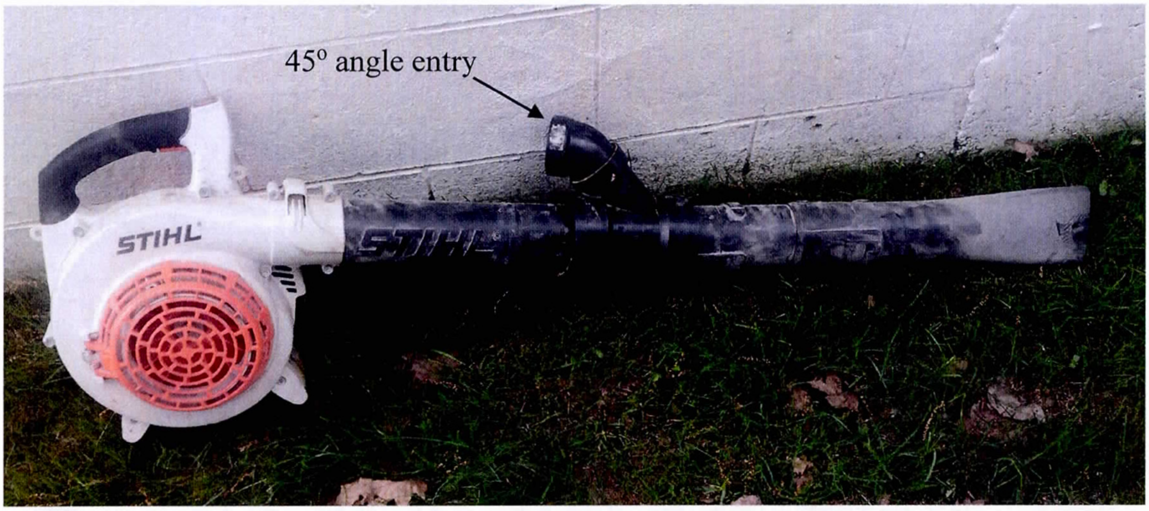

Figure A.2 Modified leaf blower. We added a two-entry conduct to the original tube of the blower. The lime was incorporated in the 45° angle entry and then blown in the forest stand.

Sapling basal area development

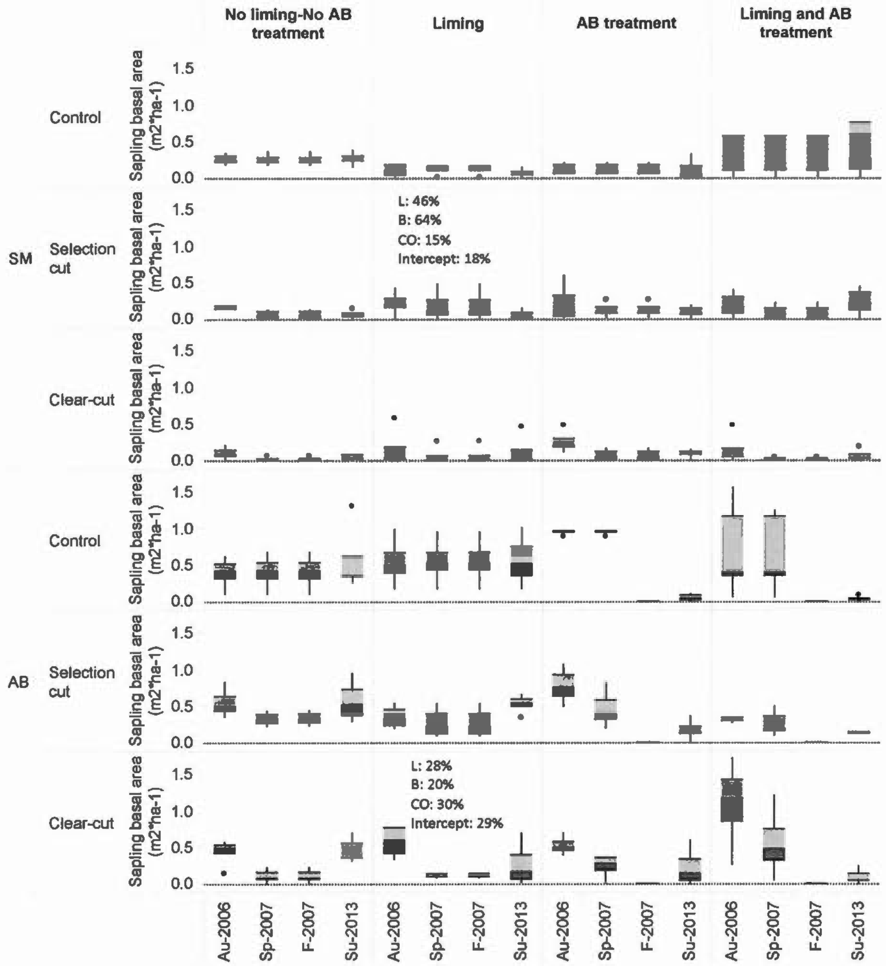

Figure A.3 Boxplots of sugar maple (SM) and American beech (AB) sapling basal area development according to the various treatments. Au: Autumn; Sp: Spring; Su: late-summer. Percentages related to L, B, CO represent the cumulative probabilities that the liming, sapling beech elimination, and canopy opening treatments be respectively included in the best model (see Methodology and Table 1.3 for details). The percentage associated to the intercept is provided for comparison. Details of the box plots are included in Figure 1.2.

Seedling density evolution

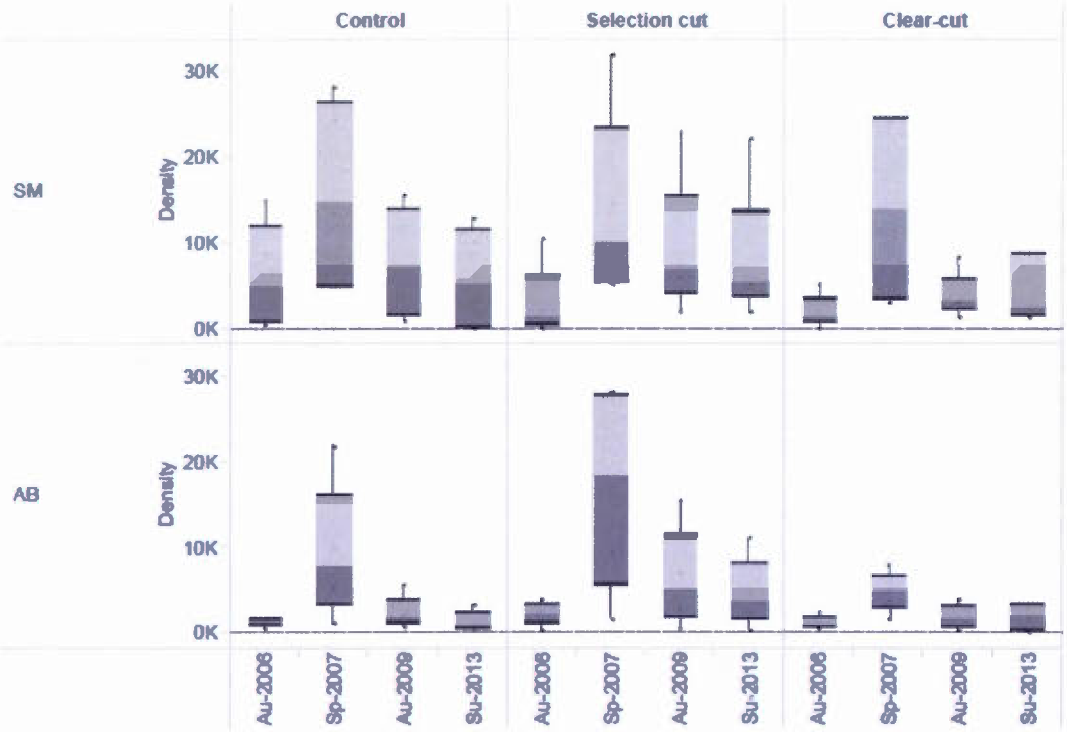

Figure A.4 Evolution of seedling density for sugar maple (SM) and American beech (AB). Only data without liming and AB sapling elimination are presented. Au: Autumn; Sp: Spring; Su: late-summer.

APPENDICE B

SUPPLEMENTARY MATERIAL TO CHAPTER II

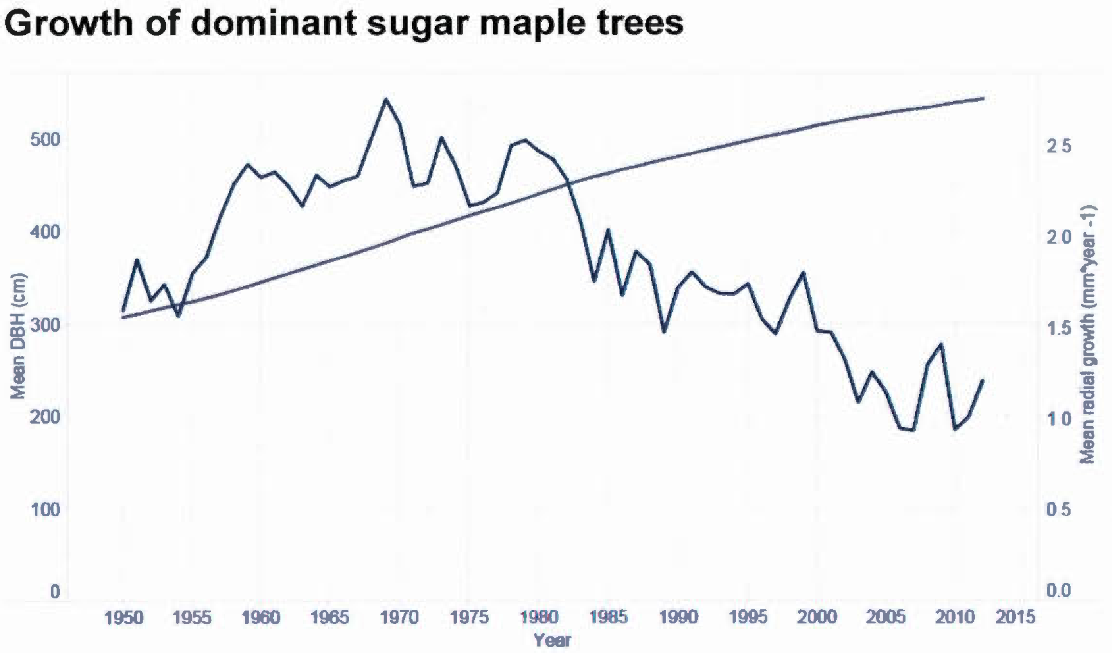

Figure B.1 Mean diameter and mean radial growth of 34 dominant sugar maple (DBH >44 cm in 2012) trees on a 60-year period. Trees were sampled in the same stands than those of Figure 2.1. Radial growth of these sugar maples when they had 40 cm in DBH (~ 1972) was about 2.2 mm*year^{-1}, which is much higher than the growth of trees of the same size nowadays (Figure 2.1C).

Additional dataset for regeneration

To support our hypothesis that sugar maple regeneration was also affected by the 1986-1989 event, we used an existing unpublished dataset. This data set has been acquired in 2001 from a territory about 100 km south of our main dataset in stands that have been strip-cut in 1988-1990. A total of forty sapling of sugar maple (from 2 to 10 cm DBH) were harvested and aged (with a disk taken at the base of the stem) in 10 strip cuts. Figure B.2 clearly shows a gap in regeneration between ~1978-1986. Our hypothesis is that this gap is also a consequence of the stressors that are responsible for the sugar maple growth drop in 1986-1989.

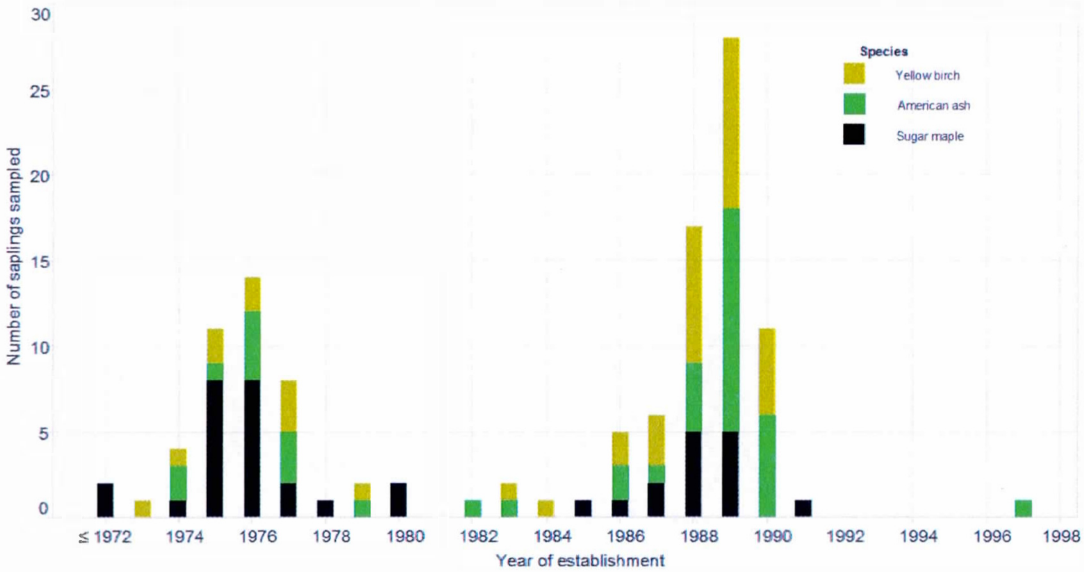

Figure B.2 Year of establishment for 40 sugar maple sampled in 2001.

Growth indices for sugar maple and American beech

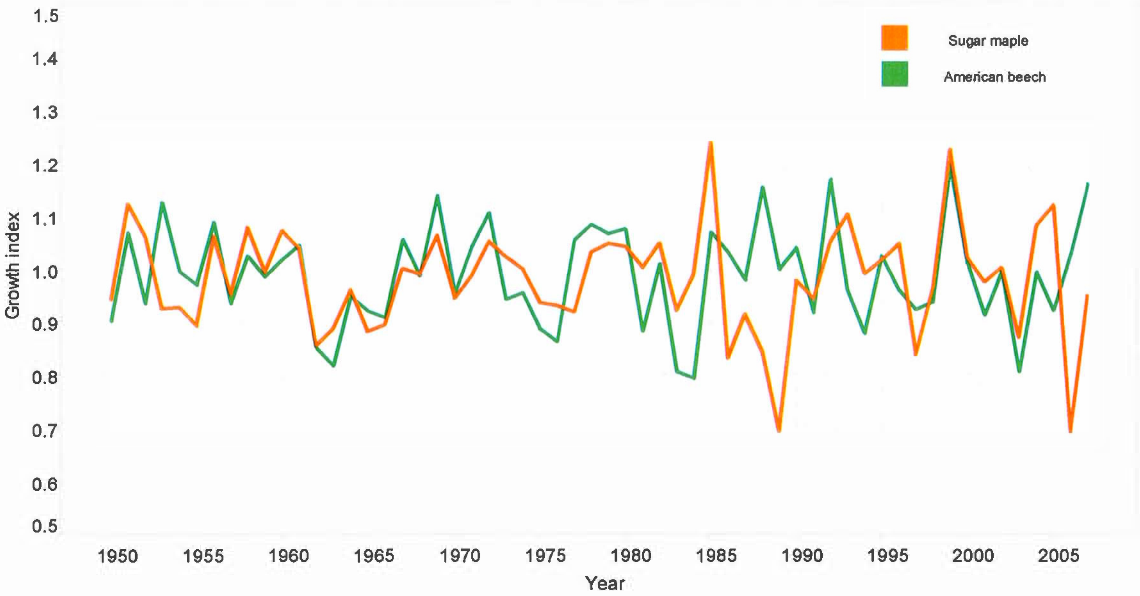

Figure B.3 **Detrended growth indices for sugar maple (orange) and American beech (green) for the 1948-2007 period.**

Correlation between climate variables and growth indices

Tableau B.1 Correlation between climate variables and growth indices for sugar maple and American beech. Only months where correlations > 0.33 for the 1950-1985 period are shown. Correlations were performed using the climate variables from both the growth year (current) and the year prededing the growth (-1).

Month	Climate variable	SM		AB	
		1950-1985	1990-2005	1950-1985	1990-2005
May (current)	Precipitations			-0.381	-0.189
May (current)	Water balance			-0.338	-0.160
June (current)	Mean temperature	-0.522	0.024	-0.410	-0.236
	Precipitations	0.341	0.216		
	Water balance	0.458	0.171	0.374	0.248
July (current)	Precipitations	0.419	-0.052		
	Water balance	0.441	-0.096		
	Mean temperature			0.346	0.346
April (-1)	Precipitations			-0.372	-0.028
	Water balance			-0.415	-0.074

Climate variables

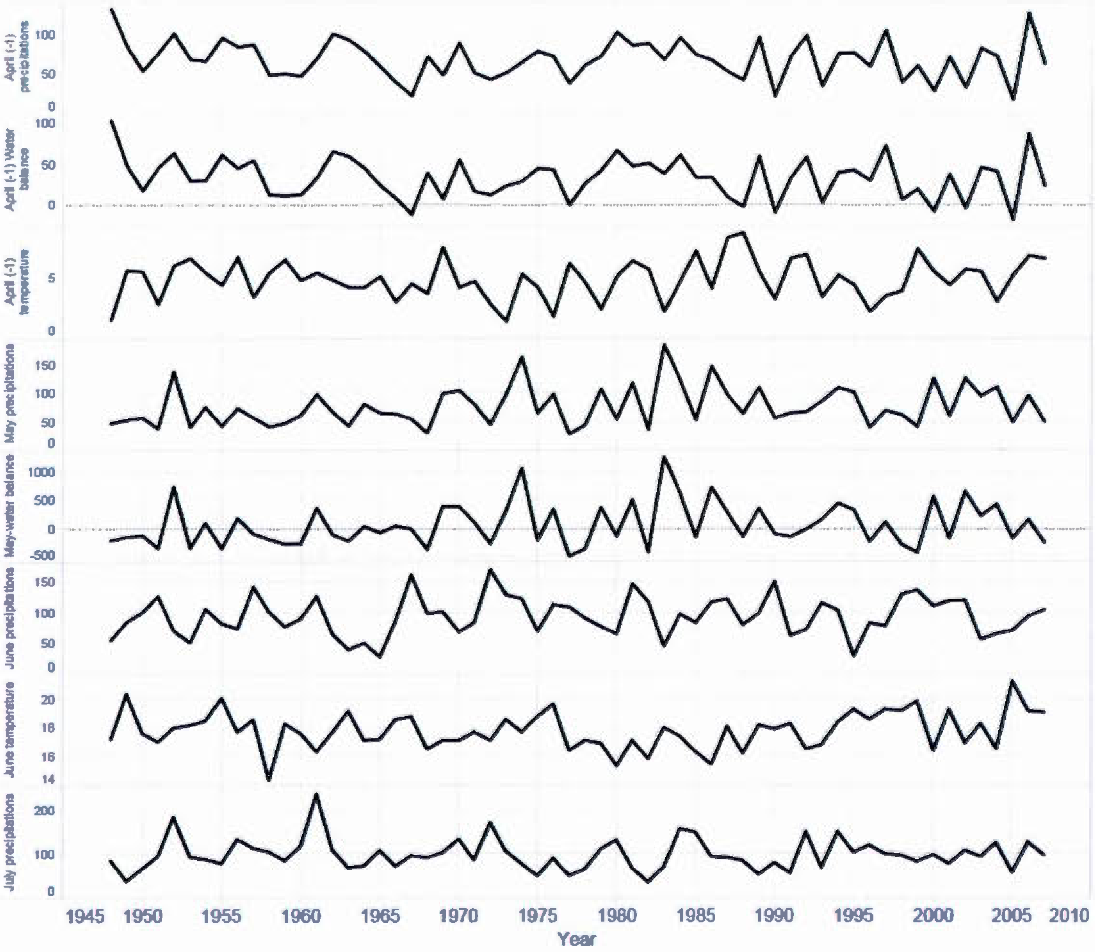

Figure B.4 Climate variables from 1948 to 2007. Only the climate variables used in Figure 2.2 and Table B.1 are shown.

Drought years

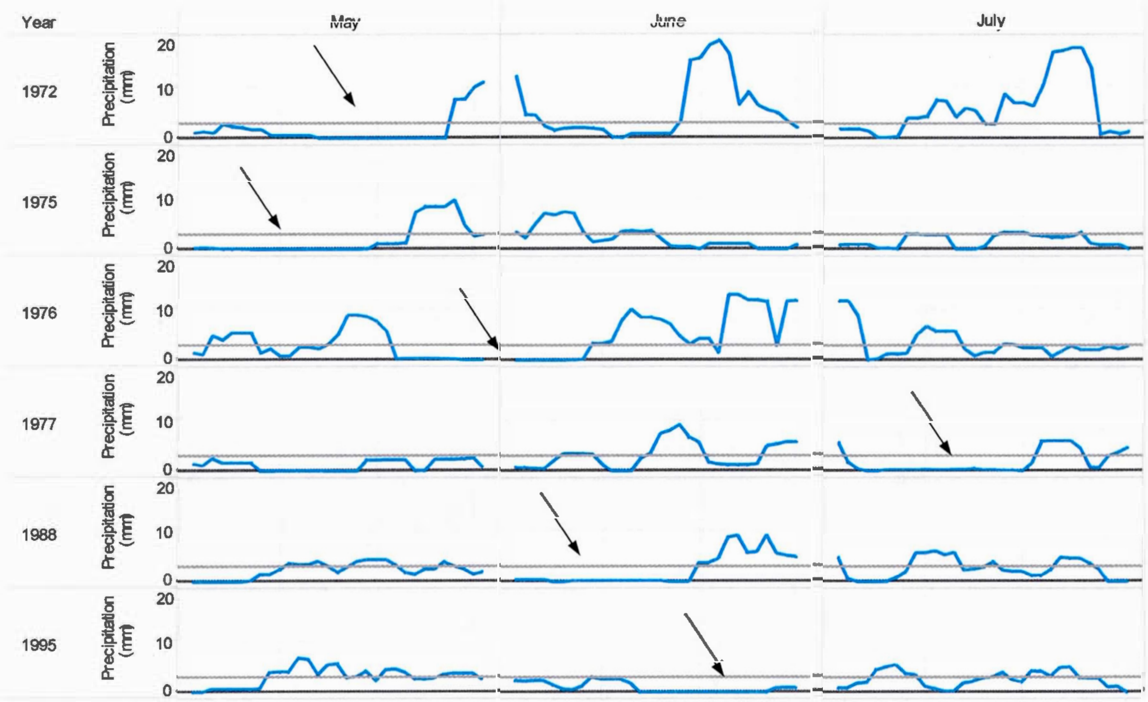

Figure B.5 Daily precipitation during the months of May to July for drought years between 1948 and 2007 according to the Mont-Laurier weather station. The grey line indicates mean daily precipitation over the period. Arrows show the periods of drought. See methodology for definition of a drought year.

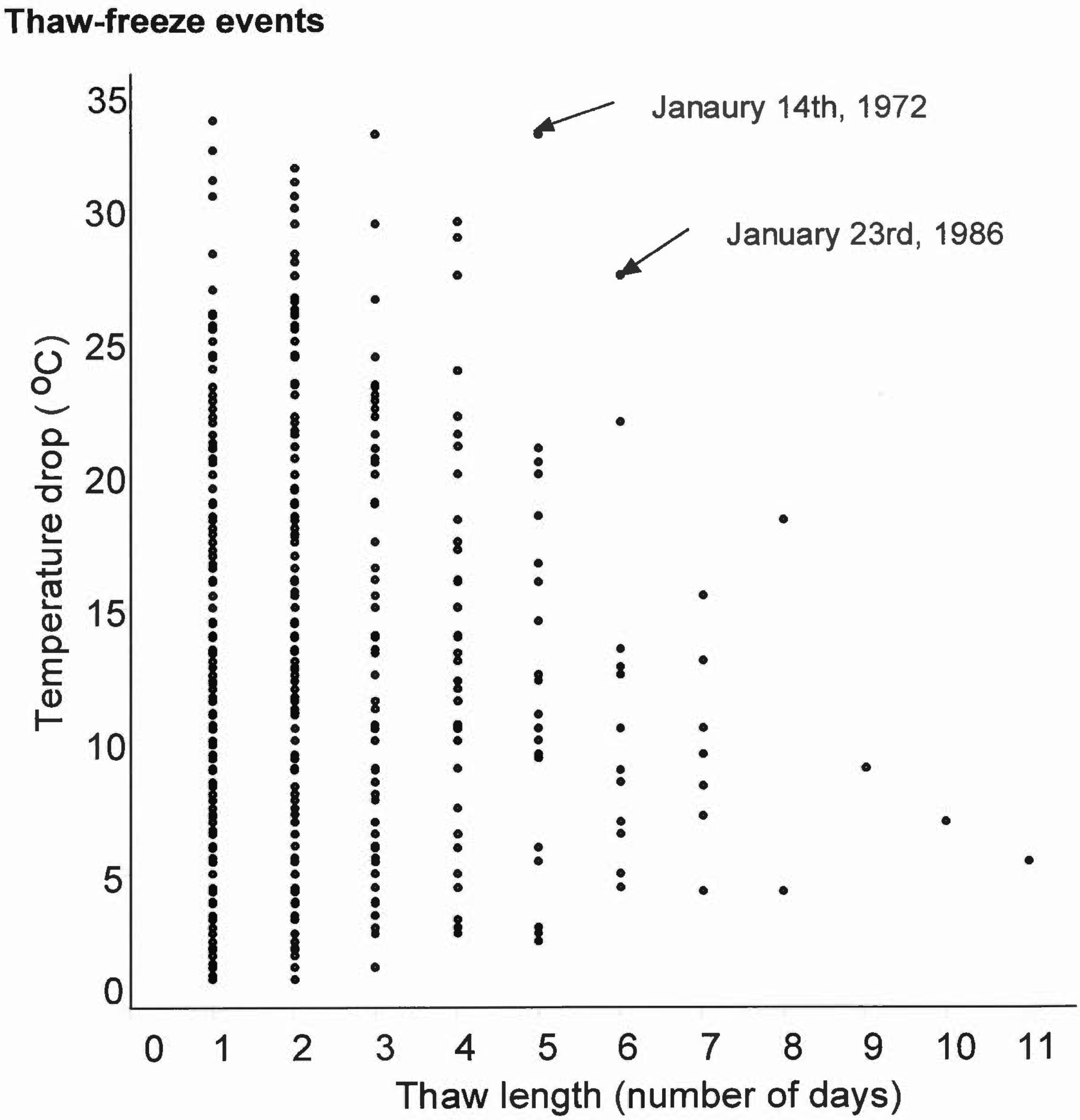

Figure B.6 Thaw-freeze events described by thaw length and subsequent temperature drop, each point representing a precise date between 1950 and 2007 for the months of January and February.

APPENDICE C

SUPPLEMENTARY MATERIAL TO CHAPTER III

Table C.1 Literature comparing even- and uneven-aged silviculture for herbs and shrubs

Elements studied	Effect	Time/spatial scale consideration	Biome	Reference
Herb diversity (Shannon)	EAS=UAS>UC	4 years after treatment/No	Temperate Deciduous Forests	Elliott and Knoepp (2005)
Vines and herbs Richness	EAS=UAS=UC	11 year after treatment/No	Tropical Moist Forests	Parrotta et al. (2002)
Vernal herbs richness and diversity	EAS=UAS=UC	3-9 years after treatment/No	Temperate Deciduous Forests	Fredericksen et al. (1999)
Vascular plant cover	UC=UAS; UC>EAS	1 year after treatment/No	Boreal Forests	Jalonen and Vanha-Majamaa (2001)
Spring herb richness Summer herb richness	EAS=UAS=UC	10 years for UAS; 27 years for EAS/No	Temperate Deciduous Forests	Kern et al. (2006),
Shrub Richness	UAS>EAS=UC	Undefined/No	Mediterranean Forests	Torras and Saura (2008)
Understory species richness	EAS=UAS	~ 12 years after treatment/Yes	Temperate Evergreen Forests	James (2012)

Understory species richness	EAS=UAS	Undefined/No	Temperate Deciduous Forests	Lenoir et al. (2010)
Shrub diversity Herb layer diversity	UAS>EAS pole stands, UAS=EAS mature stands EAS=UAS	Various development stages used for EAS/No	Mediterranean Forests	Alberti et al. (2013)
Diversity of functionnal types	EAS>UAS	EAS from 2 to 50 years/No	Temperate Deciduous Forests	Decocq et al. (2013)
Abundance of an invasive plant	EAS and UAS changed with deer and earthworm densities	~ 17 years after treatment/Yes	Temperate Deciduous Forests	Powers and Nagel (2008)
Understory plant diversity	UAS>EAS=UC	Various development stages used for EAS/No	Temperate forests in general	Duguid and Ashton (2013)
Understory plant richness Understory plant composition	UC>EAS=UAS EAS or UAS alone may lead a composition divergent	Various development stages used for EAS/No	Boreal Forests	Haeussler et al. (2007)

	from natural disturbances			

Table C.2 Literature comparing even- and uneven-aged silviculture for structural elements

Elements studied	Effect	Time/spatial scale consideration	Biome	Reference
Down woody debris and standing dead trees	UC>UAS>EAS	1-3 years/Yes	Boreal Forests	Atlegrim and Sjöberg (2004)
Snags basal area Down woody debris Vertical diversity	UC>EAS=UAS EAS=UAS>UC UC>UAS>EAS	~ 10 years after treatment/Yes	Temperate Deciduous Forests	Doyon et al. (2005)
Snags density	EAS>UC>UAS	Undefined/No	Mediterranean Forests	Torras and Saura (2008)
Snag volume Down woody debris	EAS>UAS UAS>EAS	Various ages/No	Temperate Deciduous Forests	Jenkins and Webster (2004)
Indices of compositional and structural change	UAS>EAS	1500-year span/Yes	Temperate Deciduous Forests	Rüger et al. (2007)
Cavity tree density	UC>UAS>EAS	Simulation study/Yes	Temperate Grasslands,	Fan et al. (2004)

			Savannas & Shrublands	
Horizontal and vertical diversity	EAS or UAS alone may lead a composition divergent from natural disturbances	Various development stages used for EAS/Yes	Boreal Forests	Haeussler et al. (2007)

Table C.3 Literature comparing even- and uneven-aged silviculture for mycorhizae, lichens, bryophytes, fungi and bacteries

Elements studied	Effect	Time/spatial scale consideration	Biome	Reference
Bryophytes cover	UC>UAS>EAS	1 year after treatment/No	Boreal Forests	Jalonen and Vanha-Majamaa (2001)
Ectomycorrhizal fungi richness	UC>UAS>EAS	16 years for EAS; 10 years for thinning/No	Temperate Evergreen Forests	Kropp and Albee (1996)
Fungal diversity	EAS=UAS=UC	65-70 years for EAS and at least 4 years since harvesting for UAS/Yes	Temperate Deciduous Forests	Lindner et al. (2006)
Microbial biomass and communities	EAS=UAS=UC	5 years after harvest/No	Boreal Forests	Hannam et al. (2006)
Microbial communities	EAS=UAS=UC	46 years for EAS and 12 years since harvesting for UAS/No	Deserts & Xeric Shrublands	Chatterjee et al. (2008)

Table C.4 Literature comparing even- and uneven-aged silviculture for mammals

Elements studied	Effect	Time/spatial scale consideration	Biome	Reference
Small mammals populations	Effets of EAS and UAS are species-specific	EAS: 0-20 years/No	Biomes of North America	Zwolak (2009)
Small mammals populations	EAS=UAS=UC for most species	1 to 4 years after treatment/No	Temperate Evergreen Forests	Klenner and Sullivan (2009)
Small rodents populations	Effets of EAS and UAS are species-specific	1-2 years after treatment/No	Temperate Deciduous Forests	Kang et al. (2013)
Populations of *Peromyscus* spp.	EAS=UAS>UC	4-7 years/No	Temperate Deciduous Forests	Fantz and Renken (2013)
Rabbit populations	UC> =UAS= EAS (< 15 years); EAS (15-40 years)> UAS=UC	Various stands ages for EAS/Yes	Temperate Evergreen Forests	Thornton et al. (2012)
Flying squirrel populations	UC>EAS=UAS	Not mentionned/ No	N.A.	Holloway and Smith (2011)
Species richness	EAS=UAS>UC	2-3 years after	Boreal Forests	Le Blanc et al. (2010)

Small mammals populations	Effets of EAS and UAS are species-specific	treatment/Yes		

Table C.5 Literature comparing even- and uneven-aged silviculture for birds

Elements studied	Effect	Time/spatial scale consideration	Biome	Reference
Mature forest species populations Early-successional species populations	UC>EAS=UAS EAS>UAS=UC	14-years monitoring after treatment/Yes	Temperate Deciduous Forests	Morris et al. (2013)
Bird species populations	Effets of EAS and UAS are species-specific	~ 10 years after treatment/Yes	Temperate Deciduous Forests	Doyon et al. (2005)
Population nesting	Forest-interior and interior-edge guilds: UC>UAS>EAS Early-successional species: EAS>UAS>UC	14-years monitoring after treatment/Yes	Temperate Deciduous Forests	Becker et al. (2011)
Abundance and richness of breeding birds	UAS>EAS (old) EAS (young)>EAS	Studies various stand age development for EAS/Yes	Temperate Deciduous Forests	Thill and Koerth (2005)

Early-succession species	EAS>UAS generally	12-years monitoring after treatment/Yes	Temperate Deciduous Forests	Perry and Thill (2013)
Migratory early-succession species	EAS>UAS	6 to 11 years/Yes	Temperate Deciduous Forests	Alterman et al. (2013)
Bird species richness	EAS>UAS	Various stands ages for EAS/Yes	Temperate Deciduous Forests	du Bus de Warnaffe and Deconchat (2008)
Cerulean warbler populations	EAS>UAS	1-2 years after treatment/No	Temperate Deciduous Forests	Kaminski and Islam (2013)
Species richness Birds populations	EAS-UAS>UC Effets of EAS and UAS are species-specific	2-3 years after treatment/Yes	Boreal Forests	Le Blanc et al. (2010)

Table C.6 Literature comparing even- and uneven-aged silviculture for herps

Elements studied	Effect	Time/spatial scale consideration	Biome	Reference
Salamander abundance	UC>UAS>EAS	Recovery with time/ No	North America	Tilghman et al. (2012)
red-backed salamanders abundance	UC>UAS>EAS	6-7 years after treatment/ No	Temperate Deciduous Forests	Hocking et al. (2013)
Salamander abundance	UC>UAS>EAS	13 yrs after treatment/ Yes	Temperate Deciduous Forests	Homyack and Haas (2009)
Amphibians Reptiles	UAS>EAS Sp-specific	3-4 years after treatment/ Yes	Temperate Deciduous Forests	Renken et al. (2004)
Amphibians specialist sp Amphibians generalist sp	UC>UAS>EAS EAS = UAS = UC	6 years after treatment/ No	Temperate Deciduous Forests	Popescu et al. (2012),
Salamanders survival Juvenile survival	UC>EAS	2-3 years/No	Temperate Deciduous Forests /	Todd et al. (2014)

	UAS=UC		Mediterranean Forests	
Amphibians oviposition and larval stage	EAS >UAS	4 years after treatment/ No	Temperate Evergreen Forests /Temperate Deciduous Forests	Semlitsch et al. (2009)
Amphibians juvenile and adult stages	EAS > UAS			

Table C.7 Literature comparing even- and uneven-aged silviculture for invertebrates

Elements studied	Effect	Time/spatial scale consideration	Biome	Reference
Ants, ground beetles and spiders communities	EAS=UAS=UC	5-20 years/No	Temperate Deciduous Forests	Johnston and Holberton (2009)
Dung beetle richness and diversity	EAS=UAS=UC	7 years after treatment/ Yes	Temperate Deciduous Forests	Masís and Marquis (2009)
Soil mites richness diversity and composition	EAS=UAS=UC	17 years after treatment/ No	Boreal Forests	Déchêne and Buddle (2009)
Gound beetle community	EAS=UAS=UC	Not mentionned	Boreal Forests	Atlegrim et al (1997)
Nematodes abundance Nematodes diversity	UC=UAS>EAS UC=UAS=EAS	6-7 months after harvesting/ No	Temperate Evergreen Forests	Panesar et al. (2005)

Carabid beetles richness Carabid beetles rare species	EAS>UC=UAS UC>EAS=UAS	EAS represented by various development stages/Yes	Temperate Deciduous Forests	du Bus dewarnaffe et Lebrun (2004)
Ground beetles	UC=UAS=EAS	EAS : ~ 70 years since treatment UAS : 7 years since last treatment/ Yes	Temperate Deciduous Forests	Latty et al. (2006)
Lepidoptera species	UC>EAS>UAS	2 years after treatment/ Yes	Temperate Deciduous Forests	Summerville (2011)
Herbivorous species richnesss	EAS>UAS for white oak EAS=UAS for black oak	7 years after treatment/ Yes	Temperate Deciduous Forests	Forkner et al. (2006)
Ground beetles	UC>UAS>EAM	3 years after treatment	Boreal forests	Graham-Sauvé et al. 2013

Table C.8 Literature comparing even- and uneven-aged silviculture for respiration and carbon sequestration

Elements studied	Effect	Time/spatial scale consideration	Biome	Reference
Soil surface CO2 efflux	UC=EAS>UAS	1 year after treatment/ No	Boreal Forests	Laporte et al. (2003)
Soil surface CO2 efflux	UC>EAS=UAS	17 months after treatment/ No	Temperate Deciduous Forests	Messina and Schoenholtz (1997)
Soil CO2 efflux	EAS>UAS>UC	8 years after treatment/ No	Temperate Deciduous Forests	Li et al. (2012)
Annual C assimilation rate	UC>UAS>EAS	5 years after treatment/ No	Boreal Forests	Lee et al. (2002)
Total amount of carbon	UC=UAS>EAS	13 years after treatment/ No	Temperate Deciduous Forests	Li et al. (2007)
Total C pool	UC>EAS=UAS	Various stand ages	Deserts & Xeric Shrublands	Chatterjee et al. (2009)

Carbon sequestration	UAS>EAS	Whole stand revolution/ Yes	Boreal Forests	Pukkala et al. (2011)
Carbon sequestration	UC=EAS>UAS	Whole stand revolution/ Yes	Temperate Deciduous Forests	Moore et al. (2012)
Carbon sequestration	EAS>UAS	80-year period/No	Boreal Forests	Nilsen and Strand (2013)

Table C.9 Literature comparing even- and uneven-aged silviculture for soil water and nutrients

Elements studied	Effect	Time/spatial scale consideration	Biome	Reference
Soil density, pH, C, N, Ca, Mg, K , CEC	EAS=UAS=UC	4 years after treatment/No	Temperate Deciduous Forests	Elliott and Knoepp (2005)
Organic matter, total nitrogen, soil density	EAS=UAS=UC	46 years for EAS and 12 years since harvesting for UAS/No	Deserts & Xeric Shrublands	Chatterjee et al. (2008)
Soil density and porosity, water nutrient concentrations	EAS=UAS=UC	17 months after treatment/No	Temperate Deciduous Forests	Messina and Schoenholtz (1997)
Light soil disturbances Heavy soil disturbances	EAS=UAS UAS>EAS	Immediately after harvesting/No	Mediterranean Forests	Spinelli et al. (2010)
Soil water nitrates and calcium concentration	Strong negative effects of management intensity	3-year monitoring/No	Temperate Deciduous Forests	Siemion et al. (2011)

Stream chemistry	UC>UAS>EAS	3-year monitoring/No	Temperate Deciduous Forests	Wang et al. (2006)

LISTE DES RÉFÉRENCES

Aakala, T., Kuuluvainen, T., Wallenius, T., Kauhanen, H., 2011. Tree mortality episodes in the intact Picea abies-dominated taiga in the Arkhangelsk region of northern European Russia. J. Veg. Sci. 22, 322–333. doi:10.1111/j.1654-1103.2010.01253.x

Adams, M.B., 1999. Acidic deposition and sustainable forest management in the central Appalachians, USA. For. Ecol. Manage. 122, 17–28. doi:10.1016/S0378-1127(99)00029-8

Alberti, G., Boscutti, F., Pirotti, F., Bertacco, C., De Simon, G., Sigura, M., Cazorzi, F., Bonfanti, P., 2013. A LiDAR-based approach for a multi-purpose characterization of Alpine forests: an Italian case study. iForest - Biogeosciences For. 6, 156–168. doi:10.3832/ifor0876-006

Allen, C.D., Macalady, A.K., Chenchouni, H., Bachelet, D., McDowell, N., Vennetier, M., Kitzberger, T., Rigling, A., Breshears, D.D., Hogg, E.H. (Ted), Gonzalez, P., Fensham, R., Zhang, Z., Castro, J., Demidova, N., Lim, J.-H., Allard, G., Running, S.W., Semerci, A., Cobb, N., 2010. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. For. Ecol. Manage. 259, 660–684. doi:10.1016/j.foreco.2009.09.001

Allen, D.C., Bauce, E., Barnett, J.C., Manion, P.D., Lachance, D., 1992. Sugar maple declines- causes, effects, and recommendations, in: Forest Decline Concepts. APS Press, pp. 491–498.

Alterman, L.E., Bednarz, J.C., Thill, R.E., The, S., Bulletin, W., Dec, N., 2013. Use of Group-Selection and Seed-Tree Cuts by Three Early-Successional Migratory Species in Arkansas Wilson Ornithological Soci 117, 353–363.

Amoroso, M.M., Daniels, L.D., Villalba, R., Cherubini, P., 2015. Does drought incite tree decline and death in Austrocedrus chilensis forests? J. Veg. Sci. 26, n/a–n/a. doi:10.1111/jvs.12320

Anderegg, W.R.L., Schwalm, C., Biondi, F., Camarero, J.J., Koch, G., Litvak, M., Ogle, K., Shaw, J.D., Shevliakova, E., Williams, A.P., Wolf, A., Ziaco, E., Pacala, S., 2015. Pervasive drought legacies in forest ecosystems and their implications for carbon cycle models. Science (80-.). 349, 528–532. doi:10.1126/science.aab1833

Anderson, D.R., Burnham, K.P., Thompson, W.L., 2000. Null Hypothesis Testing: Problems, Prevalence, and an Alternative. J. Wildl. Manage. doi:10.2307/3803199

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. For. Ecol. Manage. 217, 275–293. doi:10.1016/j.foreco.2005.06.008

Arii, K., Lechowicz, M.J., 2002. The influence of overstory trees and abiotic factors on the sapling community in an old-growth Fagus-Acer forest. Ecoscience 9, 386–396.

Atlegrim, O., Sjöberg, K., 2004. Selective felling as a potential tool for maintaining biodiversity in managed forests. Biodivers. Conserv. 1123–1133. doi:10.1023/B:BIOC.0000018148.84640.fd

Atlegrim, O., Sjöberg, K., Ball, J.P., 1997. Forestry effects on a boreal ground beetle community in spring: selective logging and clear-cutting compared. Entomol. Fenn. 8, 19–26.

Auclair, A., Eglinton, P., Minnemeyer, S., 1997. Principal forest dieback episodes in northern hardwoods: Development of numeric indices of areal extent and severity. Water. Air. Soil Pollut. doi:10.1007/BF02404755

Auclair, A.N.D., Lill, J.T., Revenga, C., 1996. The role of climate variability and global warming in the dieback of Northern Hardwoods. Water. Air. Soil Pollut. 91, 163–186. doi:10.1007/BF00666255

Auclerc, A., Nahmani, J., Aran, D., Baldy, V., Callot, H., Gers, C., Iorio, E., Lapied, E., Lassauce, A., Pasquet, A., Spelda, J., Rossi, J.-P., Guérold, F., 2012. Changes in soil macroinvertebrate communities following liming of acidified forested catchments in the Vosges Mountains (North-eastern France). Ecol. Eng. 42, 260–269. doi:10.1016/j.ecoleng.2012.02.024

Baldocchi, D.D., Wilson, K.B., Gu, L., 2002. How the environment, canopy structure and canopy physiological functioning influence carbon, water and energy fluxes of a temperate broad-leaved deciduous forest--an assessment with the biophysical model CANOAK. Tree Physiol. 22, 1065–77. doi:10.1093/treephys/22.15-16.1065

Bannon, K., Delagrange, S., Bélanger, N., Messier, C., 2015. American beech and sugar maple sapling relative abundance and growth are not modified by light availability following partial and total canopy disturbances. Can. J. For. Res. 45, 632–638. doi:10.1139/cjfr-2014-0240

Bauce, E., Allen, D.C., 1991. Etiology of a Sugar Maple Decline. Can. J. For. Res. 21, 686–693. doi:10.1139/x91-093

Beaudet, M., Brisson, J., Gravel, D., Messier, C., 2007. Effect of a major canopy disturbance on the coexistence of Acer saccharum and Fagus grandifolia in the understorey of an old-growth forest. J. Ecol. 95, 458–467. doi:10.1111/j.1365-2745.2007.01219.x

Beaudet, M., Messier, C., Paré, D., Brisson, J., Bergeron, Y., 1999. Possible mechanisms of sugar maple regeneration failure and replacement by beech in the Boise-des-Muir old-growth forest, Quebec. Ecoscience 6, 264–271.

Becker, D.A., Wood, P.B., Keyser, P.D., Wigley, T.B., Dellinger, R., Weakland, C.A., 2011. Threshold responses of songbirds to long-term timber management on an active industrial forest. For. Ecol. Manage. 262, 449–460. doi:10.1016/j.foreco.2011.04.011

Bell, J.L., Sloan, L.C., Snyder, M. a, 2004. Regional Changes in Extreme Climate Events: A Future Climate Scenario. J. Clim. 17, 81–87. doi:10.1175/1520-0442(2004)017<0081:rciece>2.0.co;2

Bergeron, Y., Harvey, B., Leduc, A., Gauthier, S., 1999. Forest management guidelines based on natural disturbance dynamics: stand-and forest-level considerations. For. Chron. 75, 49–54.doi.org/10.5558/tfc75049-1

Bergeron, Y., Leduc, A., Harvey, B., Gauthier, S., 2002. Natural fire regime: a guide for sustainable management of the Canadian boreal forest. Silva Fenn. 36, 81–95. doi:10.1139/x91-093

Bishop, D.A., Beier, C.M., Pederson, N., Lawrence, G.B., Stella, J.C., Sullivan, T.J., 2015. Regional growth decline of sugar maple (Acer saccharum) and its potential causes. Ecosphere 6, art179. doi:10.1890/ES15-00260.1

Blanc, M.-L. Le, Fortin, D., Darveau, M., Ruel, J.-C., 2010. Short Term Response of Small Mammals and Forest Birds to Silvicultural Practices Differing in Tree Retention in Irregular Boreal Forests. Ecoscience 17, 334–342. doi:10.2980/17-3-3340

Bose, a. K., Harvey, B.D., Brais, S., Beaudet, M., Leduc, a., 2013. Constraints to partial cutting in the boreal forest of Canada in the context of natural disturbance-based management: a review. Forestry 87, 11–28. doi:10.1093/forestry/cpt047

Bourque, C.P.-A., Cox, R.M., Allen, D.J., Arp, P.A., Meng, F.-R., 2005. Spatial extent of winter thaw events in eastern North America: historical weather records in relation to yellow birch decline. Glob. Chang. Biol. 11, 1477–1492. doi:10.1111/j.1365-2486.2005.00956.x

Bréda, N., Huc, R., Granier, A., Dreyer, E., 2006. Temperate forest trees and stands under severe drought: a review of ecophysiological responses, adaptation processes and long-term consequences. Ann. For. Sci. 63, 625–644. doi:10.1051/forest:2006042

Breshears, D.D., Cobb, N.S., Rich, P.M., Price, K.P., Allen, C.D., Balice, R.G., Romme, W.H., Kastens, J.H., Floyd, M.L., Belnap, J., Anderson, J.J., Myers, O.B., Meyer, C.W., 2005. Regional vegetation die-off in response to global-change-type drought. Proc. Natl. Acad. Sci. U. S. A. 102, 15144–8. doi:10.1073/pnas.0505734102

Brisson, J., De, I., Hx, Q., 1994. Beech-maple dynamics in an old-growth forest in southern Québec , Canada 1 1, 40–46.

Bunn, A.G., 2010. Statistical and visual crossdating in R using the dplR library. Dendrochronologia 28, 251–258. doi:10.1016/j.dendro.2009.12.001

Cale, J.A., McNulty, S.A., Teale, S.A., Castello, J.D., 2012. The impact of beech thickets on biodiversity. Biol. Invasions 15, 699–706. doi:10.1007/s10530-012-0319-5

Camarero, J.J., Gazol, A., Sangüesa-Barreda, G., Oliva, J., Vicente-Serrano, S.M., 2015. To die or not to die: early warnings of tree dieback in response to a severe drought. J. Ecol. 103, 44–57. doi:10.1111/1365-2745.12295

Canham, C.D., 1988. Growth and Canopy Architecture of Shade-Tolerant Trees : Response to Canopy Gaps. Ecology 69, 786–795. doi:10.2307/1941027

Canham, C.D., 1989. Different Responses to Gaps Among Shade-Tolerant Tree Species. Ecology 70, 548–550. doi:10.2307/1940200

Canham, C.D., 1990. Suppression and release during canopy recruitment in Fagus grandifolia. Bull. Torrey Bot. Club 1–7. doi:10.2307/2997123

Carpenter, S., Walker, B., Anderies, J.M., Abel, N., 2001. From Metaphor to Measurement: Resilience of What to What? Ecosystems 4, 765–781. doi:10.1007/s10021-001-0045-9

Chatterjee, A., Vance, G.F., Pendall, E., Stahl, P.D., 2008. Timber harvesting alters soil carbon mineralization and microbial community structure in coniferous forests. Soil Biol. Biochem. 40, 1901–1907. doi:10.1016/j.soilbio.2008.03.018

Chatterjee, A., Vance, G.F., Tinker, D.B., 2009. Carbon pools of managed and unmanaged stands of ponderosa and lodgepole pine forests in Wyoming. Can. J. For. Res. 39, 1893–1900. doi:10.1139/X09-112

Christie, D.A., Armesto, J.J., 2003. Regeneration microsites and tree species coexistence in temperate rain forests of Chilo{é} Island, Chile. J. Ecol. 91, 776–784. doi:10.1046/j.1365-2745.2003.00813.x

Cooke, B.J., Lorenzetti, F., 2006. The dynamics of forest tent caterpillar outbreaks in Québec, Canada. For. Ecol. Manage. 226, 110–121. doi:10.1016/j.foreco.2006.01.034

Côté, B., O'Halloran, I., Hendershot, W., Spankie, H., 1995. Possible interference of fertilization in the natural recovery of a declining sugar maple stand in southern Quebec. Plant Soil 168-169, 471–480. doi:10.1007/BF00029359

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. Front. Ecol. Environ. 7, 519–524. doi.org/10.1890/080088

Déchêne, A.D., Buddle, C.M., 2009. Effects of experimental forest harvesting on oribatid mite biodiversity. For. Ecol. Manage. 258, 1331–1341. doi:10.1016/j.foreco.2009.06.033

Decocq, G., Aubert, M., Dupont, F., Alard, D., Saguez, R., Wattez-Franger, A., De Foucault, B., Delelis-Dusollier, A., Bardat, J., 2004. Plant diversity in a managed temperate deciduous forest: Understorey response to two silvicultural systems. J. Appl. Ecol. 41, 1065–1079. doi:10.1111/j.0021-8901.2004.00960.x

Delagrange, S., Messier, C., Lechowicz, M.J., Dizengremel, P., 2004. Physiological, morphological and allocational plasticity in understory deciduous trees: importance of plant size and light availability. Tree Physiol. 24, 775–784. doi:10.1093/treephys/24.7.775

Denny, M.W., Hunt, L.J.H., Miller, L.P., Harley, C.D.G., 2009. On the prediction of extreme ecological events. Ecol. Monogr. 79, 397–421. doi:http://dx.doi.org/10.1890/08-0579.1

Doyon, F., Gagnon, D., Giroux, J.-F., 2005. Effects of strip and single-tree selection cutting on birds and their habitat in a southwestern Quebec northern hardwood forest. For. Ecol. Manage. 209, 101–116. doi:10.1016/j.foreco.2005.01.005

Drever, C.R., Peterson, G., Messier, C., Bergeron, Y., Flannigan, M., 2006. Can forest management based on natural disturbances maintain ecological resilience? Can. J. For. Res. 36, 2285–2299. doi:10.1139/x06-132

Driscoll, C.T., Driscoll, K.M., Mitchell, M.J., Raynal, D.J., 2003. Effects of acidic deposition on forest and aquatic ecosystems in New York State. Environ. Pollut. 123, 327–336. doi:10.1016/S0269-7491(03)00019-8

du Bus de Warnaffe, G., Deconchat, M., 2008. Impact of four silvicultural systems on birds in the Belgian Ardenne: implications for biodiversity in plantation forests. Biodivers. Conserv. 17, 1041–1055. doi:10.1007/s10531-008-9364-x

du Bus dewarnaffe, G., Lebrun, P., 2004. Effects of forest management on carabid beetles in Belgium: implications for biodiversity conservation. Biol. Conserv. 118, 219–234. doi:10.1016/j.biocon.2003.08.015

Duchesne, L., Ouimet, R., Houle, D., 2002. Basal area growth of sugar maple in relation to acid deposition, stand health, and soil nutrients. J. Environ. Qual. 31, 1676–1683. doi:10.2134/jeq2002.1676

Duchesne, L., Ouimet, R., Moore, J.D., Paquin, R., 2005. Changes in structure and composition of maple-beech stands following sugar maple decline in Québec, Canada. For. Ecol. Manage. 208, 223–236. doi:10.1016/j.foreco.2004.12.003

Duguid, M.C., Ashton, M.S., 2013. A meta-analysis of the effect of forest management for timber on understory plant species diversity in temperate forests. For. Ecol. Manage. 303, 81–90. doi:10.1016/j.foreco.2013.04.009

Duraiappah, A.K., Naeem, S., Agardy, T., Assessment, M.E., 2005. Ecosystems and human well-being: biodiversity synthesis. Island Press Washington, DC.

Easterling, D.R., Meehl, G. a, Parmesan, C., Changnon, S. a, Karl, T.R., Mearns, L.O., 2000. Climate extremes: observations, modeling, and impacts. Science 289, 2068–2074. doi:10.1126/science.289.5487.2068

Elbakidze, M., Angelstam, P., Andersson, K., Nordberg, M., Pautov, Y., 2011. How does forest certification contribute to boreal biodiversity conservation? Standards and outcomes in Sweden and NW Russia. For. Ecol. Manage. 262, 1983–1995. doi:10.1016/j.foreco.2011.08.040

Elliott, K.J., Knoepp, J.D., 2005. The effects of three regeneration harvest methods on plant diversity and soil characteristics in the southern Appalachians. For. Ecol. Manage. 211, 296–317. doi:10.1016/j.foreco.2005.02.064

Fan, Z., Shifley, S.R., Thompson, F.R., Larsen, D.R., 2004. Simulated cavity tree dynamics under alternative timber harvest regimes. For. Ecol. Manage. 193, 399–412. doi:10.1016/j.foreco.2004.02.008

Fantz, D.K., Renken, R.B., 2013. Short-term landscape-scale effects on Peromyscus spp . forest mnanagement mice within Missouri Ozark forests. Wildl. Soc. Bull. 33, 293–301. doi:10.2193/0091-7648(2005)33[293:SLEOFM]2.0.CO;2

FAO, 2009. State of the World's Forests.

Forcier, L.K., 1975. Reproductive Strategies and the Co-occurrence of Climax Tree Species. Science (80-.). 189, 808–810.

Forkner, R.E., Marquis, R.J., Lill, J.T., Le Corff, J., 2006. Impacts of Alternative Timber Harvest Practices on Leaf-Chewing Herbivores of Oak. Conserv. Biol. 20, 429–440. doi:10.1111/j.1523-1739.2006.00346.x

Foster, D., 1988. Species and stand responce to catastrophic wind incantral New England, U.S.A. J. Ecol. 76, 135–151. doi:10.2307/2260458

Franklin, J.F., Berg, D.R., Thornburgh, D.A., Tappeiner, J.C., 1997. Alternative silvicultural approaches to timber harvesting: variable retention harvest systems.

Creat. a For. 21st century Sci. Ecosyst. Manag. Isl. Press. Washington, DC 111–139.

Fredericksen, T.S., Ross, B.D., Hoffman, W., Morrison, M.L., Beyea, J., N. Johnson, B., Lester, M.B., Ross, E., 1999. Short-term understory plant community responses to timber-harvesting intensity on non-industrial private forestlands in Pennsylvania. For. Ecol. Manage. 116, 129–139. doi:10.1016/S0378-1127(98)00452-6

Frost, E.E., Levia, D.F., 2014. Hydrologic variation of stemflow yield across co-occurring dominant canopy trees of varying mortality. Ecohydrology 7, 760–770. doi:10.1002/eco.1397

Fyles, J.W., Côté, B., Courchesne, F., Hendershot, W.H., Savoie, S., 1994. Effects of base cation fertilization on soil and foliage nutrient concentrations, and litter-fall and throughfall nutrient fluxes in a sugar maple forest. Can. J. For. Res. 24, 542–549. doi:10.1139/x94-071

Gasser, D., Messier, C., Beaudet, M., Lechowicz, M.J., 2010. Sugar maple and yellow birch regeneration in response to canopy opening, liming and vegetation control in a temperate deciduous forest of Quebec. For. Ecol. Manage. 259, 2006–2014. doi:10.1016/j.foreco.2010.02.011

Gauthier, S., 2009. Ecosystem management in the boreal forest. PUQ.

Gavin, D., 2008. Forest dynamics and the growth decline of red spruce and sugar maple on Bolton Mountain, Vermont: a comparison of modeling methods. Can. J. For. Res. 38, 2635–2649. doi:10.1139/X08-106

Gillis, A.M., 1990. The new forestry. Bioscience 558–562. doi.org/10.2307/1311294

Graham-Sauvé, L., Work, T.T., Kneeshaw, D., Messier, C., 2013. Shelterwood and multicohort management have similar initial effects on ground beetle assemblages in boreal forests. For. Ecol. Manage. 306, 266–274. doi:10.1016/j.foreco.2013.06.019

Gravel, D., Beaudet, M., Messier, C., 2011. Sapling age structure and growth series reveal a shift in recruitment dynamics of sugar maple and American beech over the last 40 years. Can. J. For. Res. 41, 873–880. doi:10.1139/X10-242

Gravel, D., Canham, C.D., Beaudet, M., Messier, C., 2006. Reconciling niche and neutrality: the continuum hypothesis. Ecol. Lett. 9, 399–409. doi:10.1111/j.1461-0248.2006.00884.x

Gutschick, V.P., BassiriRad, H., 2003. Extreme events as shaping physiology, ecology, and evolution of plants: Toward a unified definition and evaluation of their consequences. New Phytol. 160, 21–42. doi:10.1046/j.1469-8137.2003.00866.x

Hacke, U.G., Sperry, J.S., 2001. Functional and ecological xylem anatomy. Perspect. Plant Ecol. Evol. Syst. 4, 97–115. doi:10.1078/1433-8319-00017

Haeussler, S., Bergeron, Y., Brais, S., Harvey, B.D., 2007. Natural dynamics-based silviculture for maintaining plant biodiversity in Populus tremuloides -dominated boreal forests of eastern Canada. Can. J. Bot. 85, 1158–1170. doi:10.1139/B07-108

Hallett, R.A., Bailey, S.W., Horsley, S.B., Long, R.P., 2006. Influence of nutrition and stress on sugar maple at a regional scale. Can. J. For. Res. 36, 2235–2246. doi:10.1139/x06-120

Hannam, K., Quideau, S., Kishchuk, B., 2006. Forest floor microbial communities in relation to stand composition and timber harvesting in northern Alberta. Soil Biol. Biochem. 38, 2565–2575. doi:10.1016/j.soilbio.2006.03.015

Hartmann, H., Messier, C., 2008. The role of forest tent caterpillar defoliations and partial harvest in the decline and death of sugar maple. Ann. Bot. 102, 377–87. doi:10.1093/aob/mcn104

Helms, J.A., 1998. The dictionary of forestry.

Hill, J.D., Silander, J. a, 2001. Distribution and dynamics of two ferns: Dennstaedtia punctilobula (Dennstaedtiaceae) and Thelypteris noveboracensis (Thelypteridaceae) in a Northeast mixed hardwoods-hemlock forest. Am. J. Bot. 88, 894–902. doi:10.2307/2657041

Hocking, D.J., Babbitt, K.J., Yamasaki, M., 2013. Comparison of silvicultural and natural disturbance effects on terrestrial salamanders in northern hardwood forests. Biol. Conserv. 167, 194–202. doi:10.1016/j.biocon.2013.08.006

Holloway, G.L., Smith, W.P., 2011. A meta-analysis of forest age and structure effects on northern flying squirrel densities. J. Wildl. Manage. 75, 668–674. doi:10.1002/jwmg.77

Holmes, R.L., 1983. Computer-assisted quality control in tree-ring dating and measurement. Tree-ring Bull. 43, 69–78.

Homyack, J.A., Haas, C.A., 2009. Long-term effects of experimental forest harvesting on abundance and reproductive demography of terrestrial salamanders. Biol. Conserv. 142, 110–121. doi:10.1016/j.biocon.2008.10.003

Hooper, M.C., Arii, K., Lechowicz, M.J., 2001. Impact of a major ice storm on an old-growth hardwood forest. Can. J. Bot. 79, 70–75. doi:10.1139/cjb-79-1-70

Horsley, S.B., Long, R.P., Bailey, S.W., Hallett, R.A., Hall, T.J., 2000. Factors associated with the decline disease of sugar maple on the allegheny plateau. Can. J. For. Res. 30, 1365–1378. doi:10.1139/x00-057

Houston, D.R., 1999. History of sugar maple decline, in: Sugar Maple Ecology and Health: Proceedings of an International Symposium. USDA Forest Service Northeastern Research Station, Warren, Pennsylvania, pp. 19–26.

Hubbell, S.P., 1997. A unified theory of biogeography and relative species abundance and its application to tropical rain forests and coral reefs. Coral reefs 16, S9–S21. doi:10.1007/s003380050237

IUFRO, 2016. No Title [WWW Document]. URL http://www.iufro.org/science/divisions/division-1/10000/10500/ (accessed 1.5.16).

Jalonen, J., Vanha-Majamaa, I., 2001. Immediate effects of four different felling methods on mature boreal spruce forest understorey vegetation in southern Finland. For. Ecol. Manage. 146, 25–34. doi:10.1016/S0378-1127(00)00446-1

James, C., 2012. Comparison of Floristic Diversity between Young Conifer Plantations and Second-Growth Adjacent Forests in California's Northern Interior. West. J. Appl. For. J. Appl. For. 27, 60–71. doi:10.5849/wjaf.11-006

Jenkins, M., Webster, C., 2004. Coarse woody debris in managed central hardwood forests of Indiana, USA. For. Sci. 50, 781–792.

Johnston, J.C., Holberton, R.L., 2009. Forest management and temporal effects on food abundance for a ground-foraging bird (Catharus guttatus). For. Ecol. Manage. 258, 1516–1527. doi:10.1016/j.foreco.2009.07.012

Juice, S.S.M., Fahey, T.T.J., Siccama, T.T.G., Driscoll, C.T., Denny, E.G., Eagar, C., Cleavitt, N.L., Minocha, R., Richardson, A.D., 2006. Response of sugar maple to calcium addition to northern hardwood forest. Ecology 87, 1267–1280. doi:10.1890/0012-9658(2006)87[1267:ROSMTC]2.0.CO;2

Kaminski, K., Islam, K., 2013. Effects of Forest Treatments on Abundance and Spatial Characteristics of Cerulean Warbler Territories. Am. Midl. Nat. 170, 111–120. doi:10.1674/0003-0031-170.1.111

Kang, J.-H., Son, S.-H., Kim, K., 2013. Effects of Logging Intensity on Small Rodents in Deciduous Forests. J Anim Vet Adv 12, 248–252.

Keeton, W.S., 2006. Managing for late-successional/old-growth characteristics in northern hardwood-conifer forests. For. Ecol. Manage. 235, 129–142. doi:10.1016/j.foreco.2006.08.005

Kern, C.C., Palik, B.J., Strong, T.F., 2006. Ground-layer plant community responses to even-age and uneven-age silvicultural treatments in Wisconsin northern hardwood forests. For. Ecol. Manage. 230, 162–170. doi:10.1016/j.foreco.2006.03.034

Klenner, W., Sullivan, T.P., 2009. Partial and clearcut harvesting of dry Douglas-fir forests: Implications for small mammal communities. For. Ecol. Manage. 257, 1078–1086. doi:10.1016/j.foreco.2008.11.012

Kneeshaw, D.D., Leduc, A., Messier, C., Drapeau, P., Gauthier, S., Paré, D., Carignan, R., Doucet, R., Bouthillier, L., 2000. Development of integrated ecological standards of sustainable forest management at an operational scale. For. Chron. 76, 481–493.

Kobe, R.K., Likens, G.E., Eagar, C., 2002. Tree seedling growth and mortality responses to manipulations of calcium and aluminum in a northern hardwood forest. Can. J. For. Res. 32, 954–966. doi:10.1139/x02-018

Kolb, T.E., McCormick, L.H., 1993. Etiology of sugar maple decline in four Pennsylvania stands. Can. J. For. Res. 23, 2395–2402. doi:10.1139/x93-296

Kropp, B.R., Albee, S., 1996. The effects of silvicultural treatments on occurrence of mycorhizal sporocarps in a Pinus contorta forest: A preliminary study. Biol. Conserv. 70, 313–318. doi:10.1016/S0006-3207(96)00140-1

Kruger, E.L., Reich, P.B., 1997. Responses of hardwood regeneration to fire in mesic forest openings. III. Whole-plant growth, biomass distribution, and nitrogen and carbohydrate relations. Can. J. For. Res. 27, 1841–1850. doi:10.1139/x97-138

Kurz, W. a, Stinson, G., Rampley, G.J., Dymond, C.C., Neilson, E.T., 2008. Risk of natural disturbances makes future contribution of Canada's forests to the global carbon cycle highly uncertain. Proc. Natl. Acad. Sci. U. S. A. 105, 1551–1555. doi:10.1073/pnas.0708133105

Labrecque, P., Nolet, P., Lesage, G., 2006. Projet Sylviculture par objectifs 2005-2006- Rapport technique, Institut québécois d'Aménagement de la Forêt .... Ripon, Québec, Canada.

Lane, C., Reed, D., 1993. Width of sugar maple (Acer saccharum) tree rings as affected by climate. Can. J. For. Res. 23, 2370–2375. doi:10.1139/x93-29

Laporte, M.F., Duchesne, L.C., Morrison, I.K., 2003. Effect of clearcutting, selection cutting, shelterwood cutting and microsites on soil surface CO2 efflux in a tolerant hardwood ecosystem of northern Ontario. For. Ecol. Manage. 174, 565–575. doi:10.1016/S0378-1127(02)00072-5

Latty, E.F., Werner, S.M., Mladenoff, D.J., Raffa, K.F., Sickley, T.A., 2006. Response of ground beetle (Carabidae) assemblages to logging history in northern hardwood–hemlock forests. For. Ecol. Manage. 222, 335–347. doi:10.1016/j.foreco.2005.10.028

Lee, J., Morrison, I.K., Leblanc, J.-D., Dumas, M.T., Cameron, D.A., 2002. Carbon sequestration in trees and regrowth vegetation as affected by clearcut and partial cut harvesting in a second-growth boreal mixedwood. For. Ecol. Manage. 169, 83–101. doi:10.1016/S0378-1127(02)00300-6

Lemoine, D., Cochard, H., Granier, A., 2002. Within crown variation in hydraulic architecture in beech (Fagus sylvatica L): evidence for a stomatal control of xylem embolism. Ann. For. Sci. 59, 19–27. doi:10.1051/forest:2001002

Lenoir, J., Gégout, J.C., Dupouey, J.L., Bert, D., Svenning, J.-C., 2010. Forest plant community changes during 1989-2007 in response to climate warming in the Jura Mountains (France and Switzerland). J. Veg. Sci. 21, 949–964. doi:10.1111/j.1654-1103.2010.01201.x

Li, Q., Chen, J., Moorhead, D.L., 2012. Respiratory carbon losses in a managed oak forest ecosystem. For. Ecol. Manage. 279, 1–10. doi:10.1016/j.foreco.2012.05.011

Li, Q., Chen, J., Moorhead, D.L., DeForest, J.L., Jensen, R., Henderson, R., 2007. Effects of timber harvest on carbon pools in Ozark forests. Can. J. For. Res. 37, 2337–2348. doi:10.1139/X07-086

Lindenmayer, D.B., Franklin, J.F., Lõhmus, A., Baker, S.C., Bauhus, J., Beese, W., Brodie, A., Kiehl, B., Kouki, J., Pastur, G.M., Messier, C., Neyland, M., Palik, B., Sverdrup-Thygeson, A., Volney, J., Wayne, A., Gustafsson, L., 2012. A major shift to the retention approach for forestry can help resolve some global forest sustainability issues. Conserv. Lett. 5, 421–431. doi:10.1111/j.1755-263X.2012.00257.x

Lindner, D., Burdsall, H., Stanosz, G., 2006. Species diversity of polyporoid and corticioid fungi in northern hardwood forests with differing management histories. Mycologia 98, 195–217. doi:10.3852/mycologia.98.2.195

Long, R.P., Horsley, S.B., Hall, J.T., 2011. Long-term impact of liming on growth and vigor of northern hardwoods. Can. J. For. Res. 41, 1295–1307. doi:10.1139/x11-049

Long, R.P., Horsley, S.B., Lilja, P.R., 1997. Impact of forest liming on growth and crown vigor of sugar maple and associated hardwoods. Can. J. For. Res. doi:10.1139/x97-074

Lorenzetti, F., Delagrange, S., Bouffard, D., Nolet, P., 2008. Establishment, survivorship, and growth of yellow birch seedlings after site preparation treatments in large gaps. For. Ecol. Manage. 254, 350–361. doi:10.1016/j.foreco.2007.08.010

Lusk, C.H., Smith, B., 1998. Life history differences and tree species coexistence in an old-growth New Zealand rain forest. Ecology 79, 795–806. doi:10.1890/0012-9658(1998)079[0795:LHDATS]2.0.CO;2

Mamet, S.D., Chun, K.P., Metsaranta, J.M., Barr, A.G., Johnstone, J.F., 2015. Tree rings provide early warning signals of jack pine mortality across a moisture gradient in the southern boreal forest. Environ. Res. Lett. 10, 84021. doi:10.1088/1748-9326/10/8/084021

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

Martin, T.E., 1988. On the advantage of being different: nest predation and the coexistence of bird species. Proc. Natl. Acad. Sci. 85, 2196–2199. doi:10.1073/pnas.85.7.2196

Masís, A., Marquis, R.J., 2009. Effects of even-aged and uneven-aged timber management on dung beetle community attributes in a Missouri Ozark forest. For. Ecol. Manage. 257, 536–545. doi:10.1016/j.foreco.2008.09.036

Matthews, J.D., 1989. Silvicultural Systems. Clarendon/Oxford University Press, Oxford, UK.

McDowell, N.G., Beerling, D.J., Breshears, D.D., Fisher, R.A., Raffa, K.F., Stitt, M., 2011. The interdependence of mechanisms underlying climate-driven vegetation mortality. Trends Ecol Evol 26, 523–532. doi:10.1016/j.tree.2011.06.003

McLaughlin, S.B., Wimmer, R., 1999. Tansley Review No. 104 Calcium physiology and terrestrial ecosystem processes. New Phytol. 373–417.

Mérian, P., Lebourgeois, F., 2011. Size-mediated climate–growth relationships in temperate forests: A multi-species analysis. For. Ecol. Manage. 261, 1382–1391. doi:10.1016/j.foreco.2011.01.019

Messier, C., Bélanger, N., Brisson, J., Lechowicz, M.J., Gravel, D., 2011. Comment on “Present-day expansion of American beech in northeastern hardwood forests: Does soil base status matter?”Appears in Can. J. For. Res. 39: 2273–2282 (2009). Can. J. For. Res. 41, 649–653. doi:10.1139/X10-239

Messier, C., Puettmann, K.J., Coates, K.D., 2013. Managing Forests as Complex Adaptive Systems: Building Resilience to the Challenge of Global Change. Routledge.

Messina, M.M.G., Schoenholtz, S.H.S., Lowe, M.W., Wang, Z., Gunter, D.K., Londo, A.J., 1997. Initial responses of woody vegetation, water quality, and soils to harvesting intensity in a Texas bottomland hardwood ecosystem. For. Ecol. Manage. 90, 201–215. doi:10.1016/S0378-1127(96)03895-9

Millar, C.I., Stephenson, N.L., Stephens, S.L., 2007. Climate change and forests of the future : Managing in the face of uncertainty. Ecol. Appl. 17, 2145–2151. doi:10.1890/06-1715.1

Millers, I., Shriner, D., Rizzo, D., 1989. History of hardwood decline in the eastern United States. General technical report NE No.126., General technical report NE. Broomall, PA, USA.

Moore, J.D., Ouimet, R., 2006. Ten-year effect of dolomitic lime on the nutrition, crown vigor, and growth of sugar maple. Can. J. For. Res. 36, 1834–1841. doi:10.1139/x06-081

Moore, J.-D., Ouimet, R., Duchesne, L., 2012. Soil and sugar maple response 15years after dolomitic lime application. For. Ecol. Manage. 281, 130–139. doi:10.1016/j.foreco.2012.06.026

Moore, P.T., DeRose, R.J., Long, J.N., van Miegroet, H., 2012. Using silviculture to influence carbon sequestration in southern appalachian spruce-fir forests. Forests 3, 300–316. doi:10.3390/f3020300

Morris, D.L., A. Porneluzi, P., Haslerig, J., Clawson, R.L., Faaborg, J., 2013. Results of 20 years of experimental forest management on breeding birds in Ozark forests of Missouri, USA. For. Ecol. Manage. 310, 747–760. doi:10.1016/j.foreco.2013.09.020

Mueller, R.C., Scudder, C.M., Porter, M.E., Talbot Trottier, R., Gehring, C.A., Whitham, T.G., 2005. Differential tree mortality in response to severe drought: evidence for long-term vegetation shifts. J. Ecol. 93, 1085–1093. doi:10.1111/j.1365-2745.2005.01042.x

Mueller, R.C., Scudder, C.M., Porter, M.E., Talbot Trottier, R., Gehring, C.A., Whitham, T.G., 2005. Differential tree mortality in response to severe drought: evidence for long-term vegetation shifts. J. Ecol. 93, 1085–1093. doi:10.1111/j.1365-2745.2005.01042.x

Nelson, A.S., Wagner, R.G., 2014. Spatial coexistence of American beech and sugar maple regeneration in post-harvest northern hardwood forests. Ann. For. Sci. 1–9. doi:10.1007/s13595-014-0376-2

Neubert, M.G., Caswell, H., 1997. Alternatives to Resilience for Measuring the Responses of Ecological Systems to Perturbations. Ecology 78, 653–665. doi:10.1890/0012-9658(1997)078[0653:ATRFMT]2.0.CO;2

Niese, J.N., Strong, T.F., 1992. Economic and tree diversity trade-offs in managed northern hardwoods. Can. J. For. Res. doi:10.1139/x92-236

Nilsen, P., Strand, L., 2013. Carbon stores and fluxes in even-and uneven-aged Norway spruce stands. Silva Fenn. 47, 1–15.

Nolet, P., Bouffard, D., Doyon, F., Delagrange, S., 2008. Relationship between canopy disturbance history and current sapling density of Fagus grandifolia and Acer saccharum in a northern hardwood landscape. Can. J. For. Res. 38, 216–225. doi:10.1139/X07-160

Nolet, P., Doyon, F., Messier, C., 2014. A new silvicultural approach to the management of uneven-aged northern hardwoods: frequent low-intensity harvesting. Forestry 87, 39–48. doi:10.1093/forestry/cpt044

Novotny, V., Basset, Y., Miller, S.E., Weiblen, G.D., Bremer, B., Cizek, L., Drozd, P., 2002. Low host specificity of herbivorous insects in a tropical forest. Nature 416, 841–844. doi:10.1038/416841a

O'Hara, K.L., 2002. The historical development of uneven-aged silviculture in North America. Forestry 75, 339–346. doi:10.1093/forestry/75.4.339

O'Hara, K.L., Ramage, B.S., 2013. Silviculture in an uncertain world: utilizing multi-aged management systems to integrate disturbance. Forestry 86, 401–410. doi:10.1093/forestry/cpt012

Paillet, Y., Bergès, L., Hjältén, J., Odor, P., Avon, C., Bernhardt-Römermann, M., Bijlsma, R.-J., De Bruyn, L., Fuhr, M., Grandin, U., Kanka, R., Lundin, L., Luque, S., Magura, T., Matesanz, S., Mészáros, I., Sebastià, M.-T., Schmidt, W., Standovár, T., Tóthmérész, B., Uotila, A., Valladares, F., Vellak, K., Virtanen, R., 2010. Biodiversity differences between managed and unmanaged forests: meta-analysis of species richness in Europe. Conserv. Biol. 24, 101–12. doi:10.1111/j.1523-1739.2009.01399.x

Panesar, T., Marshall, V., Barclay, H., 2000. The impact of clearcutting and partial harvesting systems on population dynamics of soil nematodes in coastal Douglas-fir forests. Pedobiologia (Jena). 665, 641–665. doi:10.1078/S0031-4056(04)70079-7

Parrotta, J.A., Francis, J.K., Knowles, O.H., 2002. Harvesting intensity affects forest structure and composition in an upland Amazonian forest. For. Ecol. Manage. 169, 243–255. doi:10.1016/S0378-1127(01)00758-7

Payette, S., Fortin, M.-J., Morneau, C., 1996. The recent sugar maple decline in southern Quebec: probable causes deduced from tree rings. Can. J. For. Res. 26, 1069–1078. doi:10.1139/x26-118

Peng, C., Ma, Z., Lei, X., Zhu, Q., Chen, H., Wang, W., Liu, S., Li, W., Fang, X., Zhou, X., 2011. A drought-induced pervasive increase in tree mortality across Canada's boreal forests. Nat. Clim. Chang. 1, 467–471. doi:10.1038/nclimate1293

Perry, R.W., Thill, R.E., 2013. Long-term responses of disturbance-associated birds after different timber harvests. For. Ecol. Manage. 307, 274–283. doi:10.1016/j.foreco.2013.07.026

Pfennig, D.W., Rice, A.M., Martin, R.A., 2006. Ecological opportunity and phenotypic plasticity interact to promote character displacement and species coexistence. Ecology 87, 769–779. doi:10.1890/05-0787

Pockman, W.T., Sperry, J.S., 1997. Freezing-induced xylem cavitation and the northern limit of Larrea tridentata. Oecologia 109, 19–27. doi:10.1007/s004420050053

Pommerening, A., Murphy, S.T., 2004. A review of the history, definitions and methods of continuous cover forestry with special attention to afforestation and restocking. Forestry 77, 27–44. http://dx.doi.org/10.1093/forestry/77.1.27

Popescu, V.D., Patrick, D. a., Hunter, M.L., Calhoun, A.J.K., 2012. The role of forest harvesting and subsequent vegetative regrowth in determining patterns of amphibian habitat use. For. Ecol. Manage. 270, 163–174. doi:10.1016/j.foreco.2012.01.027

Poulson, T.L., Platt, W.J., 1996. Replacement patterns of beech and sugar maple in Warren Woods, Michigan. Ecology 77, 1234–1253. doi:10.2307/2265592

Powers, M., Nagel, L., 2008. Disturbance dynamics influence Carex pensylvanica abundance in a northern hardwood forest. J. Torrey Bot. Soc. 135, 317–327. doi:10.3159/08-RA-034.1

Pro Silva, 2012. Pro Silva Principles. Pro Silva Europe. Union européenne des forestiers aux conceptions de gestion proche de la Nature.

Puettmann, K., Messier, C., Coates, K.D., 2013. 1 Managing forests as complex adaptive systems, in: Managing Forests as Complex Adaptive Systems: Building Resilience to the Challenge of Global Change. Routledge, p. 1.

Pukkala, T., Lähde, E., Laiho, O., 2011. A multifunctional comparison of even-aged and uneven-aged forest management in a boreal region. Can. J. For. Res. 862, 851–862. doi:10.1139/X11-009

R Core Team, 2013. R: A Language and Environment for Statistical Computing.

Rask, M., Nyberg, K., Markkanen, S.-L., Ojala, A., 1998. Forestry in catchments: effects on water quality, plankton, zoobenthos and fish in small lakes. Boreal Environ. Res. 3, 75–86.

Régnière, J., Saint-Amant, R., 2008. BioSIM 9: manuel de l'utilisateur. Centre de foresterie des Laurentides.

Reid, C., Watmough, S., 2014. Evaluating the effects of liming and wood-ash treatment on forest ecosystems through systematic meta-analysis. Can. J. For. Res. 44, 867–885. doi:10.1139/cjfr-2013-0488

Renken, R.B., Gram, W.K., Fantz, D.K., Richter, S.C., Miller, T.J., Ricke, K.B., Russell, B., Wang, X., 2004. Effects of Forest Management on Amphibians and Reptiles in Missouri Ozark Forests. Conserv. Biol. 18, 174–188. doi:10.1111/j.1523-1739.2004.00312.x

Ricciardi, A., 2007. Are modern biological invasions an unprecedented form of global change? Conserv. Biol. 21, 329–336. doi:10.1111/j.1523-1739.2006.00615.x

Robitaille, A., Saucier, J.-P., 1998. Paysages régionaux du Québec méridional. Les Publications du Québec, Québec, QC, Canada.

Rosenzweig, C., Iglesias, A., Yang, X.B., Epstein, P.R., Chivian, E., 2001. Climate change and extreme weather events. Glob. Chang. Hum. Heal. 2, 90–104. doi:10.1023/A:1015086831467

Royo, A.A., Carson, W.P., 2006. On the formation of dense understory layers in forests worldwide: consequences and implications for forest dynamics, biodiversity, and succession. Can. J. For. Res. 36, 1345–1362. doi:10.1139/x06-025

Rüger, N., Gutiérrez, Á.G., Kissling, W.D., Armesto, J.J., Huth, A., 2007. Ecological impacts of different harvesting scenarios for temperate evergreen rain forest in southern Chile—A simulation experiment. For. Ecol. Manage. 252, 52–66. doi:10.1016/j.foreco.2007.06.020

Runkle, J., 1981. Gap Regeneration in Some Old-growth Forests of the Eastern United States. Ecology 62, 1041–1051. doi:10.2307/1937003

Runkle, J., 2013. Thirty-two years of change in an old-growth Ohio beech – maple forest. Ecology 94, 1165–1175. doi:10.1890/11-2199.1

Sage, R., Porter, W., Underwood, H., 2003. Windows of opportunity: white-tailed deer and the dynamics of northern hardwood forests of the northeastern US. J. Nat. Conserv. 10, 213–220. doi:10.1078/1617-1381-00021

Schütz, J.P., 2002. Silvicultural tools to develop irregular and diverse forest structures. Forestry 75, 329–337. doi:10.1093/forestry/75.4.329

Semlitsch, R.D., Todd, B.D., Blomquist, S.M., Calhoun, A.J.K., Gibbons, J.W., Gibbs, J.P., Graeter, G.J., Harper, E.B., Hocking, D.J., Hunter, M.L., Patrick, D. a., Rittenhouse, T. a. G., Rothermel, B.B., 2009. Effects of Timber Harvest on Amphibian Populations: Understanding Mechanisms from Forest Experiments. Bioscience 59, 853–862. doi:10.1525/bio.2009.59.10.7

Seymour, R.S., Hunter, M.L., 1992. New forestry in eastern spruce-fir forests: principles and applications to Maine. College of Forest resources, University of Maine.

Seymour, R.S., White, A.S., deMaynadier, P.G., 2002. Natural disturbance regimes in northeastern North America—evaluating silvicultural systems using natural scales and frequencies. For. Ecol. Manage. 155, 357–367. doi:10.1016/S0378-1127(01)00572-2

Sharpe, W.E., Driscoll, C.T., Lawrence, G.B., Bulger, A.J., Butler, T.J., Cronan, C.S., Eagar, C., Lambert, K.F., Likens, G.E., Stoddard, J.L., Weathers, K.C., 2002. Acid deposition explains sugar maple decline in the east [2] (multiple letters). Bioscience 52, 4–6. doi:10.1641/0006-3568(2002)052[0005:ADESMD]2.0.CO;2

Siemion, J., Burns, D.A., Murdoch, P.S., Germain, R.H., 2011. The relation of harvesting intensity to changes in soil, soil water, and stream chemistry in a northern hardwood forest, Catskill Mountains, USA. For. Ecol. Manage. 261, 1510–1519. doi:10.1016/j.foreco.2011.01.036

Simard, S.W., 2009. The foundational role of mycorrhizal networks in self-organization of interior Douglas-fir forests. For. Ecol. Manage. 258, S95–S107. doi:10.1016/j.foreco.2009.05.001

Soil Landscapes of Canada Working Group (SLCWG), 2010. Soil landscapes of Canada version 3.2, Agriculture and Agri-Food Canada.(digital map and database at 1: 1 million scale).

Spinelli, R., Magagnotti, N., Nati, C., 2010. Benchmarking the impact of traditional small-scale logging systems used in Mediterranean forestry. For. Ecol. Manage. 260, 1997–2001. doi:10.1016/j.foreco.2010.08.048

Summerville, K.S., 2011. Managing the forest for more than the trees: effects of experimental timber harvest on forest Lepidoptera. Ecol. Appl. 21, 806–816. doi:10.1890/10-0715.1

Tardif, J., Brisson, J., Bergeron, Y., 2001. Dendroclimatic analysis of Acer saccharum, Fagus grandifolia, and Tsuga canadensis from an old-growth forest, southwestern Quebec. Can. J. For. Res. Can. Rech. For. 31, 1491–1501. doi:10.1139/cjfr-31-9-1491

Thill, R.E., Koerth, N.E., 2005. Breeding Birds of Even- and Uneven-Aged Pine Forests of Eastern Texas. Southeast. Nat. 4, 153–176. doi:10.1656/1528-7092(2005)004[0153:BBOEAU]2.0.CO;2

Thompson, I., Mackey, B., McNulty, S., Mosseler, A., 2009. Forest Resilience, Biodiversity, and Climate Change. A synthesis of the biodiversity/resilience/stability relationship in forest ecosystems, Technical Series. doi:10.1007/978-3-642-10445-9_5

Thornton, D.H., Wirsing, A.J., Roth, J.D., Murray, D.L., 2012. Complex effects of site preparation and harvest on snowshoe hare abundance across a patchy forest landscape. For. Ecol. Manage. 280, 132–139. doi:10.1016/j.foreco.2012.06.011

Tilghman, J.M., Ramee, S.W., Marsh, D.M., 2012. Meta-analysis of the effects of canopy removal on terrestrial salamander populations in North America. Biol. Conserv. 152, 1–9. doi:10.1016/j.biocon.2012.03.030

Todd, B.D., Blomquist, S.M., Harper, E.B., Osbourn, M.S., 2014. Effects of timber harvesting on terrestrial survival of pond-breeding amphibians. For. Ecol. Manage. 313, 123–131. doi:10.1016/j.foreco.2013.11.011

Torras, O., Saura, S., 2008. Effects of silvicultural treatments on forest biodiversity indicators in the Mediterranean. For. Ecol. Manage. 255, 3322–3330. doi:10.1016/j.foreco.2008.02.013

Vadeboncoeur, M.A., 2010. Meta-analysis of fertilization experiments indicates multiple limiting nutrients in northeastern deciduous forests. Can. J. For. Res. 40, 1766–1780. doi:10.1139/X10-127

Walker, B., Holling, C.S., Carpenter, S.R., Kinzig, A., 2004. Resilience, adaptability and transformability in social-ecological systems. Ecol. Soc. 9. doi:5

Wang, X., Burns, D.A., Yanai, R.D., Briggs, R.D., Germain, R.H., 2006. Changes in stream chemistry and nutrient export following a partial harvest in the Catskill Mountains, New York, USA. For. Ecol. Manage. 223, 103–112. doi:10.1016/j.foreco.2005.10.060

West, J.M., Julius, S.H., Kareiva, P., Enquist, C., Lawler, J.J., Petersen, B., Johnson, A.E., Shaw, M.R., 2009. U.S. natural resources and climate change: concepts and approaches for management adaptation. Environ. Manage. 44, 1001–21. doi:10.1007/s00267-009-9345-1

Whittaker, R.H., 1965. Dominance and Diversity in Land Plant Communities Numerical relations of species express the importance of competition in community function and evolution. Science (80-.). 147, 250–260.

Williams, J.W., Jackson, S.T., Kutzbach, J.E., 2007. Projected distributions of novel and disappearing climates by 2100 AD. Proc. Natl. Acad. Sci. U. S. A. 104, 5738–5742. doi:10.1073/pnas.0606292104

Wilmot, T.R., Ellsworth, D.S., Tyree, M.T., 1996. Base cation fertilization and liming effects on nutrition and growth of Vermont sugar maple stands. For. Ecol. Manage. 84, 123–134. doi:10.1016/0378-1127(96)03743-7

Wright, J.S., 2002. Plant diversity in tropical forests: a review of mechanisms of species coexistence. Oecologia 130, 1–14. doi:10.1007/s004420100809

Yamamoto, S.-I., Nishimura, N., Matsui, K., 1995. Natural disturbance and tree species coexistence in an old-growth beech-dwarf bamboo forest, southwestern Japan. J. Veg. Sci. 875–886. doi:10.2307/3236402

Zhou, D., Zhao, S.Q., Liu, S., Oeding, J., 2013. A meta-analysis on the impacts of partial cutting on forest structure and carbon storage. Biogeosciences 10, 3691–3703. doi:10.5194/bg-10-3691-2013

Zobel, M., 1992. Plant species coexistence: the role of historical, evolutionary and ecological factors. Oikos 314–320. doi:10.2307/3545024

Zwolak, R., 2009. A meta-analysis of the effects of wildfire, clearcutting, and partial harvest on the abundance of North American small mammals. For. Ecol. Manage. 258, 539–545. doi:10.1016/j.foreco.2009.05.033