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COMPÉTIVITÉ DE L'ÉRABLE À SUCRE ET DU HÊTRE À GRANDES FEUILLES ET DYNAMIQUE DE LEUR REMPLACEMENT DANS LES ÉRABLIÈRES DU SUD OUEST DU QUÉBEC

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KIM BANNON

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TABLE DES MATIÈRES

LISTE DES FIGURES

LISTE DES TABLEAUX

LISTE DES ABBRÉVIATIONS

AP1	0-5 years after disturbance
AP2	6-10 years after disturbance
AS	*Acer saccharum*
AV	before DHT
BA_{AS}	Basal area of AS
BA_{FG}	Basal area of FG
CC	Clear cut
CJ	Coupe de jardinage
CO	Canopy opening
CT	Coupe totale
DFPP	Densité du flux photonique photosynthétisant
DHT	Disturbance history type
FG	*Fagus grandifolia*
L	Limed
LA	Light availability
LAR	Leaf area ratio
LMA	Leaf mass per area
LWR	Leaf weight ratio
NL	Not limed

PC	Partial cut
RelSD$_{AS}$	Relative sapling density of AS
RWR	Roots weight ratio
SD$_{AS}$	Sapling density of AS
SD$_{FG}$	Sapling density of FG
SeeD$_{AS}$	Seedling density of AS
SeeD$_{FG}$	Seedling density of FG
ST	Soil treatment
T	Forêts non aménagées
UF	Unmanaged forest

RÉSUMÉ

Les forêts de feuillus dans le Nord-Est de l'Amérique du Nord font face à de grands changements au niveau de la composition et de la coexistence d'espèces tolérantes à l'ombre. Parmi ces espèces, on retrouve le hêtre à grandes feuilles (FG : *Fagus grandifolia*) et l'érable à sucre (AS : *Acer saccharum*). Durant les dernières décennies, plusieurs études ont observé une augmentation considérable de jeunes tiges de FG en sous-étage alors que AS montrait un dépérissement généralisé dans les canopées des forêts feuillues du sud du Québec. Il a été proposé que le dépérissement des AS matures soit lié à des changements dans les propriétés du sol qui affecterait sa croissance et sa vigueur. De plus, d'autres études ont proposé que ces mêmes modifications de propriétés du sol lorsque associées avec une diminution de l'intensité de perturbation du couvert pourraient favoriser l'établissement et la croissance d'une régénération en hêtre plutôt qu'en érable à sucre.

Deux études ont été établies. (i) Dans un premier temps, un territoire de 1272 km^2 à été couvert en Outaouais et 56 peuplements d'érablières y ont été échantillonnés. Les peuplements ont été sélectionnés selon un gradient de lumière et de fertilité de sol. Le gradient de lumière a été obtenu en sélectionnant un gradient de perturbations du couvert, des peuplements ayant été subies dans le passé (T : forêts non aménagées; CJ : coupe de jardinage; CT : coupe totale). Ensuite, la sélection des sites a été faite en fonction de la fertilité du sol prédite par cartographie (sites pauvres, moyens, riches). Dans chaque peuplement, des mesures sur la surface terrière, la croissance radiale, la densité en gaules des deux essences ont été prises et analysées en fonction de la disponibilité en lumière et la fertilité des sols à l'aide de modèles mixtes. (ii) Dans un second temps, une étude semi-contrôlée a été réalisée dans un peuplement d'érablière de 15.36 ha à proximité du Lac Gagnon au Nord-Est de Duhamel. Dans cette étude des combinaisons de traitement (ouverture du couvert et chaulage) ont été réalisées aléatoirement sur 24 sites de 0.64 ha. Les mêmes paramètres (lumière et sol) ont été à l'étude mais un effort d'échantillonnage supplémentaire a été mis dans l'estimation de la performance des semis de AS et FG. Des mesures sur la densité, la croissance annuelle en hauteur, la morphologie, la physiologie et l'allocation de biomasse des semis ont été prises et analysées en fonction de la disponibilité en lumière et de la fertilité des sols.

Pour l'étude sur l'historique de perturbation, nos résultats n'ont montré aucune variabilité dans la fertilité des sols échantillonnés (malgré la présélection) et que ceux-ci se sont tous avérés relativement pauvres (*e.i.,* Ca, Mg et P) suite à nos analyses. Sur une période de 50 ans, l'intensité de l'historique de perturbations a grandement modifié la composition de la canopée. Par contre, la fertilité du sol, l'historique de perturbations ainsi que leur interaction n'ont pas eu d'effets significatifs pouvant expliquer la variation de la densité actuelle, absolue ou relative, des gaules de AS et FG. Les résultats montrent que la croissance radiale des gaules de AS a effectivement mieux répondu à une grande ouverture de la canopée (CT), sur sols pauvres, mais n'a pas pu surpasser la croissance des gaules de FG. Un seuil critique de disponibilité en lumière où la performance des 2 espèces serait inversée n'a cependant pas pu être confirmé. Pour l'étude semi-contrôlée, l'abondance en semis de AS a eu tendance à augmenter avec la combinaison d'une grande ouverture de la canopée (CT) et le chaulage du sol. La croissance annuelle en hauteur des semis de AS a également été avantagée par ses mêmes conditions. Les semis de AS et de FG ont montré très peu de différences dans leur réponse morphologique et physiologique à un grand gradient d'ouverture du couvert et au chaulage.

Mots clefs: *Acer saccharum*, *Fagus grandifolia*, fertilité des sols, historique de perturbations, lumière

INTRODUCTION GÉNÉRALE

La problématique

Durant le dernier siècle, l'aménagement forestier a créé de nombreux changements dans la structure et la composition du paysage. Dans la forêt feuillue de l'Est de l'Amérique du Nord une modification de la dynamique entre le hêtre à grandes feuilles (FG : *Fagus grandifolia*) et l'érable à sucre (AS : *Acer saccharum*) a notamment été observée (Kelty et Nyland, 1981; Horsley, 1994; Ray, Nyland et Yanaj, 1999; Dyer, 2001). Plusieurs de ces auteurs ont d'ailleurs énoncé le terme d'envahissement des érablières par FG. Parallèlement, plusieurs études ont rapporté un dépérissement des AS matures (Long et al., 1997; Moore et al., 2000) pendant lequel FG se serait graduellement établi en sous-étage modifiant la structure et la composition du sous-couvert des érablières (Duchesne et Ouimet, 2005). La baisse de croissance, la défoliation des cimes, la forte mortalité et la baisse de recrutement en AS, observées par ces mêmes auteurs, seraient à la base d'un déclin observé de leur population. Il est généralement extrêmement difficile d'isoler la cause de tels déclins en raison des divers facteurs qui contrôlent la dynamique des populations. Pourtant, il est primordial de comprendre tout facteur pouvant influencer la dynamique de régénération des essences forestières puisque c'est le paramètre clé qui régit l'évolution des populations. La croissance et la vigueur de AS en régénération semblent résulter de l'interaction de deux principaux facteurs : 1) la disponibilité en lumière qui varie avec l'aménagement forestier et les caractéristiques du couvert forestier (Canham, 1985; Kobe et al., 1995) et 2) la fertilité du sol (Ouimet et Camiré, 1995; Duchesne et al., 2002; Duchesne, Ouimet et al., 2005). Il est à noter que ces deux facteurs agissent probablement en interaction (Nolet et al., 2008a).

En se basant sur cette littérature ainsi que dans le cadre de la théorie des niches écologiques (Grubb, 1977), les changements de composition entre ces deux espèces reposeraient directement sur des différences au niveau de leur autoécologie et donc de leur compétitivité à utiliser différentes conditions environnementales. Ainsi, il existerait des conditions environnementales où l'une ou l'autre de ces deux espèces performerait mieux que sa compétitrice. Selon Nolet et al. (2008a), il existerait au moins deux mécanismes qui avantageraient l'établissement de FG sous sa propre canopée. La faible proportion de lumière transmise au sol après avoir traversé une canopée de FG (Canham et al., 1994) favoriserait les espèces très tolérantes à l'ombre, comme FG. La présence du FG affecterait négativement les conditions chimiques du sol, ce qui aurait un effet négatif sur la survie des semis de AS (Hane, 2003). Par contre, ces effets allélopathiques ne sont pas bien connus et d'autres études sont nécessaires afin de confirmer ces résultats. Plusieurs études ont également examiné la coexistence de FG et de AS selon différentes intensités de perturbations (Poulson et Platt, 1996; Arii et Lechowicz, 2002; Nolet et al., 2008a). Une ouverture partielle de la canopée transmettant moins de 30% de lumière au sol bénéficierait aux semis de FG par rapport à ceux de AS (Poulson et Platt, 1996). D'autres auteurs sont allés plus loin en élaborant des modèles où l'intensité de lumière en plus de la qualité du sol influenceraient la régénération des semis/gaules de AS et de FG (Arii et Lechowicz, 2002; Nolet et al., 2008a). Nolet et al. (2008a) suggèrent que de larges trouées (offrant plus de 30% de lumière au sol) sont nécessaires pour favoriser la régénération de AS au détriment de FG sur des sites ayant une faible fertilité. Ainsi, AS dominerait les peuplements là où l'intensité de lumière serait plus élevée, puisque les semis/gaules de AS auraient un meilleur succès de régénération que les semis/gaules de FG (Arii et Lechowicz, 2002). Sur des sols plus fertiles, de fréquentes perturbations, même partielles, assureraient une régénération continuelle de AS (Poulson et Platt, 1996). Par contre, sous un même régime de perturbation mais sur des sites plus pauvres (sols acides), et donc moins propices pour la régénération de AS, ce succès serait inversé à l'avantage de FG (Arii et Lechowicz, 2002).

Ainsi, il semblerait que AS et le FG possèdent chacune des adaptations et des acclimatations qui leurs sont propres et qui leur permettraient de répondre différemment aux traitements sylvicoles qui leur sont imposés tout au long de leur cycle de vie. Compte tenu de ces différences, cette étude a tenté de déterminer quels étaient les conditions environnementales, produites par différents traitements sylvicoles, qui favoriseraient la régénération de AS par rapport au FG sur un même site. Une telle étude pourrait permettre de mieux orienter les techniques sylvicoles et même de développer de nouvelles approches sylvicoles pour mitiger ou contrecarrer l'envahissement du hêtre dans les érablières du Québec.

Pour cela, deux études ont été conduites en parallèles. Dans un premier temps, un grand nombre de peuplements ont été visités avec pour objectifs principaux: 1) vérifier si la fertilité des sols et l'historique de perturbation ainsi que de leur interaction avaient un effet sur la canopée de AS et de FG; 2) évaluer si l'historique de perturbation a eu des répercussions sur la densité des gaules de AS et de FG; 3) vérifier les différences dans la croissance radiale des gaules des deux espèces à l'origine des perturbations. Dans un deuxième temps, une étude semi-contrôlée a été établie afin de vérifier si l'interaction de la disponibilité en lumière et des traitements de chaulage du sol avaient un effet sur: 4) la proportion des semis de AS et de FG; 5) la croissance annuelle en hauteur relative des semis de AS et de FG; et 6) l'allocation de la biomasse, la morphologie et physiologie des semis de ces 2 espèces.

État des connaissances

Dynamique des changements de la composition dans les érablières

Historique des changements compositionnels

Dans l'historique des paysages forestiers, il est courant de retrouver des changements de composition où les espèces se remplacent de façon naturelle tout au long d'une succession (Oliver et Larson, 1996; Nolet et al., 2001; Bouffard et al., 2003). Ces nombreux changements de dominance ont notamment été observés entre AS et FG dans les forêts du nord-est de l'Amérique du Nord (Bouliane, 1969; Duchesne, Ouimet et al., 2005).

Bouleversements récents de la composition des érablières

Depuis la fin des années 1970, un dépérissement et un déclin de AS ont été observés (Duchesne, Ouimet et al., 2005; Duchesne, et al., 2006) qui pourraient modifier la composition et structure des écosystèmes feuillus du Sud du Québec. Puisque AS est favorisé pour la qualité de son bois et a une grande valeur économique pour la production de sirop d'érable, plusieurs études se sont donc penchées sur cette problématique afin de déterminer la cause du déclin et du dépérissement de AS. Il a été révélé que les facteurs causant cette diminution seraient plutôt de natures anthropiques (influence de la pollution, coupes et aménagement des forêts). Dans le sud du Québec, l'accroissement de AS mature aurait diminué de 10% et le recrutement de 30% (Duchesne, Moore et al., 2008). De plus, le taux de recrutement de gaules de FG aurait augmenté considérablement de sorte que ce changement pourrait être caractérisé comme un envahissement. En effet, une fois en place, les gaules et semis de FG profiteraient de la disponibilité accrue de lumière causée par le déclin de AS mature. Cette augmentation pourrait alors compromettre la composition des érablières dans leurs formes actuelles, notamment dans les érablières moins fertiles (Duchesne et al., 2003).

Plusieurs études ont essayé d'élucider ce changement soudain dans la dynamique entre les deux espèces sans toutefois avoir de réponses claires et précises. Par exemple, Hane (2003) supporte l'hypothèse que l'ombrage serait le mécanisme d'interférence. Dans son expérience, l'enlèvement du gaulis de FG a grandement amélioré la survie des semis de AS. Cependant, la compétition pour la lumière ne semblerait être qu'une partie de l'effet global de FG sur AS. Il y aurait possiblement un effet négatif des gaules de FG sur la survie des semis de AS via une compétition pour la disponibilité en eau (Hane, 2003). D'autres effets négatifs de la présence de FG pourraient inclure la compétition pour les nutriments ou des effets phytotoxiques. Certains auteurs croient qu'une allélopathie serait générée par la dense litière laissée au sol par FG et qu'elle pourrait freiner l'établissement des semis de AS (Brisson et al., 1994; Hane et al., 2003). Il a été montré que la superficie des feuilles ainsi que la biomasse des semis de AS auraient diminué suite à l'application de concentrations élevées de lessivats provenant du feuillage de FG (Hane et al., 2003). Cependant, d'autres recherches sont nécessaires pour confirmer l'effet allélopathique puisque certaines études réalisées en forêt ne supportent pas cette hypothèse (Beaudet, Messier et al., 1999; Nolet et al., 2008a).

D'autres facteurs pourraient contribuer à l'augmentation de gaules de FG. Nolet et al. (2008a) ont observé qu'une augmentation de la densité de gaules de FG serait reliée à l'application de coupes partielles. Plusieurs facteurs pourraient expliquer la dominance de FG en sous-étage de forêts partiellement perturbées: 1) sa haute tolérance à l'ombre, ce qui lui permettrait un meilleur taux de survie sous une canopée fermée (Canham, 1988; Forcier, 1975) ou suite à une perturbation de faible intensité (<30%) (Poulson et Platt, 1996); 2) sa capacité à se reproduire végétativement (Forcier, 1975; Brisson et al., 1994; Beaudet, Messier et al., 1999; Bohn et Nyland, 2003; Beaudet et Messier, 2008); 3) une meilleure résistance ou un risque moins élevé de se faire brouter par le cerf de Virginie (*Odocoileus virginianus*) (Ward, 1961; Nyland et al., 2006), et finalement 4) les blessures faites sur les racines pendant l'exploitation forestière ainsi que la maladie corticale du hêtre (*Neonectria faginata*) qui permettent de maintenir ou d'augmenter la proportion de FG par drageonnement (Nyland et al., 2006). On notera d'ailleurs qu'aux États-Unis, la maladie corticale du hêtre est directement responsable de la diminution de la valeur commerciale de FG (Bohn et Nyland, 2003).

Facteurs influençant la performance de Fagus grandifolia et d'Acer saccharum

Les sols

AS est très exigeant en nutriments et s'établit mieux dans des sols fertiles, profonds, humides et bien drainés (Kobe et al., 1995; Moore et al., 2000; Horsley, Long et al., 2002). Selon Duchesne et al. (2002), une diminution de la fertilité des sols serait le facteur qui contribuerait à la décroissance de AS. Des sols pauvres en éléments nutritifs de même qu'une concentration élevée en aluminium (Al) ayant un effet toxique, diminueraient l'abondance des AS matures au Québec (Ouimet et Camire, 1995; Moore et al., 2000; Duchesne, Ouimet et al., 2002). Il a été rapporté que cette décroissance pourrait être à l'origine d'une modification de sa distribution à l'échelle du peuplement (Duchesne, Ouimet et al., 2005).

Quelques évidences incluant la physiologie, les relations entre les espèces et le sol, et celles entre l'écosystème et le budget nutritif suggèrent que des changements dans le ratio entre le Ca et l'Al échangeable peuvent influencer la dynamique de la forêt (Kobe et al., 2002). En effet, l'Al dissout interférerait avec l'assimilation du Ca par les racines (Long et al., 1997). Le Ca est un des éléments importants pour l'érable (Adams et Hutchinson, 1992). Il joue un rôle dans la croissance des radicelles (Adams et Hutchinson, 1992) et dans différents processus physiologiques incluant la résistance contre les maladies, le signal de transduction, la synthèse et le fonctionnement des membranes et parois cellulaires, et la régulation des stomates (Kobe et al., 2002). Certains auteurs ont effectivement observé une augmentation significative de la survie des semis de AS sur des sols calcaires et élevés en azote (Kobe et al., 1995; Arii et Lechowicz, 2002). AS est une espèce exigeante envers cet élément nutritif. On retrouve de grandes quantités de Ca dans la litière foliaire de AS. À l'inverse, la litière foliaire retrouvée sous FG contient des concentrations de Ca très basses (Côté et Fyles, 1993). Par ce fait même, le sol des forêts deviendra plus pauvre en termes de disponibilité du Ca suite à l'établissement grandissant de FG, ce qui contribuera davantage à une diminution de la régénération et à une augmentation de la mortalité des semis d'AS (Duchesne, Ouimet et al., 2005). Par contre Nolet et al. (2008b) n'ont pas trouvé le Ca ni le Mg comme étant des facteurs importants influençant de manière significative la régénération de ces deux espèces. Dans cette étude, les auteurs ont suggéré que la transmission de la lumière au sol était si limitante pour le développement des semis d'érable que l'effet d'autres facteurs comme la fertilité des sols était négligeable (cf. aussi Ricard et al., 2003).

Une autre théorie, associée à l'envahissement des érablières par FG, suppose que les apports anthropiques de sulfates (SO_4^{2-}) et de nitrates (NO_3^-) amèneraient une acidification des sols et donc un épuisement des cations, ce qui affecterait la dynamique de régénération entre AS et FG (Duchesne, Ouimet et al., 2005). FG serait, en effet, capable de s'établir sur des sols pauvres (Kobe, Likens et al., 2002) ou très acides où la disponibilité en Ca serait très faible (Arii et Lechowicz, 2002; Duchesne et al., 2005). Cependant, il existe encore une controverse sur l'exactitude des causes possibles associées à cet envahissement par le FG, à travers la littérature (Duchesne et al., 2009; Messier et al., 2011; Duchesne, 2011).

Quelques autres facteurs sembleraient aussi affecter la survie des semis de AS, soit l'humidité du sol et le manganèse (Mn). En ce qui a trait à l'humidité du sol, un des avantages de FG est qu'il produit des drageons lorsque les conditions deviennent plus difficiles. Non seulement cela lui permet de croître sur des sites moins favorables mais d'avoir aussi une croissance plus élevée que les semis naturels de AS (Beaudet et Messier, 2008). Contrairement aux semis, les drageons ont la possibilité d'avoir accès aux racines de l'arbre principal et par conséquent d'avoir accès à des nappes d'eau plus profonde (Ward, 1961). Ainsi, les drageons de FG auraient un avantage certain sur les semis de AS lors de périodes de sécheresse. Pour ce qui est du Mn, une autre étude a soulevé aussi que les peuplements en déclin auraient une concentration de Mn et de Mg considérablement plus élevée dans leurs structures en bois et un ratio Ca/Mn plus faible. Des concentrations plus élevées de Mn et de faibles concentrations de Ca et d'Al se retrouvaient dans le feuillage (Houle et al., 2007). Cependant, il était difficile de déterminer si ces différences étaient une cause ou un symptôme de la santé de AS (Houle et al., 2007).

La disponibilité en lumière

La lumière est l'un des facteurs abiotiques les plus documentés en ce qui concerne son influence sur la régénération et la survie de plusieurs espèces, et notamment de AS et de FG (Canham, 1985 et 1988; Lei et Lechowicz, 1990; Kobe et al., 1995; Poulson et Platt, 1996; Beaudet et Messier, 1998; Beaudet et Messier et al., 2000; Brisson, 2001; Delagrange, Messier et al., 2004; Nolet et al., 2008b). AS et FG sont considérés comme tolérants à l'ombre. Ils sont capable de survivre plusieurs années sous une canopée fermée tout en minimisant les coûts associés à l'entretien des tissus ligneux et d'être capables de supporter plusieurs épisodes de suppression (Canham, 1985; Kobe et al., 1995; Beaudet et Messier, 1998). Par contre, on retrouve plusieurs différences entre les deux essences dans la littérature, notamment le fait que AS démontre un taux de mortalité plus élevé au stade semis que FG, dans des conditions très ombragées (Canham, 1985; Canham, 1988; Kobe et al., 1995; Poulson et Platt, 1996). Selon Lei et Lechowicz (1990), les semis AS seraient capables de persister pendant plusieurs années sous une canopée fermée jusqu'à l'apparition d'une trouée. Cependant, les semis d'AS ne pourraient acquérir cette capacité qu'en demeurant de petite taille, c'est-à-dire en arrêtant leur croissance en hauteur et en développant des racines adventives (Delagrange et al., 2004; Woods, 2008) alors que le hêtre peut conserver une croissance en hauteur minimale sous fort ombrage. Ainsi, certains auteurs ont rapporté que le taux de croissance en hauteur des semis de AS est plus faible que ceux de FG sous une canopée fermée (Poulson et Platt, 1996) et même jusqu'à des disponibilités en lumière allant à 50% de densité du flux photonique photosynthétisant (DFPP) (Beaudet et Messier, 1998). Par contre, les semis de AS répondraient mieux lorsque l'intensité de la lumière augmente et surpasserait même celle des semis de FG dans des grandes trouées (Canham, 1988; Kobe et al., 1995; Poulson et Platt, 1996; Nolet et al., 2008b). Ainsi, il n'existe pas de consensus en ce qui concerne la croissance des semis de FG et de AS et la dominance de l'un par rapport à l'autre en fonction de la disponibilité en lumière. En fait, il est probable que ces divergences dans la littérature proviennent de la fertilité des sites (Beaudet et Messier, 1998; Nolet et al., 2008a), empêchant par conséquent la généralisation.

En ce qui a trait à la réponse morphologique face aux variations de lumière, peu de différences sont retrouvées entre les deux espèces. Lorsque la lumière est élevée, la couronne des semis est davantage allongée (Beaudet et Messier, 1998; Nolet et al., 2008b), alors qu'à l'ombre, leur couronne s'étale plus à l'horizontal (Beaudet et Messier, 1998; Brisson, 2001; Delagrange, Messier et al., 2004). La différence retrouvée est que le feuillage des semis de FG s'étale plus horizontalement, qu'il devient plus dense et qu'il conserve des feuilles plus profondément à l'ombre par rapport à celui des semis de AS (Beaudet, Messier et al., 1999). Ceci a pour conséquence d'intercepter plus de lumière ce qui est avantageux pour FG mais également d'établir un ombrage plus intense qui sera désavantageux pour ses compétiteurs (*e.g.*, AS) (Nolet et al., 2008a). Une relation négative entre la superficie de la feuille du semis et la disponibilité en lumière a été observée pour les deux espèces (Beaudet et Messier, 1998). À l'ombre, cette superficie est plus grande, et maximise donc l'interception de la lumière.

Cependant, si la morphologie des deux essences a déjà été étudiée pour des disponibilités en lumière inférieures à 50% de DFPP, peu de choses ont été faites pour des valeurs de lumière plus élevées. Or, sous fortes lumières, la régénération de AS démontre une plasticité morphologique importante, lui permettant d'être très compétitif (Nolet et al., 2008b). Plusieurs autres études ont démontré aussi qu'avec une augmentation de la disponibilité en lumière: 1) les semis de AS allouaient une plus grande biomasse foliaire et racinaire (Beaudet et Messier, 1998); 2) les semis de AS augmentaient la longueur moyenne des pétioles (Beaudet et Messier, 1998); et 3) les semis/gaules de AS étalaient leurs feuilles de façon plus efficace (Canham, 1988; Beaudet et Messier, 1998) que ceux de FG. AS pourrait donc posséder une meilleure capacité d'acclimater sa physiologie et son patron d'allocation que le FG lorsque la disponibilité en lumière augmente beaucoup (Nolet et al., 2008b). En effet, l'augmentation de la disponibilité en lumière doit être supérieure à 50% de la lumière totale car avant cela, l'avantage compétitif des semis de AS sur les semis de FG n'est pas démontré (Beaudet et Messier, 1998; Beaudet, Messier et al., 2000).

Traitement sylvicole

Plusieurs études ont été faites proposant le traitement sylvicole idéal pour aider à la régénération de AS. Par contre, beaucoup de facteurs peuvent intervenir et empêcher d'obtenir des résultats concrets.

Une étude a suggéré que dans un peuplement âgé, le nombre de microsites (trouées) où la lumière disponible est assez élevée pour maintenir la survie de la régénération de AS, est plus faible que dans un peuplement aménagé (Beaudet, Messier et al., 1999). Dans le peuplement âgé, la lumière disponible peut être proche du seuil minimum pour la survie de la régénération de AS (Beaudet, Messier et al., 1999). Selon Canham (1990), qu'importe si les trouées sont proches ou au-dessus de l'espèce, celles-ci favorisent le développement des semis ou des gaules de FG. Ceci serait dû au fait que le seuil minimal de disponibilité en lumière pour la survie est plus faible pour les gaules de FG que celles de AS (Canham, 1990).

À l'échelle du peuplement, Forget et al. (2007), ont noté que la croissance de AS sur des sites fertiles augmentait avec des coupes partielles de 30% mais que la croissance de FG augmentait tout autant sinon plus dans ces mêmes conditions. Par contre, des trouées plus larges causées par le retrait d'individus dominants favoriseraient le développement des semis de AS (Bohn et Nyland, 2003). Il a été rapporté aussi que les semis de AS feraient partie de la nouvelle cohorte seulement s'ils ne sont pas supprimés par la régénération de FG (Poulson et Platt, 1996). Les gaules de AS pourraient aussi exiger une ouverture de la canopée directement au-dessus d'eux afin de maximiser sa régénération (Canham, 1985). Selon Canham (1988), FG et AS seraient chacun à leur façon, des spécialistes de trouées. Il a noté que les semis de FG répondaient, en terme de croissance, de façon modeste à une intensité lumineuse faible provenant d'une trouée, mais étaient hautement efficaces dans la façon dont ils étalaient leurs feuilles sous une canopée fermée. L'inverse était observé chez les semis de AS (Canham, 1988).

Duchesne, Ouimet et al. (2003) ont observé une augmentation du nombre de gaules de FG aux dépends de AS dans les forêts où il n'y a eu aucun traitement sylvicole. D'autres études ont vu une augmentation de la proportion de gaules de FG dans les forêts de feuillus suite à différents types de perturbations mais généralement de faibles intensités. Nolet et al., (2008a) ont étudié des peuplements dominés par AS qui se distinguaient par leur historique de perturbation (coupe à blanc, feux et coupe partielle). Ils ont constaté que les différents types de perturbation de la canopée du 20^e siècle influençaient la dynamique actuelle des gaules de FG et de AS. Les perturbations partielles avaient tendance à favoriser les gaules de FG. Par contre, des éclaircies d'intensités différentes (1.1 à 3.7 m^2/ha de surface terrière) dans les peuplements d'érable à sucre, auraient favorisé la croissance des gaules de AS (Pothier, 1996). À l'inverse, des perturbations plus sévères comme une coupe totale ou un feu, pourraient favoriser la régénération de AS plutôt que celle de FG et cela particulièrement dans la zone nordique de son aire de répartition (Nolet et al., 2008a; Nolet et al., 2008b). Cependant, il sera important de vérifier la fréquence avec laquelle AS récupère une dominance après la création d'une perturbation sévère puisque selon Nyland et al. (2006), si FG ou AS se retrouvaient abondamment dans le peuplement avant une coupe totale, ces deux espèces peuvent acquérir la dominance dans la nouvelle cohorte.

Traitements d'adaptation à l'envahissement de FG

Différentes méthodes de fertilisations ont été développées dans le but de remédier à la pauvreté des sols, de permettre une meilleure croissance de AS et une diminution des symptômes de dépérissement. Par exemple, la fertilisation aurait permis de diminuer les symptômes de dépérissement de 25%, de hausser la fréquence d'arbres en santé de 70%, d'accroître le développement de la surface terrière et la vigueur des tiges de AS (Duchesne, Moore et al., 2008; Moore et al., 2006). De plus, Long et al. (1997) ont fertilisé avec de la chaux dolomitique (22.4 Mg.ha^{-1}) des peuplements mixtes de AS et de FG afin d'augmenter le Ca, le Mg et le pH du sol. Leurs résultats ont démontré, pour AS, une augmentation de la croissance, de la survie et de la reproduction. Une méta-analyse conduite sur 26 études de fertilisation réalisées sur l'érable, a démontré qu'il existe des effets positifs significatifs provenant de la fertilisation au Ca et de fertilisation à nutriments multiples mais aucun effet significatif provenant de N et P seuls (Vadeboncoeur, 2010). De plus, une réponse synergique de la part de AS a été obtenue en combinant une coupe sélective avec fertilisation. Le fait que FG n'ait pas réagi suite à l'ajout de 22.4 Mg.ha^{-1} de chaux dolomitique suggère qu'il n'est pas limité par la faible teneur du Ca dans les sols (Long et al., 1997).

Une autre méthode employée afin d'augmenter les chances de survie de l'AS est un dégagement du sous-étage de toutes autres espèces pouvant interférer avec la croissance des semis/gaules de l'AS et particulièrement la régénération de FG (Nyland et al., 2006). Après l'application d'un tel traitement de dégagement, Delagrange et al. (2007) ont pu effectivement ramener à 100% la proportion de l'AS.

Hypothèses de travail

Compte tenu de la littérature, plusieurs études ont soulevé des points importants concernant la réponse différente de AS et FG aux divers traitements sylvicoles actuellement pratiqués. Cependant, l'ensemble de ces renseignements est très dispersé et il est difficile de réellement conclure sur l'interaction possible de ces différents facteurs sur la régénération de ces deux espèces. Dans le but de clarifier certaines de ces interactions, cette étude a été planifiée pour analyser la performance de la régénération de AS et FG en fonction de la disponibilité en lumière et de la fertilité des sols. Pour cela, un large spectre de régimes de perturbations de la canopée était à l'étude en plus d'intégrer la qualité du site (*i.e.*, sa fertilité) des peuplements. De même, une étude spécifique combinant diverses ouvertures du couvert et une fertilisation à la chaux dolomitique a été conduite. En résumé, il est suggéré que les répercussions de différentes intensités de perturbations du couvert peuvent amener une inversion dans le succès de régénération des semis et gaules de FG et de AS. De plus, la fertilité du sol jouerait aussi un rôle dans la régénération des deux espèces. Afin de vérifier si ces deux facteurs ont une influence sur le succès de régénération entre les gaules et les semis de AS et de FG, 5 hypothèses alternatives ont été testées pour la région des Outaouais. Celles-ci s'énoncent comme suit;

1) Dans les peuplements où on retrouve AS et FG, il existe un gradient de fertilité des sols, allant de pauvre à riche, qui permet d'expliquer des différences

dans la régénération des deux essences sous des conditions lumineuses identiques.

2) Une grande ouverture de la canopée (> 50% DFPP) favoriserait la dominance de AS en canopée ainsi que la croissance radiale des gaules de AS qui surpasserait celle de FG .

3) Un sol fertile combiné avec une disponibilité de lumière plus élevée à 50% de DFPP auraient un effet synergique positif sur le succès de régénération (*e.i.,* croissance et abondance) des gaules de AS par rapport à FG de même qu'une baisse de ces deux facteurs auraient un effet inverse.

4) Un traitement de la canopée laissant entrer plus de 50% de lumière combiné avec un traitement de chaulage avantageraient la densité et permettraient une meilleure croissance annuelle en hauteur des semis de AS par rapport à ceux de FG.

5) Il existe des différences physiologiques, morphologiques et d'allocation de biomasse entre les semis de AS et FG qui expliqueraient leur différence de performance (*e.i.,* croissance et/ou abondance).

En se basant sur le modèle de la croissance potentielle au niveau de l'individu de Nolet et al. (2008a) (Fig. 1) pour expliquer le succès de régénération des deux espèces, trois sous-hypothèses sont proposées:

1a) La croissance des gaules/semis de AS surpassera celle de FG seulement lorsque le seuil critique de disponibilité en lumière est atteint.

1b) À l'inverse, la croissance des gaules/semis de FG surpassera celle de AS tant et aussi longtemps que le seuil critique de disponibilité en lumière n'est pas atteint.

1c) La valeur du seuil de disponibilité en lumière entre les deux espèces augmente avec la diminution de la fertilité du sol.

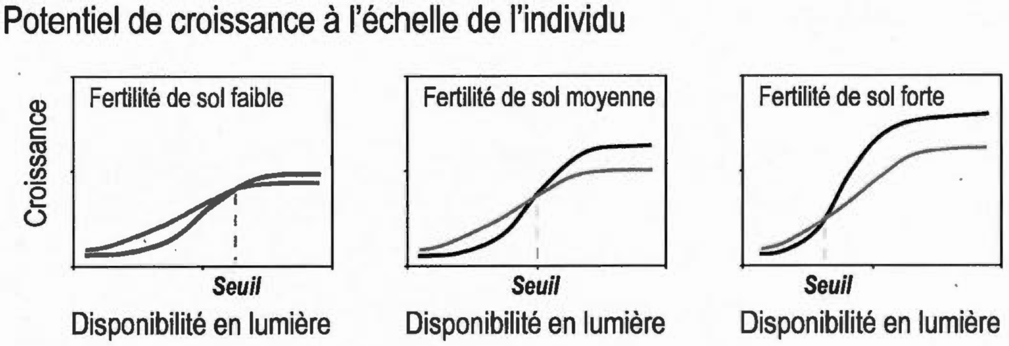

Figure 1: Les trois modèles figurant le potentiel de croissance à l'échelle de l'individu de la régénération des gaules de AS (trait foncé) et de FG (trait pâle) en fonction de la disponibilité en lumière. Le seuil de la disponibilité en lumière serait variable en fonction des conditions du sol (faible, moyenne, riche) (Nolet et al., 2008a).

Méthodologie

Ce projet est divisé en 2 parties complémentaires où la problématique globale de ce présent mémoire sera traitée à l'aide (1) d'une étude régionale où un grand nombre de peuplements ont été inventoriés et (2) d'une étude semi-contrôlée où des traitements spécifiques ont été appliqués.

Étude régionale

Un total de 56 peuplements dominés par AS a été échantillonné dans l'ouest de l'Outaouais (Québec) faisant partie du domaine bioclimatique de l'Érablière à bouleau jaune. Les peuplements ont été choisis en fonction de leur historique de perturbation et de classes de fertilité de sol. La surface terrière, la densité des gaules et la croissance de AS et de FG ont été mesurées en plus d'une caractérisation des facteurs abiotiques actuels (lumière et sol). L'interaction ainsi que l'effet de chacun de ces deux facteurs ont été évalués sur les gaules des deux espèces.

Étude semi-contrôlée

Un total de 24 parcelles de 0.64 ha a été échantillonné dans un peuplement dominé par AS et FG dans le secteur Nord-Est de Duhamel (Québec). Ces parcelles ont été soumises à des combinaisons de traitements d'ouverture du couvert et de chaulage afin d'obtenir un gradient de lumière et de fertilité du sol. Les mêmes mesures ont été prises que dans l'étude régionale mais en plus, une estimation de la performance à l'échelle des semis de AS et FG a été faite. L'interaction ainsi que l'effet de chacun des deux facteurs ont été évalués sur les semis des deux espèces.

Une description détaillée du protocole d'échantillonnage pour ces deux études est présentée dans la section « Material and Methods » de leur chapitre respectif.

CHAPTER I

IMPACT OF SOIL AND DISTURBANCE HISTORY TYPE ON SUGAR MAPLE AND AMERICAN BEECH COMPETITIVENESS IN SOUTHERN QUEBEC

Kim Bannon[1], Sylvain Delagrange[1,3], Nicolas Bélanger[1,2], and
Christian Messier[1]

[1]Centre d'étude de la forêt (CEF), Université du Québec à Montréal,
Département des sciences biologiques, Montréal (Québec) H3C 3P8, Canada.

[2]UER Science et Technologie, Université du Québec à Montréal (TELUQ),
Montréal (Québec) H2X 3P2, Canada.

[3]Institut Québécois d'Aménagement de la Forêt Feuillue (IQAFF), Ripon
(Québec) J0V 1V0, Canada.

1.1 Abstract

Recent studies have reported divergent results on the effect of soil nutrient (*i.e.*, Ca and Mg) and light availability on sapling and seedling density and growth of sugar maple (AS: *Acer saccharum*) and American beech (FG: *Fagus grandifolia*). The main objective of this study was to evaluate the effect of light availability and soil fertility on the density and growth of AS and FG saplings throughout the Outaouais region of Québec. We investigated 56 stands subjected to different disturbance history types (DHT) (UF, unmanaged forest; PC, partial cuts and; CC, clear cuts) along a soil fertility gradient. AS and FG absolute and relative sapling density varied a lot between the 56 stands, but no significant effect of DHT, soil nutrients and their interactions were found. However, after analyzing them, all 56 stands turned out to be on relatively nutrient poor sites. Radial growth of both species responded positively to canopy opening. CC permitted AS saplings to maintain more its radial growth in time than FG, thus the gain loss in radial growth in PC was higher for AS saplings than FG. Large changes in the intensity of canopy disturbance mainly caused a large (but equivalent) increase of growth for both species. Little could be done to shift dominance to advantage AS regeneration on such poor sites. PC disturbance regime created a certain discrepancy in growth rate between the two species 10 years after the disturbance occurred, but to the advantage of FG.

Keywords: *Fagus grandifolia*, *Acer saccharum*, soil fertility, light availability, saplings, clear cut, partial cut

1.2 Introduction

Throughout the last century, forest management has changed the structure and composition of forested landscapes in the temperate deciduous forest in Québec. Most notably, several experimental evidences indicate that management practices affect the dynamic coexistence (*i.e.*, the replacement pattern) of sugar maple (AS: *Acer saccharum*) and American beech (FG: *Fagus grandifolia*) in deciduous forests (Forcier, 1975; Kelty and Nyland, 1981; Horsley, 1994; Poulson and Platt, 1996; Beaudèt, Messier et al., 1999; Ray, Nyland et al., 2006; Dyer, 2001; Nolet et al., 2008a). A key factor determining the replacement pattern in maple-beech forest is the competitive regeneration of AS and FG in the understory (Arii and Lechowicz, 2002). These patterns have been investigated by numerous authors (Brisson, Bergeron et al., 1994; Poulson and Platt, 1996; Beaudet, Messier et al., 1999; Arii and Lechowicz, 2002; Nolet et al., 2008a; Gravel, Beaudet et al., 2010), but the identification of the biotic and abiotic factors responsible for these replacements remains unclear.

Environmental factors (*i.e.*, light availability, soil moisture, and soil nutrients) are known to influence AS regeneration patterns, however their effects on AS regeneration have rarely been studied simultaneously (Arii and Lechowicz, 2002, Nolet et al., 2008a). Yet, AS regeneration growth and vigor appear to be controlled by two principal factors and their interaction; 1) light availability which varies according to previous forests management and the characteristics of the forest canopy (Canham, 1985; Kobe et al., 1995) and 2) soil fertility (Kobe, 1996; Dijkstra and Smits, 2002; Hamburg, Yanai et al., 2003; Bailey, Horsley et al., 2004). It thus seems likely that these two dominant factors, and their interaction, dictate the temporal and spatial patterns of AS – FG coexistence.

Recently, several studies have reported dieback, defoliation of the crown, increases in mortality, and decreases in recruitment and growth of AS trees

(Long, Horsley et al., 1997; Moore, Camiré et al., 2000; Horsley, Long et al., 2002; Duchesne, Ouimet et al., 2005). These factors are all thought to be responsible for a decreasing AS population and in modifying the composition of the deciduous forest of Quebec (Duchesne and Ouimet, 2005; Duchesne et al., 2006). At the same time, FG appears to be increasing its relative dominance in these ecosystems, as FG saplings gradually gain dominance in the understory (Doyon et al., 2005; Gravel et al., 2010), modifying the structure and composition of sugar maple stands (Duchesne and Ouimet, 2005).

In order to delineate the performance and coexistence of AS and FG according to different disturbances, several studies have investigated the effects of light intensity and soil fertility on AS and FG seedling and sapling regeneration (Arii et Lechowicz, 2002; Nolet et al., 2008a). Nolet et al. (2008a) suggested that large gaps (*e.g.*, >30% of total incident light) are necessary to favor AS growth and regeneration success over FG. Moreover, subsequent frequent disturbances in those stands would assure AS regeneration continuously (Poulson and Platt, 1996) and allow it to maintain its dominance. However, other studies have suggested that both species respond similarly to an increase in light availability (Beaudet et al., 2007). Indeed, following the important canopy opening caused by the 1998 ice storm event, the hierarchical ranking of both species in the forest understory was not modified (Beaudet et al., 2007).

To clarify the possible synergetic effect of both light availability and soil fertility on the regeneration success of both AS and FG, this study sampled 56 stands which experienced contrasting historical canopy disturbances. This allowed focusing on the effects of disturbance history types (DHT) on the performance and relative abundance of AS and FG sapling regeneration, while also integrating soil fertility effects on regeneration. As such, a large range of canopy disturbance regimes were studied along with site quality.

The objectives for the present study were to i) verify if the variability between AS and FG abundance at the regeneration level, could be explained by the range of soil fertility found in the Outaouais region (Quebec, Canada); ii) examine the effect of this gradient of soil fertility, DHT and their interactions on the present AS and FG sapling density by testing the validity of Nolet et al.'s (2008a) model, and iii) test for a difference in radial growth response between AS and FG in relation to the intensity of canopy disturbances.

1.3 Methods

1.3.1 Study Sites

This study was carried out in the region of Outaouais, Quebec, Canada (Fig. 2). This region is part of the Canadian Shield and also part of the sugar maple – yellow birch bioclimatic zone (Ordre des ingénieurs forestiers du Québec, 2009; MRNF, 2003, Robitaille et Saucier, 1998). The forest canopy is mainly dominated by sugar maple (*Acer saccharum*), American beech (*Fagus grandifolia*) and yellow birch (*Betula alleghaniensis*). Mean annual temperature is 3.7 °C and annual precipitation ranges from 900 – 1000 mm (Ordre des ingénieurs forestiers du Québec, 2009). The Outaouais region is characterized by thin glacial till soils (Ordre des ingénieurs forestiers du Québec, 2009).

1.3.2 Stand Selection

Using a geographic information system software (ArcGIS v.9.0.), stand selection was made in order to get a gradient of intensities of historical canopy disturbance and of soil fertility. From this map, we pre-selected 72 mature AS and FG dominated stands with a minimum area of 4 ha (Fig 2). To obtain a gradient of intensities of historical canopy disturbance, three disturbance history types (DHT) affecting the canopy were delineated. These included, unmanaged forests (UF) as a control group, partial cuts (PC) implemented approximately 20 years ago and clear cuts (CC) implemented approximately 50 years ago. Within each DHT, stands were sorted into 3 fertility classes, based on the surface deposits given in ArcGIS inventory data, to cover a range in soil fertility. Selected stands were also located a minimum of 30 m from roads to avoid edge effects. The data inventory were not always accurate for local conditions and upon field visits and lab soil testing, pre-selected stands were eliminated if they did not fit the chosen criteria (*i.e.,* to have the presence of both species in the selected stand). Of the 72 pre-selected stands, 56 were used for this study and sampled (18 stands in UF, 18 stands in PC, and 20 stands in CC) (Fig. 2).

1.3.3 Experimental Design

The experimental design was based on Delagrange et al. (2007). For each 4 hectare stand, we established two sampling areas, at a distance of 150 m apart from each other, of 5 sample plots each (for a total of 10 sample plots with a radius of 3.09 m). The two sampling areas were spaced enough from each other to be referred to as two different experimental units or as two different stands (Fig. 3). Each experimental unit covered an area of 0.015 ha (Fig. 3). A total of 280 sample plots were measured throughout the Outaouais region (*i.e.*, 56 sampling areas x 5 plots). The central plot of the experimental unit (sample plot A) was randomly established with a flagpole once we entered the stand according to our GPS points given by ArcGIS (Fig. 3). AS and FG had to be present in both the understory and in the canopy before establishing the sampling area. After sample plot A was established, 4 extra flagpoles (B, C, D, E) were put in each of the four cardinal directions at a distance of 15 m from sample plot A (Fig. 3).

1.3.4 Field Measurements

1.3.4.1 Basal Area, Sapling Density and Radial Growth of *A. saccharum* and *F. grandifolia*

In each sample plot A, we took the basal area of each species with a factor 2 prism (metric). We also took sapling (1 cm < DBH < 9.0 cm individuals) density of all species in all 5 sample plots (Fig. 3). To examine the effect of DHT on growth response, in each sample plot A, we collected one sapling disk from a large sapling (7 cm < DBH < 9 cm individuals) for both species in the UF and PC stands. Sapling disk were collected at breast height to get retroactive DBH and growth of each individual. In the CC stands, tree coring was used since large trees were targeted to get individual growth response at disturbance occurrence (*i.e.*, trees that already existed as saplings at that time of the disturbance). It was important to choose trees that were present at that time, therefore, were saplings at the moment of the disturbance. In total, 112 disks and/or cores of AS and FG were collected for dendrochronological analysis. Disks and cores were air dried for several weeks and sanded up to 600 grit. A tree-ring measuring table with a 0.01mm precision (Velmex inc. Bloomfield, NY) was used. Radial growth (mm/yr) for disks was evaluated by averaging tree-ring width taken in two directions separately, one in 90° and the second one, opposite of the first, in 180°. Radial growth measurements were recorded for all PC and CC disk and core samples and spanned the 5 years previous to the disturbance event (*i.e.*, harvest) and for the 10 years following it, including the year of the canopy disturbance. For the UF, we kept 15 years of radial growth that occurred approximately during the same period of the harvest, according to the PC and CC disks and cores to allow for growth comparisons over the same timeframe.

1.3.4.2 Light Measurements

One hemispherical picture was taken in the center of each sample plot, for a total of 5 per experimental unit, at 1 m above ground. We used a numeric Nikon Coolpix 990 camera (Nikon Corporation, Tokyo, Japon) equipped with a hemispheric lens Fisheye Converter FC-E8. A total of 280 pictures were taken from all stands. Pictures were analyzed with the Gap light Analyser v.2.0 program (GLA v.2.0).

1.3.4.3 Soil Characteristics

In the centre of each sample plot within each stand, we collected soil from the B horizon and pooled all 5 samples into the same bag (*i.e.,* one bag per experimental unit) for a total of 56 soil samples. Soil samples were air dried for several weeks. Each soil sample was then sieved with a 2 mm lattice and sent for analysis (Soil and Plant Analysis Service, Sherbrooke University). From these samples, carbon and nitrogen concentrations (mg C g^{-1}, mg N g^{-1}) were determined by high temperature combustion (960°C), followed by thermo-conductometric detection (Vario MACRO, Elementar Analysensysteme, Haan, Germany). Base cations (Ca^{2+}, Mg^{2+}) and phosphate, were extracted with mehlich III solution and concentrations were determined by atomic absorption spectroscopy (AAnalyst 100, Perkin Elmer, Norwalk, CT) (San Tran et al., 1993). Lastly, soil pH was measured in water with a soil to water ratio of 1:2 (Hendershot et al., 2007).

1.3.5 Data Analysis

1.3.5.1 Stand Characteristics

The basal area of AS, FG and their total were calculated from the prism point in sample plot A of each stand. Measurements taken from each sample plot were averaged to estimate values for the stand and the relative and absolute sapling density of both species were calculated (saplings/hectare).

Linear models (LM) were used to test for differences between the stand and soil characteristics within the DHT (Tab. 1, 2, 3). Dependent variables were the basal area (BA) of both species and total stand basal area (BA_{stand}), sapling density (SD) of AS and FG, relative sapling density (SD_{Rel}) of both species, light availability and soil properties.

1.3.5.2 Sapling Density of *A. saccharum* and *F. grandifolia*

Linear mixed models (LME) were employed to independently test for interactions between SD_{AS}, SD_{FG}, and SD_{Rel} and soil nutrients and DHT. The Ca, C, P, Mg were used as continuous soil variables and the DHT as categorical variables. Since the experimental design was nested, because saplings of both species were measured in the same sample plots/stand, a random effect parameter was added in order to maintain independence between observations. Pearson correlation coefficients were calculated to test for correlations between SD_{AS}, SD_{FG}, and SD_{Rel} and each of the continuous soil data for Ca, C, P, Mg, C/N ratio among the DHT.

1.3.5.3 Radial Growth Response of *A. saccharum* and *F. grandifolia*

LME were employed to test the possible interactions between the radial growth response of AS and FG saplings in different time period (AV; before disturbance; AP1, 0-5 years after disturbance; AP2, 5-10 years after disturbance) among the DHT. The dependant variable used was the direct gain in radial growth (*i.e.*, subtracting AP1 from AV and AP2 from AV) for the PC and CC.

Log transformations were applied to dependant variables when needed to meet fit assumptions of normality. For all analyses I used the R statistical software (2009). Model outputs were considered significant at $\alpha = 0.05$.

1.4 Results

1.4.1 Stand Characteristics

The BA_{AS} was significantly higher in UF than in PC and CC stands, while BA_{FG} was significantly higher in CC than in UF and PC stands (Tab. 1). There were no significant differences for the BA_{Stand} among DHT. UF and CC stands had a significantly higher light transmission than PC stands (Table 1). In terms of understory composition, there were no significant differences between AS and

FG sapling density, nor relative sapling density, among DHT (Tab. 2 and Fig. 4). While there were more AS trees than FG trees in the canopy, there were more FG saplings in the understory in UF and PC (Tab. 1 and 2). In CC stands, the proportion of AS and FG appeared similar for both canopy trees and understory saplings (Tab. 1 and 2).

1.4.2 Soil Characteristics

Except for Mg, all soil nutrients showed significant differences among some, or all, of the DHT (Tab. 3). Ca (mg/kg) decreased as DHT severity increased (*i.e.,* severity increases from UF to PC to CC) (Tab. 3). Similarly, P (mg/kg) was significantly lower in CC stands than in UF and PC stands, but no significant difference existed between PC and UF stands. C (mg/kg) increased in CC stands over UF and PC stands (Tab. 3). C/N ratio increased significantly with severity of DHT (Tab. 3). The pH was significantly higher in UF stands than in PC and CC stands (Tab. 3).

1.4.3 Interactions of Sapling Density of *A. saccharum* and *F. grandifolia* with Disturbance History Type (DHT) and Soil

The sampled stands were found to be poor throughout the sampled region. Thus, the soil fertility gradient used in this study was surprisingly narrow in the expected gradient of Ca (*e.i.,* 300 mg/kg up to >5000 mg/kg, pers. comm. Bélanger, N., also see Tab. 3) and prevented us from categorizing it into classes going from poor to rich soil fertility despite initial cartographic classification. In this narrow range, none of the nutrient availabilities were related to any SD_{AS}, SD_{FG} or SD_{Rel} variations (data not shown). All Pearson correlations showed no significant relationships between $RelSD_{AS}$ and the nutrient availabilities except for the C/N ratio in CC (R=-0.5; *p*-value = < 0.001).

1.4.4 Radial Growth Response of *A.saccharum* and *F. grandifolia*

Both species responded positively and significantly to the disturbance type (*i.e.*, the harvest) according to the different time period (in PC from AV-AP1, *p* value <0.002; AV-AP2, *p value* <0.004; in CC from AV-AP1, *p* value <0.000 and AV-AP2, p value <0.000) (Fig. 5). As expected, the response in both species was very small throughout the time periods in UF (Fig.5A). In PC, there was already a slight difference at the start between the two species which significantly increased, at the advantage of FG, when the disturbance occurred (Fig. 5B). Radial growth gain was similar for both species, whereas AS saplings gained 154% and FG saplings gained 148% from AV to AP1 (Fig. 5B). However, during AP2, FG saplings tended to maintain more its gain in radial growth than AS going from AV to AP2 (*e.i*, 124% and 78%, respectively) (Fig. 5B). In CC, both species significantly gained in radial growth from AV to AP1 (*i.e.*, 194% for AS and 278% for FG) but the gain between the species wasn't statistically different (Fig. 5C). In AP2, CC permitted AS saplings to maintain more its radial growth than FG (*e.i.*, a decrease of 39% vs 64%, respectively) (Fig. 5C). Thus, the gain loss in radial growth in PC was higher for AS saplings than FG and lesser for both species in CC. The overall gain in radial growth was about the same for both species in the CC (Fig. 5C).

1.5 Discussion

1.5.1 Growth Response of *A. saccharum* and *F. grandifolia* Saplings to Canopy Disturbances

At the individual level, few differences were reported between AS and FG absolute radial growth in any of the three DHT studied. The only appreciable distinction is that the growth of FG tended to be higher than AS under PC, and especially its enhancement lasted longer after perturbation than the growth of AS making the growth gap between species greater, even though FG had a slight advantage over AS before the disturbance occurred. This was also reported for trees (*i.e.,* DBH>9cm) by Forget et al. (2001). This observation thus reinforces that partial canopy disturbances may gradually favor FG regeneration as compared to AS in the northern part of their distribution range through an increase in FG growth performance under partial harvests (Nolet et al., 2008a). Noteworthy, this slight discrepancy between AS and FG growth under PC might also partly be related to climatic issues. Indeed, in our PC stands, the dates of disturbance (about 20 years ago) associated with the release period (beginning of the nineties) for AS and FG saplings also concurs with a known dry period in Southern Quebec (Bertrand et al., 1994). This may have additionally mitigated AS growth, since it is known that FG is more drought tolerant than AS (Godman et al., 1990; Tubbs and Houston, 1990).

Furthermore, both species performed similarly (i) under closed canopy, and (ii) both species growth was similarly enhanced after CC. Several studies reported the inability of AS to outgrow FG under light availability inferior to 30% and suspected AS to overgrow FG under higher light levels (Beaudet, Brisson et al., 2007; Nolet et al., 2008a; Nolet et al., 2008b). In our study, light availability could not be measured at the time of the DHT (*i.e.,* 20 and 50 years ago), but it is safe to assume that after CC, light levels were higher than 50% of total incident radiation. It is also safe to assume that ground water was abundant enough for seedlings to grow at that time. It has been shown that ground water table level significantly rises after a CC, and so does after thinning but at a lower degree (Heikurainen, 1966; Päivänen, 1966; Helzinki, 1970). Nevertheless, after CC, relative competitiveness of AS and FG saplings remains the same, between both species. Such ability of FG to respond to large canopy opening was unexpected. Under closed canopy, vegetative and especially root sprouting ability of FG has been associated to its higher growth rates than AS (Beaudet, Messier et al., 1999). In this study, the origin of FG saplings was impossible to determine but it is reasonable to assume that some of the high FG performance under high light came from sprouts (Arii and Lechowicz 2002).

Thus, at the individual level, no experimental evidence exists to suggest a shift in AS and FG competitiveness with large changes in the intensity of canopy disturbances (cf. Fig. 1), at least on nutrient poor sites such as those found in the Outaouais region. Based on the theoretical framework proposed by Meinzer (2003) and further established by Valladares et al. (2007), the absence of species differences in competitiveness or performance is likely related to the fact that, there are a limited number of phenotypic solutions for plants to acclimate to a limited environment (here soil fertility). This also agrees with previous studies, which showed that a large increase in light availability in the understory maintains AS and FG competitiveness because of very similar response of both species (Beaudet et al., 2008; Takahashi and Lechowicz, 2008). Nevertheless, it is possible that on more fertile sites, the enhancement of AS growth rate to outgrow FG in response to a significant canopy opening could occur (cf. McClure, Lee et al., 2000, Nolet et al., 2008a).

1.5.2 *A. saccharum* and *F. grandifolia* Regeneration Dynamic and Disturbance History Type (DHT)

First of all, one should acknowledge that the regeneration dynamics described in this study does not cover the whole population of maple dominated stands, but maple dominated stands where the presence of both AS and FG saplings was demonstrated in the understory in the last 5 decades. Based on this premise, DHT appears to have a critical effect on the present canopy composition which is composed of an increasing proportion of FG as the intensity of canopy disturbance increases. Several factors need to be considered to better describe such changes in composition. First, the proportion of AS and FG in the canopy and in the understory prior to disturbance could not be determined. Even if it can't refute that the composition was not similarly variable in all DHT, this could not be confirmed in this study. However, considering that during the stand selection for PC or CC, priority was given to stands with historically lower FG proportion (Bouffard et al., 2003), original PC and CC stands surely had similar or lower FG proportion in the canopy than AS. Second, composition changes may be accentuated by stem selection at harvest. Indeed, as mostly all trees were harvested in the CC stands, AS might have been preferentially harvested in the PC stands, increasing FG proportion at the stand level in this specific DHT. Third, and probably the most important factor in the present canopy composition, is the combination of the rather equal, growth competitiveness described in the previous section but distinct location of both species in the understory (*i.e.*, AS as a seedling bank and FG as a sapling bank (see also next section). As reported by our result, growth competitiveness of both species was very similar under either of the DHT studied, or slightly to the advantage of FG in PC. On the rather low fertility sites we investigated in this study, both species thus compete equally and have the same opportunity to complete their regeneration cycle. Only the rate of recruitment changes in response to DHT (no matter the species); the more intense the disturbance, the faster the recruitment. However, in the end, FG will obviously dominate in these particular low fertility sites, since FG has the substantial advantage of generating a sapling bank (Forcier, 1975; Brisson et al., 1994; Houle, 2002), while AS produces a seedling bank (Marks and Gardescu, 1998). In addition, several studies have shown that FG root sprouts can contribute to increase the presence of FG in the understorey and eventually the canopy (Forcier, 1975; Brisson et al., 1994; Beaudet et al., 1999; Houston, 2001; Arii et Lechowicz, 2002) and root sprouting may increase with increasing logging intensity. Finally, several other factors, not considered in this study, such as climate change, air pollution, soil acidification (Bouliane, 1969; Duchesne, Ouimet et al., 2005), may have interacted differently with each DHT to produce the observed changes in the understory composition (Poulson and Platt, 1996; Nolet, Forget et al., 2001; Arii and Lechowicz, 2002; Bouffard, Doyon et al., 2003; Nolet et al., 2008a), but these interactions need further investigation to be confirmed.

1.5.3 *A. saccharum* and *F. grandifolia* Sapling Density, Disturbance History Type (DHT) and Soil Fertility

In the understory, FG sapling density tended to be higher than AS, in all DHT. The understory composition did not reflect the canopy composition in relative proportions of AS and FG. This leads us to believe that the higher FG density is related to a better survival of FG seedlings and saplings in the understory. Previous research has shown that FG has a higher vertical growth rate than AS under low light conditions (*i.e.*, 1% PPFD) and a better ability to capture light by expanding its lateral branches (Poulson and Platt, 1996; Beaudet et Messier 1999; Takahashi and Lechowicz, 2008). These physiological and structural adaptations may give FG an adaptive advantage to install a sapling bank under very low light availability (Arii and Lechowicz, 2002). On the other hand, AS generally stops its height growth under low light conditions (Delagrange et al., 2004; Woods, 2008) allowing this species to survive in the seedling strata (<1 m tall) rather than in the sapling strata.

Surprisingly, there were no differences in sapling relative density due to DHT, soil fertility or the interaction of both factors. This contradicts other findings linking contrasting sapling abundances of both species with soil fertility and more specifically with Ca availability (Arii and Lechowicz 2002; Duchesne and Ouimet 2009). However, one should acknowledge that the fertility gradient (and especially for Ca) measured among our 56 stands was narrow and restricted to low values (< 1770 mg/g). This led to the conclusion that sample stands, where both species were present in the last 5 decades, only selected low fertility sites despite a cartographic classification into low, medium and rich fertility stands. This also supports that occurrence of FG in the Western Outaouais region might be limited to more unfertile sites. The absence of a linkage between relative sapling proportion and soil fertility in our study is also reinforced by the fact that contrasting fertility was found within DHT but that it did not induce any consequences for species regeneration. Indeed, significantly lower availability of Ca, P and Mg were found as the severity of DHT increased. Some factors may explain the decrease of the availabilities of these nutrients, such as forest development stage (Arthur and Yahai, 2000; Hamburg, Yanai et al., 2003) or logging (Bormann, Likens et al., 1968; Federer, Hornbeck et al., 1989; Johnson, Romanowicz et al., 1997; Arthur and Yanai, 2000). Federer, Hornbeck et al., (1989) reported that CC depleted the soil by removing 90% of each nutrient of the above ground pool, potentially resulting in decreasing exchangeable Ca faster than total Ca. However, these large scale footprints on soil fertility had no detectable impact on AS and FG sapling recruitment.

Our results also mitigate Nolet et al. (2008a) hypothesis that AS sapling recruitment on poorer soils is promoted when more severe DHT occurred. Limited below-ground resources may have greatly restrained the ability of AS to respond to higher light availability minimizing differences in growth competiveness between both species (cf. "Growth response of *A. saccharum* and *F. grandifolia* saplings to canopy disturbances" section and Beaudet et al., 2008). However, considering our small soil fertility gradient, it remains impossible to conclude on Nolet et al. (2008a) assumptions dealing with both species regeneration on richer soils.

1. 6 Conclusion

At the stand scale, contrasting DHT may critically impact the regeneration dynamic of *A. saccharum* (AS) and *F. grandifolia* (FG) on low fertility sites. However, this effect was not expressed in this study through a shift in species growth competitiveness. We report instead that large changes in the intensity of canopy disturbance mainly caused a large (but equivalent) acceleration of growth for both species. Furthermore, we did not measure any effect of soil fertility on the relative density of AS and FG saplings under any of the studied DHT, but we acknowledged that the soil fertility gradient was limited. These results suggest that on these relatively nutrient poor sites managers cannot shift dominance toward AS in the regeneration through canopy opening modifications alone.

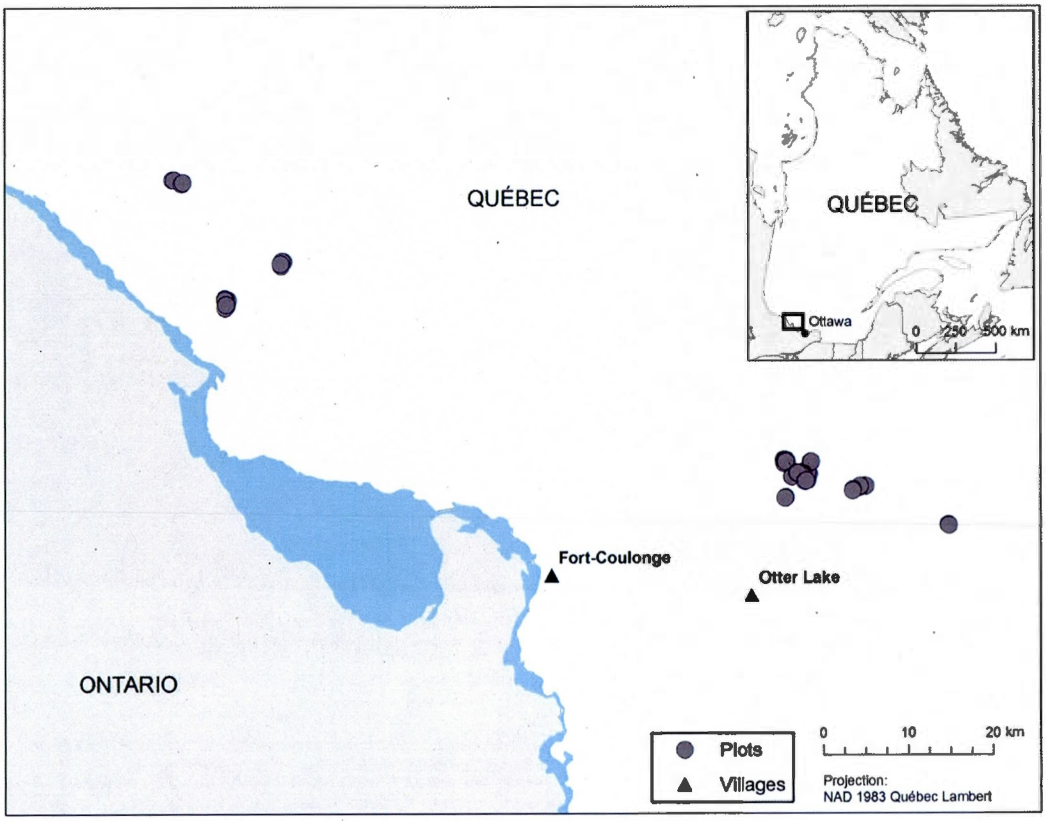

Figure 2: Study area of the 56 sugar maple and American beech stands situated throughout the Outaouais region, Québec, Canada.

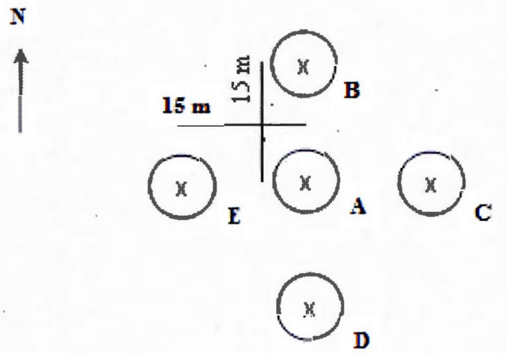

Figure 3: Sampling design representing the 5 sample plots (A, B, C, D, E) where x represents the center of the sample plot. All saplings measurements took place in all 5 plots (r = 3.09 m).

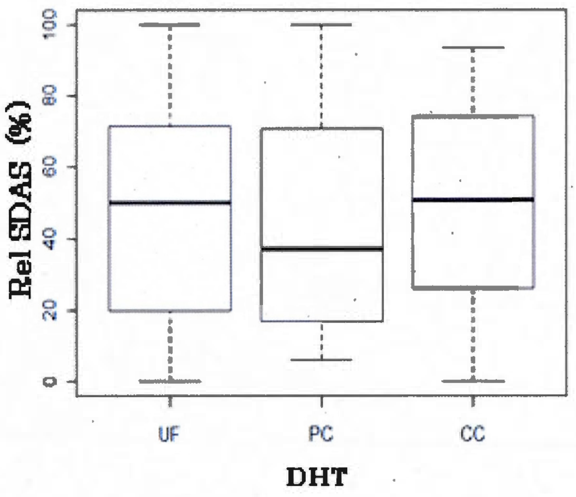

Figure 4: Relative sapling density of *A. saccharum* (RelSD$_{AS}$) compared to *F. grandifolia* (%) according to disturbance history type (DHT; UF, PC, CC) with standard deviation. Boxes are the 5th and 95th percentiles and solid lines in the box represent the median. See table 1 for abbreviations.

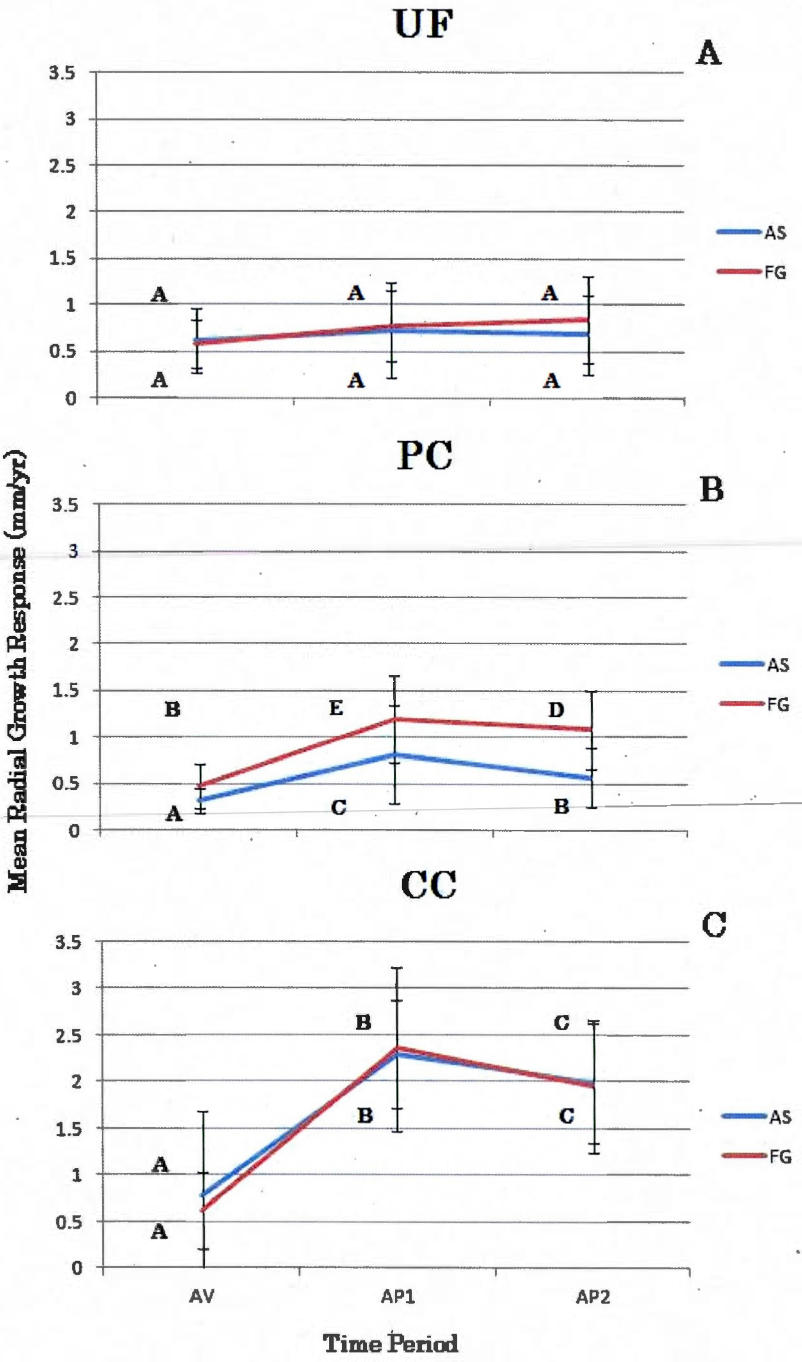

Figure 5: Mean radial growth response (mm/yr) for AS (blue) and FG (red) according to DHT (UF, PC, CC) for each time period (AV, AP1, AP2) where AV: before DHT; AP1: 0-5yrs after DHT; AP2: 6-10 yrs after DHT. Time period within each DHT with different letters are significantly different at α = 0.05.

Table 1: Characteristics of stand composition according to disturbance history type (DHT) in the Outaouais region.

Stand Characteristics *					
DHT	n	BA_{AS} (trees/ha)	BA_{FG} (trees/ha)	BA_{Stand} (trees/ha)	LA
UF	18	13.7a	1.6b	22.3a	9.1a
PC	18	9.1b	4b	19.2a	6.5b
CC	20	7.9b	8a	20.8a	8.1a

*Values are the means for LA (Light availability). Values within a column with different letters are significantly different at $\alpha = 0.05$ according to DHT.

*BA_{AS}, basal area of *Acer saccharum*; BA_{FG}, basal area of *Fagus grandifolia*; BA_{stand}, basal area of stand.

*UF, unmanaged forest; PC, partial cut; CC, clear cut.

Table 2: Characteristics of stand understory composition according to disturbance history type (DHT) in the Outaouais region.

Stand Characteristics *				
DHT	n	SD_{AS} (stem/ha)	SD_{FG} (stem/ha)	SDtotal (stem /ha)
UF	18	448a	726a	1174a
PC	18	792a	959a	1751a
CC	20	527a	670a	1197a

*Values are the means. Values within a column with different letters are significantly different at $\alpha = 0.05$ according to DHT.

*SD_{AS}, *Acer saccharum* sapling density; SD_{FG}, *Fagus grandifolia* sapling density.

*See table 1 for abbreviations.

Table 3: Characteristics of the soil in B horizon according to disturbance history type (DHT) in the Outaouais region.

	Soil characteristics (B horizon)*					
DHT	Ca (mg/kg)	C (mg/kg)	P (mg/Kg)	Mg (mg/Kg)	C/N (mg/kg)	pH
UF	641(± 449)a	34 (± 8)a	51 (±38)a	32 (± 16)a	14 (± 2)a	4.3 (±0.3)a
PC	494 (± 383)b	33 (± 8)a	46 (± 47)a	27 (± 12)a	15 (± 2)b	4.2 (± 0.2)b
CC	325 (± 263)c	40 (± 13)b	20 (± 36)b	22 (±12)a	17 (± 3)c	4.1 (± 0.2)b

*Values are the means (± SD). Values within a column with different letters are significantly different at
α = 0.05 as in function of DHT.
*Ca, calcium; C, carbon; P, phosphorus; Mg, magnesium; C/N, carbon/nitrogen ratio.

1.7 References

Arii, K. and J. Lechowicz, M (2002). "The influence of overstory trees and abiotic factors on the sapling community in an old-growth Fagus-Acer forest." Écoscience 9(3): 386-396.

Arthur, A., M, and D. Yanai, R (2000). "Distinguishing the Effects of Environmental Stress and Forest Succession on Changes in the Forest Floor." Korean J. Ecol. 23(2): 83-88.

Bailey, S. W., B. Horsley, S, et al. (2004). "Influence of Edaphic Factors on Sugar Maple Nutrition and Health on the Allegheny Plateau." Soil Sci. Soc. Am. J. 68: 243-252.

Beaudet, M. and C. Messier. (2008). "Beech regeneration of seed and root sucker origin: A comparison of morphology, growth, survival, and response to defoliation." Forest Ecology and Management 255: 3659-3666.

Beaudet, M., J. Brisson, et al. (2007). "Effect of a major canopy disturbance on the coexistence of Acer saccharum and Fagus grandifolia in the understorey of an old-growth forest." Journal of Ecology 95(3): 458-467.

Beaudet, M., C. Messier, et al. (1999). "Possible mechanisms of sugar maple regeneration failure and replacement by beech in the Boisé-des-Muir old-growth forest, Québec." Écoscience 6(2): 264-271.

Bertrand, A., G. Robitaille, et al. (1994). "Effects of soil freezing and drought stress on abscisic acid content of sugar maple sap and leaves " Tree Physiology 14(4): 413-425.

Bormann, H., F, E. Likens, G, et al. (1968). "Nutrient Loss Accelerated by Clear-Cutting of a Forest Ecosystem." Science 159: 882-884.

Bouffard, D., F. Doyon, et al. (2003). "Historique et dynamisme écologique de la végétation forestière de la réserve faunique Rouge- Matawin de 1930 à nos jours." Rapport volet II. IQAFF 1-122.

Bouliane, A. (1969). "Étude de la transformation de l'érablière à sucre en hêtraie." Mémoire demaîtrise, Faculté de foresterie et de géodésie de l'Université Laval, Québec. 77 p.

Brisson, J, Bergeron et al. (1994). "Beech-maple dynamics in an old-growth forest in southern Quebec, Canada." Écoscience 1(1): 40-46.

Canham, D., C. (1985). "Suppression and release during canopy recruitement in Acer saccharum." Torrey Botanical Club 112(2): 134-145.

Delagrange, S., C. Messier, et al. (2004). "Physiological, morphological and allocational plasticity in understory deciduous trees: importance of plant size and light availability." Tree Physiology 24: 775–784.

Delagrange, S., P. Nolet, et al. (2007). "Impact du dégagement et du chaulage sur la régénération en érable à sucre et en hêtre dans les érablières en voie d'hêtrisation soumis à différentes intensités de prélèvements du couvert. Rapport de la phase II." IQAFF: 1-19.

Dijkstra, A., F, and M. Smits, M, (2002). "Tree Species Effects on Calcium Cycling: The Role of Calcium Uptake in Deep Soils." Ecosystems 5: 385-398.

Doyon, F., D. Gagnon, et al. (2005). "Effects of strip and single-tree selection cutting on birds and their habitat in a southwestern Quebec northern hardwood forest." Forest Ecology and Management 209(1-2): 101-116.

Duchesne, L. and R. Ouimet (2009). "Present-day expansion of American beech in northeasthern hardwood forests: Does soil base status matter?" Can. J. For. Res. 39: 2273-2282.

Duchesne, L., J. Moore, D, et al. (2006). "Envahissement du hêtre dans les érablières dépérissantes au Québec." Le naturaliste canadien 130(1): 56-59.

Duchesne, L., R. Ouimet, et al. (2005). "Changes in structure and composition of maple–beech stands following sugar maple decline in Quebec, Canada." Forest Ecology and Management 208: 223–236.

Dyer, M., J (2001). "Using witness trees to assess forest change in southeastern Ohio." Can. J. For. Res. 31(10): 1708-1718.

Federer, C. A., J. W. Hornbeck, et al. (1989). "Long-term depletion of calcium and other nutrients in eastern US forests." Environmental Management 13(5): 593-601.

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

Forget, E., F. Doyon, et al. (2001). "L'évolution de la qualité des tiges: une évaluation régionale." IQAFF: 1-25.

Godman, M. R., W. H. Yawney, et al. (1990). "*Acer Saccharum* Marsh. Sugar Maple." In Silvics of North America: 2, R.M. Burns and B.H. Honkala, Department of Agriculture, Forest Service, Washington, DC, pp. 78-91.

Gravel, D., M. Beaudet, et al. (2010). "Large-scale synchrony of gap dynamics and the distribution of understory tree species in maple–beech forests." Oecologia **162**: 153-161.

Hamburg, P., S,, D. Yanai, R,, et al. (2003). "Biotic Control of Calcium Cycling in Northern Hardwood Forests: Acid Rain and Aging Forests." Ecosystems 6: 399-406.

Heikurainen, L. (1966). "Effect of cutting on the ground-water level on drained peat lands." Intern. Symp. on Forest Hydrol., Pergamon Press, pp. 345-354.

Heikurainen, L. and J. Päivänen (1970). "The effect of thinning, clear cutting, and fertilization on the hydrology of peatlands drained for forestry." Acta Forestalia Fennica 104: 1-28.

Hendershot, W.H., Lalande, H., Duquette, M. 2007. Soil reaction and exchangeable acidity In Soil sampling and methods of analysis, Second edition, M.R. Carter and E.G. Gregorich, editors, CRC Press, Boca Raton, FL, pp. 173-178.

Houle, D., L. Duchesne, et al. (2002). "Soil and Tree-Ring Chemistry Response to Liming in a Sugar Maple Stand." J. Environ. Qual 31: 1993-2000.

Houston, R. D. (2001). "Effect of Harvesting Regime on Beech Root Sprouts and Seedlings in a North-Central Maine Forest Long Affected by Beech Bark Disease." Research Paper NE-717. USDA Forest Service: 1-24.

Horsley, S. B. (1994). "Regeneration Success and Plant Species Diversity of Allegheny Hardwood Stands After Roundup Application and Shelterwood Cutting." Northern Journal of Applied Forestry 11: 109-116.

Horsley, S. B., R. P. Long, et al. (2002). "Health of Eastern North American Sugar Maple Forests and Factors Affecting Decline." Northern Journal of Applied Forestry 19: 34-44.

Johnson, E., C,, B. Romanowicz, R,, et al. (1997). "Conservation of exchangeable cations after clear-cutting of a northern hardwood forest." Can. J. For. Res. 27: 859-868.

Kelty, M. J. and R. D. Nyland (1981). "Regenerating Adirondack Northern Hardwoods By Shelterwood Cutting and Control of Deer Density." Journal of Forestry 79: 22-26.

Kobe, R. K. (1996). "Intraspecific Variation in Sapling Mortality and Growth Predicts Geographic Variation in Forest Composition." Ecological Monographs 66(2): 181-201.

Kobe, K., Richard, S. Pacala, W, et al. (1995). "Juvenile tree survivorship as as component of shade tolerance." Ecological Applications 5(2): 517-532.

Long, P., R, B. Horsley, S, et al. (1997). "Impact of forest liming on growth and crown vigor of sugar maple and associated hardwoods." Can. J. For. Res. 27: 1560-1573.

Marks, P. L. and S. Gardescu (1998). "A Case Study of Sugar Maple (Acer saccharum) as a Forest Seedling Bank Species." Journal of the Torrey Botanical Society 125(4): 287-296.

Meinzer, F. C. 2003. Functional convergence in plant responses to the environment. Oecologia 134: 1–11.

Tubbs, H. C., D. R. Houston (1990). "*Fagus grandifolia* Ehrh. American beech" In Silvics of North America: 2, R.M. Burns and B.H. Honkala, Department of Agriculture, Forest Service, Washington, DC, pp. 325-332.

Moore, J., D, C. Camiré, et al. (2000). "Effects of liming on the nutrition, vigor, and growth of sugar maple at the Lake Clair Watershed, Québec, Canada." Can. J. For. Res. 30: 725–732.

McClure, J. W., T. D. Lee, et al. (2000). "Gap capture in northern hardwoods: patterns of establishment and height growth in four species." Forest Ecology and Management 127(1-3): 181-189.

MRNF. (2003). Zones de végétation et domaines bioclimatiques du Québec. Gouv. Du Québec. Dans: http://www.mrnfp.gouv.qc.ca/forets/connaissances/connaissances-inventaire-zones.jsp

Nolet, P., D. Bouffard, et al. (2008a). "Relationship between canopy disturbance history and current sapling density of Fagus grandifolia and Acer saccharum in a northern hardwood landscape." Canadian Journal of Forest Research 38: 216-225.

Nolet, P., S. Delagrange, et al. (2008b). "The successional status of sugar maple (Acer saccharum), revisited." Ann. For. Sci. 65: 208.

Nolet, P., E. Forget, et al. (2001). "Reconstitution historique du dynamisme du paysage forestier du bassin de La Lièvre au cours du 20ième siècle." IQAFF: 1-122.

Nyland, D., R, A. Bashant, L, et al. (2006). "Interference to Hardwood Regeneration in Northeastern North America: Controlling Effects of American Beech, Striped Maple, and Hobblebush." North. J. Appl. For 23(2): 122-132.

Ordre des ingénieurs forestiers du Québec (2009). Manuel de foresterie, $2^{ème}$ ed, ouvrage collectif, éditions multimondes, Qc, 1544p + 32 p. couleurs.

Poulson, L., T and J. Platt, W (1996). "Replacement Patterns of Beech and Sugar Maple in Warren Woods, Michigan." Ecology 77(4): 1234-1253.

Robitaille, A., J-P. Saucier. (1998). Paysages régionaux du Québec méridional. Publications du Québec, Sainte-Foy, Québec.

Sen Tran T, Simard RR. 1993. Mehlich III-extractable elements. pp. 43-49. *In* Carter MR (ed.), Soil sampling and methods of analysis. Lewis Publishers, Boca Raton, FL.

Takahashi, K. and J. Lechowicz, M (2008). "Do Interspecific Differences in Sapling Growth Traits Contribute to the Co-dominance of Acer saccharum and Fagus grandifolia?" Annals of Botany 101: 103-109.

Valladares, F., E. Gianoli, et al. (2007). "Ecological limits to plant phenotypic plasticity." New Phytologist 176: 749-763.

Woods, D. K. (2008). "Living long by staying small: stem layering as an adaptive life-history trait in shade-tolerant tree seedlings." Can. J. For. Res. 38: 480-487.

CHAPTER II

REGENERATION SUCCESS OF SUGAR MAPLE AND AMERICAN BEECH IN RELATION TO OVERSTORY OPENING AND LIME TREATMENT

Kim Bannon[1], Christian Messier[1], Philippe Nolet[2] and
Sylvain Delagrange[1,2]

[1]Centre d'étude de la forêt (CEF), Université du Québec à Montréal, Département des sciences biologiques, Montréal (Québec) H3C 3P8, Canada.

[2]Institut Québécois d'Aménagement de la Forêt Feuillue (IQAFF), Ripon (Québec) J0V 1V0, Canada.

2.1 Abstract

Both low soil fertility and lower light availabilities are suspected to favor the establishment and growth of American Beech (FG: *Fagus grandifolia*) over sugar maple (AS: *Acer saccharum*) seedlings. This study is complementary to our regional experimental study in investigating the regeneration success of sugar maple and American beech. The main objective of this study is to evaluate the effect of a combination of canopy openings and liming treatment on the density and growth of AS and FG seedlings. This semi-controlled experiment used 24 stands subjected to recent canopy openings (CO; UF, PC, CC) and liming (3t per ha) soil treatment (ST). Again, AS and FG absolute and relative seedling density varied among stands, but both light and soil fertility treatments did not have any significant impact 3 years following the treatments. Wide canopy openings (*i.e.,* CC) combined with limed soils had a positive but not significant effect on absolute AS seedling density. However, this same treatment combination showed significant results on AS height growth. Each species showed very few differences in their overall physiological, morphological and allocational performance mostly related to the canopy opening, but no differences were found between the two species.

Keywords: *Acer saccharum*, *Fagus grandifolia*, canopy treatment, liming treatment, seedlings, partial cut, clear cut.

2.2 Introduction

Major transformations occurred in the temperate deciduous forest in Québec changing the composition of forested landscapes. Management practices create imbalances in the coexistence dynamics (*i.e.*, the replacement pattern) between sugar maple (AS: *Acer saccharum*) and American beech (FG: *Fagus grandifolia*) (Forcier, 1975; Kelty and Nyland, 1981; Horsley, 1994; Poulson and Platt, 1996; Beaudet, Messier et al., 1999; Ray, Nyland et al., 1999; Dyer, 2001; Nolet et al., 2008a). Since the 1980s, many of these authors have reported a considerable increase in FG saplings in the understory whereas AS trees were showing generalized dieback (Long et al., 1997; Moore, Camiré et al., 2000). It has been suggested that AS dieback could be related to changes in soil properties due to acid rain altering its growth and vigor. Meanwhile, these same changes associated with a decrease in the intensity of canopy disturbance would favor FG establishment, therefore modifying the structure and composition of the sugar maple understory (Duchesne and Ouimet, 2005). Doyon et al. (2003) reported that over 600 000 ha in the Outaouais region are invaded by an overgrowth of FG in sugar maple stands.

It has been extremely difficult to isolate the main cause of such decline in AS (*i.e.*, a decrease in growth, and recruitment, and increase in mortality) because of the many possible factors that regulate the population dynamics of such species. But, two factors have been singled out as being responsible for the AS regeneration growth and vigor decline over that of FG (Delagrange, Nolet et al., 2009). First, the low light availability found under deciduous forests could favor beech over maple (Canham, 1985; Kobe et al., 1995; Poulson and Platt, 1996; Arii and Lechowicz, 2002; Nolet et al., 2008a). Second, declining soil fertility caused by acid rain could favor beech over maple (Kobe, 1996; Dijkstra and Smits, 2002; Hamburg, Yanai et al., 2003; Bailey, Horsley et al., 2004; Duchesne, Moore et al., 2006). In the recent past (last 40 years), forest management implicates more partial cuts (PC) today and because severe fires are being suppressed, less severe canopy openings are occurring which could prevent higher light levels from reaching the understory and AS regeneration to benefit from it (Nolet et al., 2008a). AS regeneration tends to have more difficulty establishing on poor soils (*i.e.*, Ca) (Kobe, 1996) whereas FG regeneration seems to be able to establish on nutrient poor sites (Delagrange, Nolet et al., 2009). Many questions are being raised regarding the future composition of stands in the region of the Outaouais.

However, many treatments exist to prevent an overgrowth of FG in the understory and to favor AS regeneration in sugar maple stands. For example, forest management could include suppressing all above ground FG regeneration to decrease competitiveness with AS (Nyland et al., 2006). Hane (2003) showed that by removing FG saplings, AS seedlings had higher survival rates. Also, forest liming has been used to improve soils with nutritional problems affecting northern hardwood growth and health (Long et al., 1997). Lime treatments have also been used to decrease soil acidity or to increase concentrations of Ca and Mg (Lea et al., 1980). Fertilization allowed a better growth for AS, a decrease of dieback symptoms by 25%, an increase of the overall health by 70% as well as an increase of the development of basal area and vigor in AS (Moore et al., 2006; Duchesne, Moore et al., 2008). Long et al. (1997) reported a positive growth response in AS, combining selective cutting and liming treatment. On the other hand, FG lack of response to liming treatment suggested that it is not limited by lower Ca concentrations in soils (Long et al., 1997).

The interacting effect of crown opening and liming treatment on the density and growth of understory sugar maple and American beech has not been fully investigated. Some authors elaborated models where light intensity along with soil fertility would influence AS and FG seedlings and saplings regeneration (Arii and Lechowicz, 2002; Nolet et al., 2008a). Nolet et al. (2008a) suggested that large gaps (*i.e.,* >30% full sunlight) are necessary to favor AS regeneration at the expense of FG regeneration on nutrient poor sites. On such poor sites, AS would dominate stands only when some periods of high light intensity could regenerate AS seedlings and saplings (Arii and Lechowicz, 2002). Thereafter, frequent partial disturbances would ensure continuous AS regeneration (Poulson and Platt, 1996) allowing it to keep its dominance.

Thus, it is reasonable to think that combining these two factors will help in understanding how AS and FG coexist and perform and in identifying operational treatments to keep AS dominance where FG is already present. The objectives of this study were to test for interactive effects of canopy opening (CO) and liming treatment on i) AS and FG seedling density, ii) AS and FG seedling annual height growth rates and iii) AS and FG seedling physiological and morphological traits. With regards to these objectives, we hypothesized that i) higher light availability combined with liming treatment will have a stronger positive effect on AS seedling survival and will thus increase AS density over FG; ii) AS seedlings will have a higher annual height growth rate than FG seedlings in response to higher light availability and liming treatment and iii) the expected higher growth of AS seedlings will be related to a better physiological, morphological and allocational response to opening and liming as compared to FG seedlings.

2.3 Methods

2.3.1 Controlled Experiment Study Site

The study site was located in the North-East of Duhamel (Québec, Canada) near Gagnon Lake and the wildlife Papineau Labelle reserve (46°07`40``N, 75° 09`24``W) (Fig. 6). The study site is part of the Canadian Shield and also part of the sugar maple – yellow birch bioclimatic zone (Ordre des ingénieurs forestiers du Québec, 2009; MRNF, 2003). On the hill tops and when slopes were steep, rocky outcrop appeared often. In the bottom of valleys, glacial deposits were found (Delagrange, et al., 2007). This region is also characterized by thin tills with poor nutritional status on a brunisolic soil type (Agriculture

Canada, 1990). Mean annual temperature can fluctuate between 2.5 and 5.0°C and rainfall is approximately 1000 mm. Growing season varies between 170-180 days (Robitaille and Saucier, 1998). The study site was mostly covered with sugar maple (*Acer saccharum*) and American beech (*Fagus grandifolia*).

2.3.2 Selected Stands and Treatments

In the Duhamel site, 24 stands (each about 1 ha size) were submitted to one of the three following canopy opening treatments in the autumn 2006; unmanaged forest (UF), partial cuts (PC) and clear cuts (CC) (Fig. 7) (Delagrange, et al., 2007). In 2007, half of the UF, PC and CC stands were randomly selected for liming (Fig. 7) with 3t of dolomitic lime per hectare.

2.3.3 Experimental Design

The canopy opening treatment was applied on an area of 1 hectare for each stand and the liming was applied to the center of this treated hectare on an area of 0.16 ha (40 m x 40 m). The sampling design was the same as the one used in the previous study (Fig. 8) but the distance between each sample plot was 10 m instead of 15 m from sample plot A (Fig. 8). At 2 m North and South of the center of each sample plot were 2 micro-plots with a radius of 1.13 m (4 m^2) where seedling density of both species was measured. A flagpole was put in the center of all micro-plots to locate them more easily.

2.3.4 Field Measurements

2.3.4.1 Basal Area and Seedling Density of *A. saccharum* and *F. grandifolia*

For the basal area measurement, the same protocol as for the previous study was used (see section 1.3.4.1 of chapter 1 for details). Seedling density for both species was measured in each micro-plot.

2.3.4.2 Light Measurements

A light availability profile was measured in each stand. We took a total of 20 hemispheric pictures per stand, 4 per sample plots at 4 different heights from the ground; 0.50, 1, 2 and 3 m. The same camera, technique and analyzing process were used as in the previous study (see section 1.3.4.2 in chapter 1 for details).

2.3.4.3 Soil Characteristics

Horizons A and B were collected in each sample plot for a total of 48 soil samples. The same protocol and analyzing processes as for the previous study were used (see section 1.3.4.3. in chapter 1 for details).

2.3.4.4 Estimate of *A. saccharum* and *F. grandifolia* Seedlings Performance

In each sample plot, one seedling of each species was randomly harvested in summer 2009 for a total of 240 seedlings. The below-ground part was carefully excavated by hand taking care to recover most of the fine-roots. Annual height growth of each seedling was measured by measuring distance between bud scars of each year along the stem. On each seedling we measured specific traits (*e.i.,* physiological, morphological and allocational) in order to have a proxy to distinguish their differences in their performance.

For morphology measurements, crown architecture was measured by taking its height and the 2 diagonals of the crown (*i.e.*, the widest and the narrowest) perpendicularly to one another. The leaf area of each seedling was taken with the LI-3000C Portable Area Meter and LI-3050C transparent belt conveyer accessory. The above measurements were all taken the same day as the seedlings were collected throughout the summer 2009. Throughout autumn 2009, each part (leaves, branches, stems, roots) of each seedling was separated, dried at 60°C and weighted. Leaf area ratio (LAR) was calculated by taking the leaf area and the total seedling weight to have a proxy of its light interception and conversion efficiency. For the biomass allocation measurements, leaf weight ratio (LWR) and root weight ratio (RWR) were calculated. For physiological measurements, leaf per mass area (LMA) of each seedling was calculated by taking the total leaf dried mass and the leaf area. Also, relative chlorophyll concentration of the leaves of each seedling was estimated using the SPAD-502 (Minolta, Osaka, Japan). This instrument gave the mean value of 6 to 9 leaves measured in each seedling which minimized the variance caused by the special heterogeneity of chlorophyll pigmentation (Guénette, 2003).

2.3.5 Data Analysis

2.3.5.1 Stand Characteristics

The relative and absolute seedling abundance (DBH < 1 cm) of both species based on the measurements taken from each micro-plot, were calculated the same way as in the previous study (See section 1.3.5.1. of chapter 1). Linear models (LM) were used to test for differences between the stand and soil characteristics within the canopy openings (CO) and soil treatments (ST) (Tab. 4 and 5). Dependant variables were seedling density (SeeD$_{AS}$, SeeD$_{FG}$) and relative seedling density (RelSeeD$_{AS}$) of 2006 and 2009, light availability and soil characteristics (Ca, P, Mg, pH) of 2007, 2008 and 2009.

2.3.5.2 Seedling Density of *A. saccharum* and *F. grandifolia*

Two-way analysis of variance (ANOVA) were used to independently test for interactions between SeeD$_{AS}$, SeeD$_{FG}$, RelSeeD$_{AS}$ and soil treatment (ST; NL; not limed and L; limed) and CO (UF, PC, CC). Tukey was used as a posteriori test when significant differences were shown. Since the experimental design was nested, where seedlings of both species were measured in the same sample plots/stand, a random effect parameter was added in order to maintain independence between observations. Pearson correlation coefficients were calculated to test for correlations between SeeD_{AS}, SeeD_{FG}, and $\text{RelSeeD}_{\text{AS}}$ and for the continuous soil data for Ca, Mg among the CO.

2.3.5.3 Annual Height Growth Rates of *A. saccharum* and *F. grandifolia*

ANOVA were employed to test for interactions between the 2009 annual height growth rate of AS and FG seedlings and ST among CO.

2.3.5.4 Estimates of *A. saccharum* and *F. grandifolia* Seedling Performance

ANOVA were employed to independently test for interactions between LMA, LAR, LWR, RWR, chlorophyll concentration and ST and CO. Tukey was used as a posteriori test when significant differences were shown.

For all analysis, log transformations were applied to dependant variables when needed to fit assumptions of normality. For all analyses, the R statistical software (2009) was used. Model outputs were considered significant at $\alpha = 0.05$.

2.4 Results

2.4.1 Stand Characteristics

In 2006, prior to treatment, BA_{Stand} was similar for each of the 6 combinations of CO and lime treatments (Tab. 4). There were no significant differences between BA_{FG}, among the 6 combinations, but BA_{AS} was significantly higher in CC than in PC whichever soil treatment (Tab. 4). In 2009, 3 years after application of the treatments, the proportion of BA for each species remained about the same among all of the 6 treatment combinations but BA of whole stand significantly decreased with increasing CO (Tab. 4). BA of AS did increase significantly from PC to CC, in 2009 (Tab. 4).

2.4.2 Soil Characteristics and Light Availability

2.4.2.1 Soil Characteristics

In 2007, CO had an impact on Mg levels where there were significantly higher in PC and CC than in UF (*F*-statistic, 5.6; *p*-value, 0.006) (Tab. 5). PC soils were significantly more acid than in the other two CO in 2007 (*F*-statistic, 5.5; *p*-value, 0.007) (Tab. 5). Ca only showed significantly higher concentrations after being limed in the CC (*F*-statistic, 11.13; *p*-value, 0.004) and only Mg showed significantly higher concentrations in PC after being limed (*F*-statistic, 10.64; *p*-value, 0.005). In 2008, CO treatments tended to keep Ca and Mg concentrations significantly higher in PC and CC than in UF (*F*-statistic, 3.6; *p*-value, 0.003 and *F*-statistic, 3.8; *p*-value, 0.002 respectively). It was only within PC that the pH was significantly less acid after it got limed (*F*-statistic, 4.6; *p*-value, 0.04). ST head to some concentrations differences in UF and PC for Ca and Mg (*F*-statistic, 4.4; *p*-value, 0.05 and *F*-statistic, 13.73; *p*-value, 0.002 respectively) whereas concentrations of Ca and Mg in UF were lower after being limed than in NL UF and the opposite happened in the PC. In 2009, soil nutrients (*i.e.,* Ca, Mg) in the A horizon, showed the expected results only in UF and PC. Indeed, UF had significantly higher concentrations of Mg after being limed (*F*-statistic, 8.2; *p*-value, 0.01)and PC had significantly higher concentrations of Ca and Mg after being limed as well (*F*-statistic, 199; *p*-value, 0.000 and *F*-statistic, 123.8; *p*-value, 0.000 respectively). Surprisingly, concentrations of P in UF significantly increased even though it wasn't an added nutrient in the process of liming (*F*-statistic, 13.05; *p*-value, 0.002). Except for Ca, all soil nutrients showed significant differences among some of the CO in horizon B (Tab. 5). Specifically, P concentrations were significantly lower in UF than in PC and CC in horizon B (*F*-statistic, 4.77; *p*-value, 0.01) (Tab. 5). Mg concentrations tended to be higher (at α=10%) in the CC than UF and PC in B horizon (*F*-statistic, 2.43; *p*-value, 0.09) (Tab. 5). Surprisingly, after ST, Ca and Mg concentrations were significantly lower in the CC (*F*-statistic, 13.09; *p*-value, 0.02 and *F*-statistic, 18.4; *p*-value, 0.000 respectively) and as expected higher for Mg in UF (*F*-statistic, 5.3; *p*-value, 0.03 respectively) (Tab.5). Again, P concentrations were significantly higher in UF even though it wasn't an added nutrient in the liming process (*F*-statistic, 7.7; *p*-value, 0.01) (Tab.5).

2.4.2.2 Light Availability Profile

As expected, light availability profile increased significantly as CO intensified. More light was passing through the canopy going from UF to PC to CC for all light profiles, except at 3m (Tab. 5).

2.4.3 Seedling Density of *A. saccharum* and *F. grandifolia* According to Canopy Opening (CO) and Soil Treatment (ST)

Before CO treatment in 2006, absolute AS seedling was significantly higher in UF than in CC and absolute FG seedling was significantly higher in PC than in CC (Tab. 4). ST did not have any effect on absolute seedling since it did not occur before year 2007. ST, CO and their interactions didn't show any clear pattern that indicated any interactive effects on SeeD$_{AS}$, SeeD$_{FG}$ in 2009 (Tab. 4) and RelSeeD$_{AS}$ in 2006 and 2009 (Fig. 9-10). All Pearson correlations showed no significant relationships between the same dependant variables and Ca and Mg nutrients among CO.

2.4.4 Annual Growth in Height of *A. saccharum* and *F. grandifolia* Seedlings

In 2009, there were no significant species differences for annual height growth in any of the combinations of CO and ST (Fig. 11). However, AS seedlings did have a significant enhancement of annual height growth under the combination of CC and L treatments (*F* ratio, 4.77; *p* value, 0.02). FG seedlings annual height growth tended to be positively enhanced by CO but no interaction was observed with lime treatment on FG annual height growth.

2.4.5 *A. saccharum* and *F. grandifolia* Seedlings Physiology and Morphology

For both species, leaf mass per area (LMA) significantly increased in response to CO but was not affected by the ST (Tab. 6). Consequently, there were no significant differences between the two species in all combinations of treatments. There was a significant increase of chlorophyll concentration in both species according to CO (Tab. 6). FG seedlings had higher chlorophyll concentration going from UF to CC whereas AS seedlings had higher chlorophyll concentration in CC compared to UF and PC (Tab. 6). Finally in UF, LWR was slightly higher for AS seedlings compared to FG seedlings (Tab. 6) but wasn't significant at $\alpha = 0.05$ (p value = 0.08). No differences among all treatments and species were found for leaf area ratio (LAR) and roots weight ratio (RWR).

2.5 Discussion

2.5.1 *A. saccharum* and *F. grandifolia* regeneration Dynamics in Relation to Canopy Opening (CO) and Soil Treatment (ST)

At the seedling stage, the mean absolute density of AS tended to be higher than FG density before and 3 years after treatments suggesting that canopy openings and/or liming did not dramatically changed seedling establishment and survival of both species. It is known that AS can maintain a massive seedling bank in the understory and has a greater fecundity and seed dispersal than FG does (Houle, 1992). More interestingly, in comparison with 2006, a severe canopy opening (*i.e.,* CC) combined with a liming treatment tended to enhance absolute AS seedling density more than in the other combination treatments, but it also enhanced the abundance of FG seedlings. This high FG abundance in CC may be related to root sprouting. FG root sprouts are known to have higher survival and growth rates than seedlings under any environmental conditions (Beaudet et al., 2007, 2008). Unfortunately we did not measure the abundance of FG root sprouts on our site, but they may be responsible for the large representation of this species at the seedling stage several years after clear cutting (Nyland 2006). Relatively, AS seedlings tended to be higher three years after CO and ST and could be explained by a good seed year for AS.

Nevertheless, excepted for limed plots, a better post cutting survival and/or recruitment from seedling stage occurred for FG leading to reinforcement in FG dominance in the sapling stage. No interaction effect was detected between liming and intensity of canopy opening (results not shown). Consequently, as for seedlings, liming tended to mitigate the observed increase of FG in the sapling stage but it did not dramatically affect the dynamics between the 2 species.

Forest liming has been used to address the issue of depleting soils from acidification or to increase the percentage of some key nutrients (*i.e.,* Ca, Mg, P) to help accelerate tree growth (Long, Horsley et al., 1997) especially in the AS and FG replacement in adult tree dynamics observed in the north-eastern forests of North-America (Moore et al., 2000; Moore and Ouimet, 2006; Delagrange, Nolet et al., 2007, 2009). We did see in our study the increase of Ca and Mg concentrations in limed treatment stands in year 2008 followed by a decrease as soon as in year 2009 suggesting that the liming effect is already decreasing after 3 years (Tab. 5). Long, Horsley et al. (1997) identified several factors that may explain the lack of effect of liming, especially on AS regeneration; i) Ca and Mg are not lacking at the study site (data 2006, Tab. 5), ii) the quantity of liming added was not sufficient, and iii) the time lapsed between responses and applications were too short. In regards to the first factor, nutrients were not abundant in our study; the sampled stands have been reported as having a low stock of bases elements. The second factor might have impacted our results but we doubt it is the case since we based our liming concentration (3t/ha) according to Moore and Ouimet (2006). In their study, an enhancement of health, growth and vigor on limed trees was reported for liming deposit of 2 t/ha and higher. Similar thresholds have also been observed in other studies (Stone et al., 1975; Lea et al., 1980; Long Horsley et al., 1997). At this point, there were no studies based on seedlings. As for the third factor, we doubt that the measurements were made before seedling and sapling responded to the liming, since the liming effect is already diminishing after 3 years. A meta-analysis using 26 studies of fertilization experiments on AS indicated that Ca fertilization and multiple-nutrient fertilization had significant positive effects on AS production (Vadeboncoeur, 2010). Some studies reported seeing liming effects lasting for a decade after treatment but for very high (up to 50 t/ha) lime deposits (Long, Horsley et al., 1997; Moore and Ouimet, 2006).

As a result, severe CO treatment enhanced the establishment and survival of AS seedlings, but this was also the case for FG. Surprisingly, a liming of 3t/ha did not favor AS, except slightly in the CC treatment. We suggest that on our site, the concentrations of Ca and Mg in the foliage of juveniles might have been close to optimal levels and probably didn't require a lot of Ca and Mg in the first place (Bélanger, N, pers. comm.) compared to what Long, Horsley et al. (1997) have suggested. Thus, planning of adding nutrients, especially in a technically reasonable amount, might not be as important at the seedling stage as expected from the literature. In regards to past and present studies, there is still no mention of any ideal liming concentration for optimal efficiency, which is evidently intimately dependent on the fertility status of each site. Furthermore, questions should be raised regarding how much fertilizer or liming should be added for optimal results without disrupting the whole ecosystem. Indeed, from an operational and ecological point of view, introducing more than 3t of lime per hectare will represent, in natural forests, a significant technical challenge and an important environmental issue (*e.g.*, nutritive imbalances in the ecosystem).

2.5.2 Growth Response of *A. saccharum* and *F. grandifolia* Seedlings to Canopy Opening (CO) and Soil Treatment (ST)

At the individual level, minor differences were found between AS and FG absolute seedling height growth in both treatment combinations. However, limed soils combined with severe canopy opening (*i.e.*, CC) significantly enhanced AS but not FG annual height growth. Furthermore, the annual height growth of FG seedlings was not affected by liming under any canopy openings, corroborating with Long, Horsley et al. (1997) study. The lack of response to liming treatments suggests that FG seedlings height growth was not limited by Ca or Mg, also agreeing with Long, Horsley et al. (1997) study. In all other treatment combinations, FG seedling annual height growth tended to be higher than AS height growth. This was also seen by Poulson and Platt (1996) in all height classes under conditions of shade and as well partial canopy openings (Beaudet et al., 1998; 2007; Takahashi and Lechowicz, 2008). Kobe, Likens et al. (2002) found that Ca additions increased AS seedlings growth but in our study, canopy openings were responsible for the main part of AS growth enhancement (Fig. 12). Light is the primary factor limiting the performance of AS seedling in the understory (Ricard, Messier et al., 2003) and is an important driver associated with regeneration processes (McClure et al. 2000).

Although it has been suggested that compared to AS, FG grows faster in the understory and slower in a gap (Canham, 1988; Poulson and Platt, 1996; McClure et al., 2000; Ricard et al., 2003), FG grew very well and tended to grow better than AS in any of the canopy openings. Several studies have suggested that AS would not outgrow FG root sprouts and that AS would never increase in dominance in the presence of FG root sprouts (Arii et Lechowicz, 2002 Beaudet 1999). However, we specifically selected natural seedlings to compare height growth between AS and FG. Thus, we would rather suggest that FG seedlings are capable to enhance their growth as light availability increases even under very high light levels (Fig. 12). This ability for FG to sustain growth under a closed canopy allows this species to produce larger seedlings and even a sapling bank in the understory. In contrast, AS rather produces a suppressed seedling bank under a closed canopy which is able to respond to openings (Canham, 1985; Delagrange, Nolet et al., 2009). However, when both species co-exists in the understory, the height advantage of FG (being in the sapling stage) allows this species to dominate even in the case of a canopy opening. Takahashi and Lechowicz (2008) reported that the trunk of FG is more plagiotropic which gives it the ability to capture more light by expanding its lateral branches in closed-canopy and it is more efficient in maximizing production in canopy gaps by growing vertically. The same study reported a higher relative height increase in the current-year leader shoot in canopy openings with FG compared to AS. All of these factors would prevent AS seedlings from outgrowing FG even though AS seedlings are thought to double their growth in gaps (Canham, 1985, 1988, Nolet et al., 2008a).

2.5.3 *A. saccharum* and *F. grandifolia* Seedling Physiological, Morphological and Allocational Performance

The ability of understory trees to acclimate to sudden changes regarding light transmission is highly linked to their growth and survival rate (Delagrange, Messier et al., 2004). We thus tried to determine which physiological and morphological processes made AS seedling height growth respond significantly to the combination of treatments. Unfortunately, we didn't find any comprehensive differences between the two species in their response to light increase or liming. Both species showed some changes in relation to light availability but changes were similar. Few studies found significant differences between AS and FG, suggesting that these two species have many functionality traits in common, making it difficult to find differences between the two. Poulson and Platt (1996) suspected that compromises are associated with architectural differences, by referring to a previous study that observed no differences in photosynthetic processes and leaf morphology (*i.e.,* specific leaf weight) between AS and FG seedlings (Jurik, 1986a; 1986b). Adding to these findings, we didn't find any significant differences between AS and FG seedlings in chlorophyll concentration or LMA, LAR and RWR. However, there was a slight difference (at $\alpha=10\%$) between the species according to CO for LWR and chlorophyll. AS seedlings allocate more biomass in leaves in UF than FG does, suggesting AS may be less effective than FG capturing and converting light to survive in a closed understory. For chlorophyll, concentrations were higher in FG than AS, but species differences disappeared under closed canopies. Comparing *Acer* species, Lei and Lechowicz (1990) found that juvenile AS seemed limited functionally under closed canopy by showing adult characteristics, such as high wood density as well as tougher, heavier but thinner leaves. Such characteristics were found to slow down AS growth (Lei and Lechowicz, 1990), possibly being one of the reasons for FG to overtop AS in the understory of closed canopy. Furthermore, AS seedlings responded significantly to CO by increasing their leaves thickness (*i.e.*, LMA), whereas FG didn't show any response. This increase in leaf thickness with increasing light availability is well known. First, it corresponds to an enhancement of photosynthetic capacity (per unit area) by producing more and denser cells (Poorter et al., 2009). Then, it also represents an investment in sclerenchyma tissues (Lei and Lechowicz, 1990) to avoid rupture from wind (Telweski, 1995) and against herbivores (Ennos, 1997). Therefore, we agree with Lei and Lechowicz's (1990) suggestion about AS being more shade-tolerant than a shade adapted species. However, considering the efficient response of AS leaves and the low response of FG ones, more differences were expected between the two species in terms of growth in more open area. This clearly suggests that differences in leaf response may be, at the crown or whole individual level, mitigated by other traits and constraints. Indeed, in an exercise to scale up carbon gain at the crown level, Beaudet, Messier et al., (2000) showed that FG seedlings have a higher integrated daily carbon gain than AS seedlings, even in gaps.

2.6 Conclusion

Overall, canopy opening treatment had a greater impact on the regeneration dynamics of *A. saccharum* (AS) and *F. grandifolia* (FG) than our 3t/ha liming treatment. However, no major shifts in the seedling and sapling density and height growth between the two shade-tolerant species were detected under any combination of treatment, even after large canopy openings (Fig. 12). Indeed, liming did not have any critical impact on the morphology and physiology of both species. Thus, at the juvenile stages, AS and FG are capable to efficiently tolerate shade but, their differential carbon gain allows FG to grow to the sapling stage and suppress AS individuals at the seedling stage. AS height growth and density responded positively to the combination of severe canopy opening and liming allowing this species to reach the same level of performance with FG (Fig. 12). We thus propose modifications to the Nolet et al. (2008a) model where no light threshold exists that will shift the regeneration success of AS over FG even on fertilized soils (Fig. 12). This reinforces the question of applying large amount of lime in natural forest because of its low and short term impact and because of operational and environmental issues.

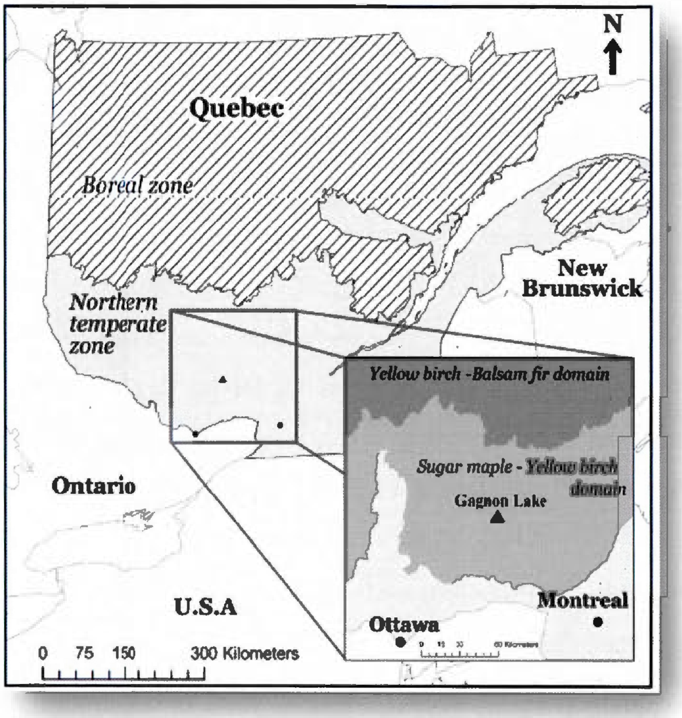

Figure 6: Study site North-East of Duhamel (Québec, Canada) near Gagnon Lake.

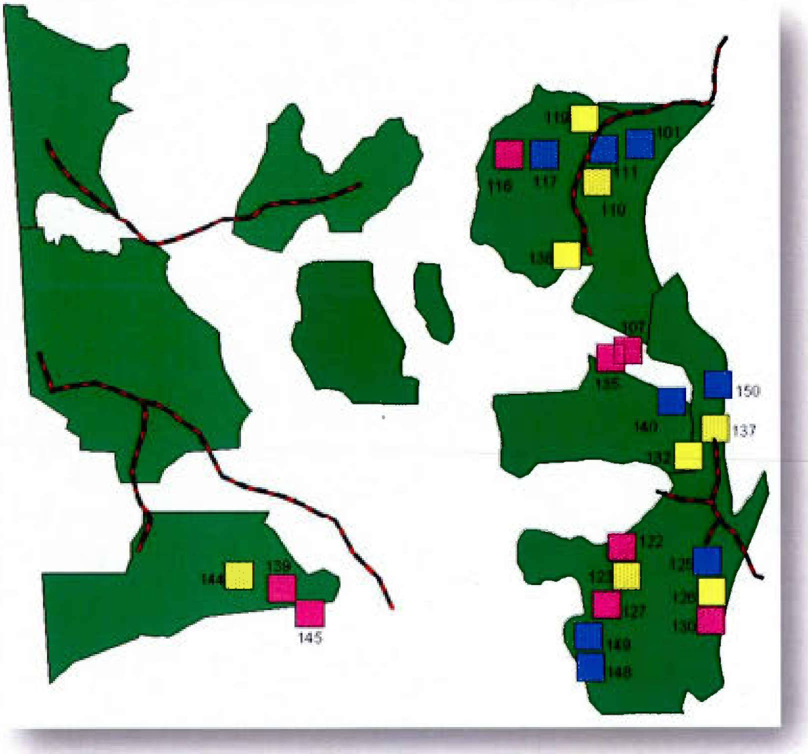

Figure 7: 24 study sites; pink squares represent unmanaged forests (UF), yellow squares represent partial cuts (PC) and blue squares represent clear cuts (CC). The black dots in 12 of the sites represent soil treatment (ST).

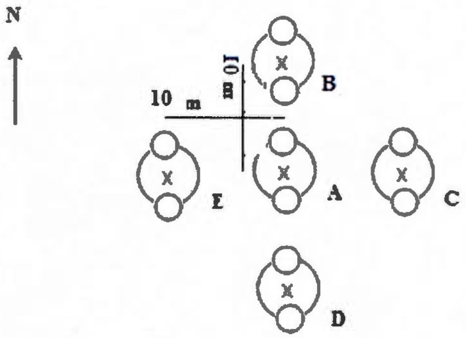

Figure 8: Sampling design representing all 5 sample plots (A, B, C, D, E) where x represents the center of the sample plots. At 2 m North and South of each sample plot were the micro-plots (r = 1.13 m) to count *A. saccharum* and *F. grandifolia* seedlings.

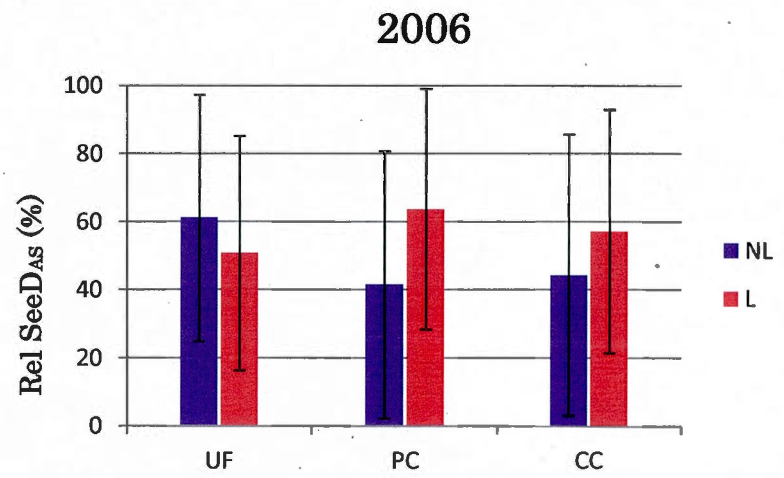

Figure 9: Relative seedling density (%) of *A. saccharum* (RelSeeD$_{AS}$) compared with *F. grandifolia* with standard deviation before soil treatment (ST; NL, not limed; L, limed) occurred in 2006 and according to canopy opening (CO; UF, PC, CC). See table 4 for abbreviations.

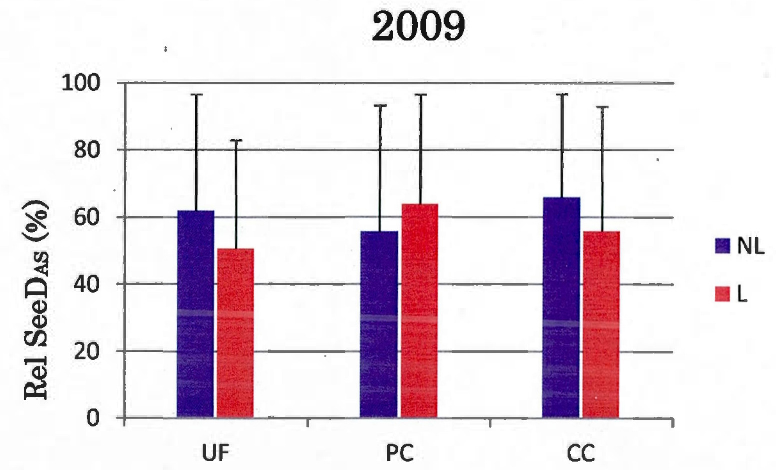

Figure 10: Relative seedling density (%) of *A. saccharum* (RelSeeD$_{AS}$) compared with *F. grandifolia* with standard deviation according to soil treatment (ST; NL, not limed; L, limed) and canopy opening (CO; UF, PC, CC), in 2009 (3yrs after treatments). See table 4 for abbreviations.

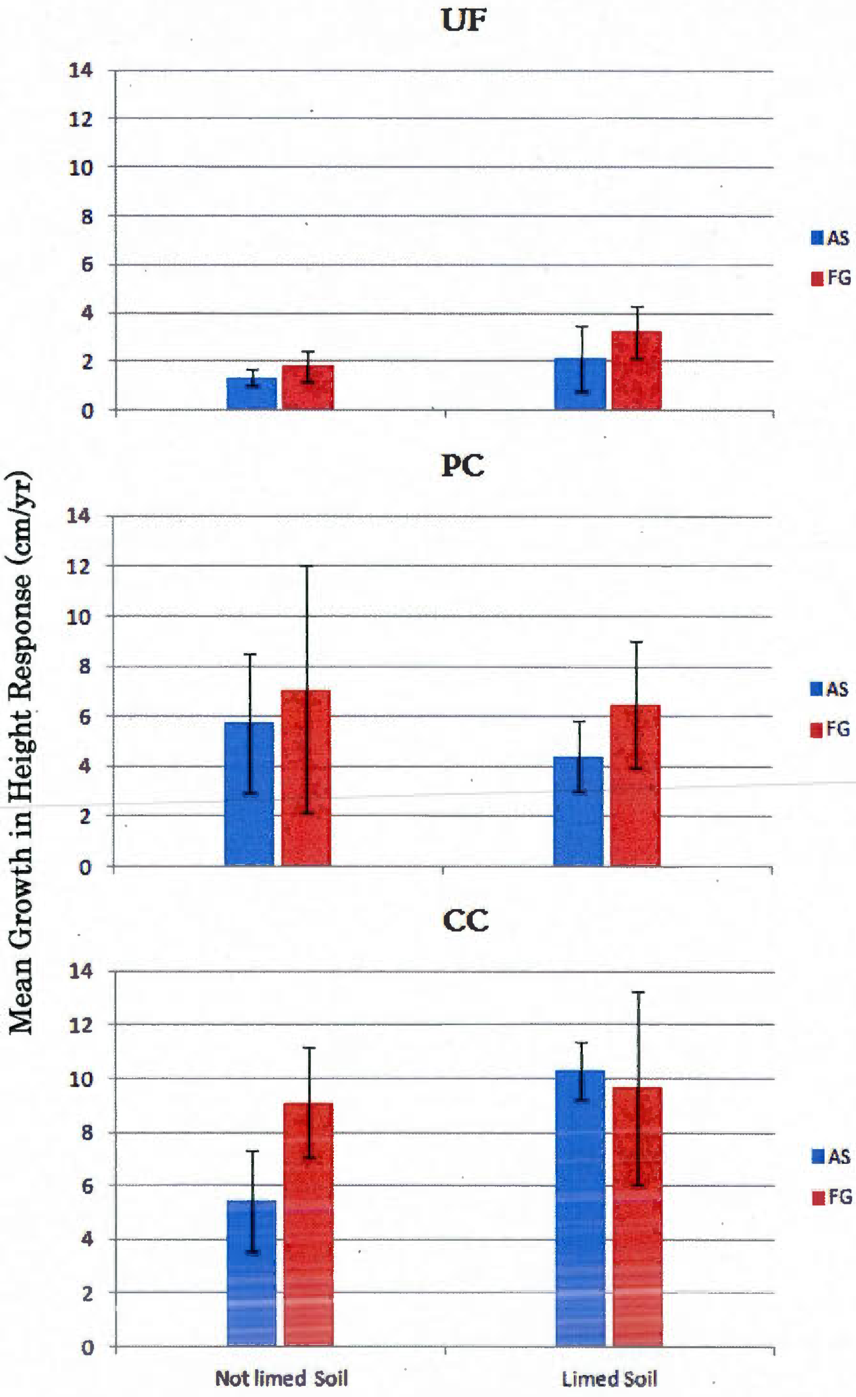

Figure 11: Mean annual growth response in height (cm/yr) of *A. saccharum* (blue) and *F. grandifolia* (red) seedlings in 2009 according to soil treatment (ST; NL and L) and canopy opening (CO; UF, PC, CC). See table 4 for abbreviations.

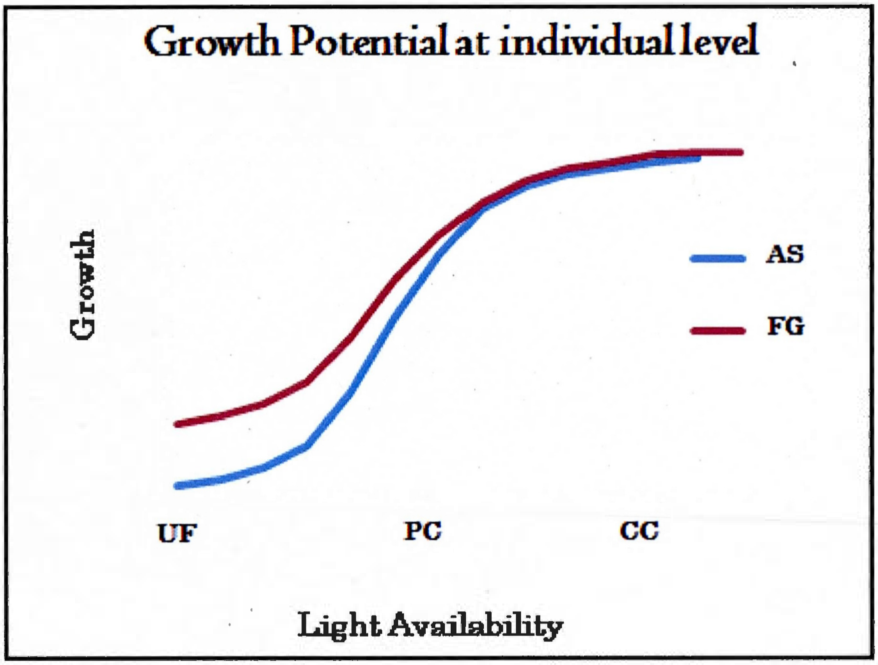

Figure 12: Model synthesis of the potential growth at the individual level of the seedling regeneration of AS (blue line) and of FG (red line) as in function of the light availability on poor soils.

Table 4: Characteristics of *A.saccharum* and *F.grandifolia* stands seedlings in stand composition according to canopy opening (CO).

Stand Characteristics*						
Treatment	UF - NL	UF -L	PC - NL	PC -L	CC - NL	CC-L
n	4	4	4	4	4	4
Canopy 2006						
BA$_{AS}$	45.7ab	53.7ab	36.5a	29.9a	52.8b	59.3b
BA$_{FG}$	40.1a	34.6a	49.5a	39.8a	35.1a	29.6a
BA$_{Stand}$	20.5a	19.2a	19.4a	21.0a	19.0a	20.2a
Canopy 2009						
BA$_{AS}$	43.8ab	54.8ab	35.5a	33.5a	66.4b	48.2b
BA$_{FG}$	37.2a	32.5a	45.2a	35.1a	20.0a	27.4a
BA$_{Stand}$	22.8a	21.3a	13.2b	17.3b	3.6c	2.1c
Seedlings 2006						
SeeD$_{AS}$	93000b	43500b	48500ab	58500ab	28750a	47250a
SeeD$_{FG}$	15750ab	32375ab	30125b	26500b	15875a	15250a
Seedlings 2009						
SeeD$_{AS}$	56375a	42500a	54313a	45938a	28438a	65938a
SeeD$_{FG}$	18000a	44938a	46563a	35875a	13063a	26438a

*Values of seedlings are the mean. Values within a row with different letters are significantly different at $\alpha = 0.05$ as in function of the canopy opening. ST effect was tested but didn't show any difference among all variables.

*Canopy opening; UF, unmanaged forest; PC, partial cut; CC, clear cut.

*Soil treatment; NL, not limed; L, limed.

*BA$_{AS}$, basal area of *A. saccharum*; BA$_{FG}$, basal area of *F.grandifolia* in percentage.

*SeeD$_{AS}$, *A. saccharum* seedling density; SeeD$_{FG}$, *F.grandifolia* seedling density.

Table 5: Soil Characteristics of A and B horizons and light availability (LA) profile as in function of the canopy opening and soil treatment.

*Soil Characteristics**

Treatments	UF:NL	UF:L	PC:NL	PC:L	CC:NL	CC:L
Horizon B 2007						
Ca (mg/kg)	639.7a	567.2a	658.9a	714.0a	597.3a(A)	937.2a(B)
P (mg/kg)	na	na	na	na	na	na
Mg (mg/kg)	75.1a	70.4a	74.0b(A)	98.5b(B)	88.8b	98.6b
pH	4.8a	4.9a	4.6b	4.5b	4.7a	4.8a
Horizon B 2008						
Ca (mg/kg)	758.4a(A)	453.9a(B)	407.2b(A)	1621.6b(B)	912.6b	1330.9b
P (mg/kg)	na	na	na	na	na	na
Mg (mg/kg)	126.3a(A)	75.8a(B)	80.2b(A)	217.2b(B)	165.4b	184.6b
pH	5.0a	4.9a	4.6a(A)	5.0a(B)	4.8a	4.9a
Horizon A 2009						
Ca (mg/kg)	2704.6a	2447.5a	722.2a(A)	4942.0a(B)	1631.0a	1794.5a
P (mg/kg)	14.1a(A)	44.5a(B)	42.4a	44.3a	63.3a	40.0a
Mg (mg/kg)	80.5a(A)	309.9a(B)	80.3a(A)	352.9a(B)	98.0a	144.9a
pH	na	na	na	na	na	na
Horizon B 2009						
Ca (mg/kg)	722.6a	306.3a	297.1a	425.1a	985.1a(A)	294.0a(B)
P (mg/kg)	3.6a(A)	10.4a(B)	14.3b	12.9b	51.5b	14.3b
Mg (mg/kg)	20.2a(A)	37.3a(A)	22.7ab	32.2ab	71.9b(A)	22.4b(B)
pH	4.6a	4.2a	4.0a	4.3a	4.1a	4.2a
Light Availability Profile 2009						
0.5 (m)	8.1a	7.9a	16.6b	11.4b	33.0c	33.6c
1 (m)	8.0a	9.3a	16.8b	10.9b	39.1c	41.5c
2 (m)	8.3a	9.0a	18.0b	12.7b	41.2c	49.3c
3 (m)	7.6a	10.1a	19.6a	11.6a	48.2c	99.3c

*Values are the mean. Values within a row with different letters (as in function of canopy opening: lower case; soil treatment: uppercase) are significantly different at $\alpha = 0.05$.

*Ca, calcium; P, phosphorus; Mg, magnesium.

*See table 4 for abbreviations.

Table 6: Summary of the ANOVA results testing the effect of canopy opening (CO: UF, PC, CC) and soil treatment (not limed and limed) on LAR, LMA, Chlorophyll, LWR and RWR of *A. saccharum* and *F. grandifolia* seedlings performance.

Variables*	Source**	df	Mean square	*F ratio*	*p*
LAR	None				
LMA	CO	2	2.61E-06	6.76	0.01
	Residuals	18	3.87E-07		
Chlorophyll	CO	2	0.052	4.73	0.02
	Residuals	18	0.01		
	CO x species	1	0.01	2.71	0.09
	Residuals	18	0.00		
LWR	CO x species	2	0.19	2.90	0.08
	Residuals	18	0.07		
RWR	none				

*LAR, leaf area ratio; LMA, leaf mass per area; LWR, leaf weight ratio and RWR, roots weight ratio.

**ST effect was tested but didn't show any difference among all variables.

Table 7: Summary of the physiological, morphological and allocational characteristics according to canopy opening (CO; UF, PC, CC) and soil treatment (ST; NL, L). Values are means (± SD).

Physiology and Morphology Characteristics*						
Treatments**	UF - NL	UF - L	PC - NL	PC - L	CC - NL	CC - L
LAR (cm2/g)						
AS	120 (± 48)	130 (± 48)	124 (± 26)	141 (± 42)	109 (± 30)	112 (± 16)
FG	161 (± 71)	171 (± 28)	129 (± 31)	131 (± 34)	114 (± 12)	126 (± 12)
LMA (g/m2)						
AS	31 (± 9)	28 (± 2)	36 (± 6)	33 (± 3)	40 (± 3)	41 (± 1)
FG	34 (± 12)	28 (± 3)	35 (± 7)	31 (± 4)	34 (± 3)	38 (± 2)
Chlorophyll (Spad unit)						
AS	26 (± 3)	28 (± 3)	25 (± 1)	25 (± 2)	26 (± 5)	30 (± 1)
FG	28 (± 2)	30 (± 1)	30 (± 2)	30 (± 2)	33 (± 3)	32 (± 2)
LWR (%)						
AS	19 (± 6)	22 (± 8)	30 (± 7)	31 (± 4)	25 (± 5)	28 (± 2)
FG	32 (± 14)	34 (± 18)	27 (± 11)	26 (± 3)	26 (± 13)	24 (± 4)
RWR (%)						
AS	49 (± 10)	44 (± 15)	40 (± 11)	40 (± 11)	40 (± 13)	51 (± 18)
FG	47 (± 12)	38 (± 14)	40 (± 11)	42 (± 8)	40 (± 13)	45 (± 13)

* For abbreviations see table 4 and 6.

2.7 References

Agriculture Canada. (1990). Pédo-paysages du Canada : Sud-ouest du Québec. Unité de cartographie et des systèmes d'information, Centre de recherche sur les terres, Direction générale de la recherche.

Arii, K. and J. Lechowicz, M (2002). "The influence of overstory trees and abiotic factors on the sapling community in an old-growth Fagus-Acer forest." Écoscience **9**(3): 386-396.

Bailey, S. W., B. Horsley, S, et al. (2004). "Influence of Edaphic Factors on Sugar Maple Nutrition and Health on the Allegheny Plateau." Soil Sci. Soc. Am. J. **68**: 243-252.

Beaudet, M. and C. Messier. (2008). "Beech regeneration of seed and root sucker origin: A comparison of morphology, growth, survival, and response to defoliation." Forest Ecology and Management **255**: 3659-3666.

Beaudet, M., J. Brisson, et al. (2007). "Effect of a major canopy disturbance on the coexistence of Acer saccharum and Fagus grandifolia in the understorey of an old-growth forest." Journal of Ecology **95**(3): 458-467.

Beaudet, M., C. Messier, et al. (2000). "Leaf- and plant-level carbon gain in yellow birch, sugar maple, and beech seedlings from contrasting forest light environments." Can. J. For. Res. 30: 390–404.

Beaudet, M., C. Messier, et al. (1999). "Possible mechanisms of sugar maple regeneration failure and replacement by beech in the Boisé-des-Muir old-growth forest, Québec." Écoscience 6(2): 264-271.

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

Canham, C. D. (1988). "Growth and Canopy Architecture of Shade-Tolerant Trees: Response to Canopy Gaps." Ecology **69**(3): 786-795.

Canham, D., C. (1985). "Suppression and release during canopy recruitement in Acer saccharum." Torrey Botanical Club 112(2): 134-145.

Delagrange, S., P. Nolet, et al. (2009). "Impact du dégagement et du chaulage sur la régénération en érable à sucre et en hêtre dans les érablières en voie d'hêtrisation soumis à différentes intensités de prélèvements du couvert. " IQAFF: 1-59.

Delagrange, S., P. Nolet, et al. (2007). "Impact du dégagement et du chaulage sur la régénération en érable à sucre et en hêtre dans les érablières en voie d'hêtrisation soumis à différentes intensités de prélèvements du couvert. Rapport de la phase II." IQAFF: 1-19.

Delagrange, S., C. Messier, et al. (2004). "Physiological, morphological and allocational plasticity in understory deciduous trees: importance of plant size and light availability." Tree Physiology 24: 775–784.

Dijkstra, A., F, and M. Smits, M, (2002). "Tree Species Effects on Calcium Cycling: The Role of Calcium Uptake in Deep Soils." Ecosystems 5: 385-398.

Doyon, F., D. Gravel, et al. (2003). L'envahissement par le hêtre dans les érablières de l'Outaouais: phénomène fantôme ou glissement de balancier? Rapport de l'Institut québécois d'aménagement de la forêt feuillue.

Duchesne, L., J. Moore, D, et al. (2008). "L'importance de la qualité de station pour l'aménagement des forêts feuillues." L'aubelle(153): 14-17.

Duchesne, L., J. Moore, D, et al. (2006). "Envahissement du hêtre dans les érablières dépérissantes au Québec." Le naturaliste canadien 130(1): 56-59.

Duchesne, L., R. Ouimet, et al. (2005). "Changes in structure and composition of maple–beech stands following sugar maple decline in Quebec, Canada." Forest Ecology and Management 208: 223–236.

Dyer, M., J (2001). "Using witness trees to assess forest change in southeastern Ohio." Can. J. For. Res. 31(10): 1708-1718.

Ennos, A. R. (1997). "Wind as an ecological factor." Trends in Ecology & Evolution 12(3): 108-111.

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

Guénette, C. (2003). Évaluation du potentiel de l'infrarouge spectral pour la détection hâtive du stress nutritif chez les végétaux de grandes cultures. Application à la culture de la pomme de terre. Maîtrise en sciences géomatiques. Faculté de foresterie et de géomatique. Université Laval.

Hamburg, P., S,, D. Yanai, R,, et al. (2003). "Biotic Control of Calcium Cycling in Northern Hardwood Forests: Acid Rain and Aging Forests." Ecosystems 6: 399-406.

Hane, N., E (2003). "Indirect effects of beech bark disease on sugar maple seedling survival." Can. J. For. Res. 33: 807–813.
Houle, G. (1992). "Spatial relationships between seed and seedling abundance and mortality in a deciduous forest of north-eastern North America." The Journal of Ecology 80(1): 99-108.

Horsley, S. B. (1994). "Regeneration Success and Plant Species Diversity of Allegheny Hardwood Stands After Roundup Application and Shelterwood Cutting." Northern Journal of Applied Forestry 11: 109-116.

Jurik, T. W. 1986a. Seasonal patterns of leaf photosynthetic capacity in successional northern hardwood tree species. American Journal of Botany 73:131-138.

____________1986b. Temporal and spatial patterns of specific leaf weight in successional northern hardwood species. American Journal of Botany 73:1083-1092.

Kelty, M. J. and R. D. Nyland (1981). "Regenerating Adirondack Northern Hardwoods By Shelterwood Cutting and Control of Deer Density." Journal of Forestry 79: 22-26.

Kobe, K., Richard, E. Likens, Gene, et al. (2002). "Tree seedling growth and mortality responses to manipulations of calcium and aluminum in a northern hardwood forest." Can. J. For. Res.: 954-966.

Kobe, K., Richard, S. Pacala, W, et al. (1995). "Juvenile tree survivorship as as component of shade tolerance." Ecological Applications 5(2): 517-532.

Kobe, R. K. (1996). "Intraspecific Variation in Sapling Mortality and Growth Predicts Geographic Variation in Forest Composition." Ecological Monographs 66(2): 181-201.

Lea, R., W. Tierson, et al. (1980). "Differential foliar responses of northern hardwoods to fertilization." Plant and Soil 54(3): 419-439.

Lei, T. T. and M. J. Lechowicz (1990). "Shade adaptation and shade tolerance in saplings of three Acer species from eastern North America." Oecologia: 224-228.

Long, P., R, B. Horsley, S, et al. (1997). "Impact of forest liming on growth and crown vigor of sugar maple and associated hardwoods." Can. J. For. Res. 27: 1560-1573.

Moore, J.-D. and R. Ouimet (2006). "Ten-year effect of dolomitic lime on the nutrition, crown vigor, and growth of sugar maple." Can. J. For. Res. 36: 1834–1841.
Moore, J., D, C. Camiré, et al. (2000). "Effects of liming on the nutrition, vigor, and growth of sugar maple at the Lake Clair Watershed, Québec, Canada." Can. J. For. Res. 30: 725–732.

McClure, J. W., T. D. Lee, et al. (2000). "Gap capture in northern hardwoods: patterns of establishment and height growth in four species." Forest Ecology and Management 127(1-3): 181-189.

MRNF. (2003). Zones de végétation et domaines bioclimatiques du Québec. Gouv. Du Québec. Dans:
http://www.mrnfp.gouv.qc.ca/forets/connaissances/connaissances-inventaire-zones.jsp

Nolet, P., D. Bouffard, et al. (2008). "Relationship between canopy disturbance history and current sapling density of Fagus grandifolia and Acer saccharum in a northern hardwood landscape." Canadian Journal of Forest Research 38: 216-225.

Nyland, D., R, A. Bashant, L, et al. (2006). "Interference to Hardwood Regeneration in Northeastern North America: Controlling Effects of American Beech, Striped Maple, and Hobblebush." North. J. Appl. For 23(2): 122–132.

Ordre des ingénieurs forestiers du Québec. 2009. Manuel de foresterie, 2ème éd, ouvrage collectif, éditions Multimondes, Qc. 1544 p. + 32 p. coul.

Poorter, H., Ü. Niinemets, et al. (2009). "Causes and consequences of variation in leaf mass per area (LMA): a meta-analysis." New Phytologist 182(3): 565-588.

Poulson, L., T and J. Platt, W (1996). "Replacement Patterns of Beech and Sugar Maple in Warren Woods, Michigan." Ecology 77(4): 1234-1253.

Ray, D. G., Nyland, R. D. et al. (1999). "Patterns of early cohort development following shelterwood cutting in three Adirondack northern hardwood stands." Forest Ecology and Management 119(1-3): 1-11.

Ricard, J., C. Messier, et al. (2003). "Do understory sapling respond to both light and below-ground competition?: a field experiment in a north-eastern American hardwood forest and a literature review." Ann. For. Sci. 60: 749–756.

Robitaille, A., Saucier, J-P. (1998). Paysages régionaux du Québec méridional. Publications du Québec, Sainte-Foy, Québec.

Stone, M., D and R. Christenson, D. (1975). "Effects of Thinning and Fertilization on Foliar Nutrient Concentrations of Sugar Maple." Canadian Journal of Forest Research 5(3): 410-413.

Takahashi, K. and J. Lechowicz, M (2008). "Do Interspecific Differences in Sapling Growth Traits Contribute to the Co-dominance of Acer saccharum and Fagus grandifolia?" Annals of Botany 101: 103-109.

Telewski, F.W. (1995) Wind-induced physiological and developmental responses in trees, in Wind and Trees. Cambridge University Press, Pp. 237-263 in http://books.google.ca/.

Vadeboncoeur, A. M. (2010). "Meta-analysis of fertilization experiments indicates multiple limiting nutrients in northeastern deciduous forests." Can. J. Bot. 40: 1766-1780.

CONCLUSION GÉNÉRALE

Cette étude avait pour but principal de déterminer quelles étaient les conditions environnementales, produites par un large spectre d'ouvertures du couvert réalisées sur un gradient de fertilité des sols, qui favorisent la régénération de l'érable à sucre (AS : *Acer saccharum*) et celle du hêtre à grandes feuilles (FG : *Fagus grandifolia*). Pour ce faire, deux études menées en parallèle ont été conduites dans la région de l'Outaouais. La première visait à suivre l'état de la régénération des gaules d'AS et de FG dans des peuplements ayant subis des coupes partielles et des coupes totales ainsi que dans des peuplements n'ayant subi aucun traitement sylvicole connu. Tous les peuplements ont été sélectionnés à travers un gradient de fertilité des sols et lorsque la présence des 2 espèces dans la régénération était avérée. La deuxième étude, exécutée dans un contexte semi-contrôlée, visait à mieux comprendre la performance des semis et gaulis de ces 2 mêmes espèces, après 3 ans, suite à un gradient d'ouverture de la canopée et un traitement de chaulage de 3 t effectué en 2007 après la réalisation des travaux sylvicoles.

Pour la première étude, il a été observé qu'il existait une très faible variabilité de fertilité de sol au sein des peuplements où la présence des espèces était avérée dans la régénération. Ainsi, toutes les érablières ayant une présence de hêtre possédaient une fertilité faible (Obj. 1). De plus, un régime différent de perturbations pourrait avoir un impact majeur sur la dynamique de régénération de *A. saccharum* (AS) et *F. grandifolia* (FG) sur ces sols pauvres (Obj. 2). D'abord, les résultats ont montré que seule une ouverture sévère du couvert (coupe totale) permettait aux gaules d'AS de rester compétitives en termes de croissance avec la régénération de FG (Obj. 3). De façon surprenante, la croissance des gaules de FG a donc bien su s'acclimater, même au sein des coupes totales (Obj. 4). En termes de densité, il semble que lorsque le territoire a subi des perturbations de nature anthropiques d'intensité partielle, le FG a une opportunité supérieure à AS de s'installer dans la canopée alors que sa proportion reste égale à AS lorsque la perturbation s'intensifie (*i.e.*, coupe totale) (Obj. 1). En ce qui concerne la composition des cohortes de gaules issues de ces peuplements, il semblerait qu'une fois le couvert refermé, peu de facteurs influence la présence de FG. Ainsi, ni la composition de la canopée, ni l'historique de perturbation, ni la fertilité des sols n'a eu d'influence sur la dominance du FG par rapport à AS lorsque les 2 espèces étaient présentes (Obj. 1-2). Il n'a donc pas été démontré qu'un renversement pouvait exister dans la dynamique de régénération entre les deux espèces en fonction d'un gradient d'ouverture de la canopée et de richesse nutritionnelle du sol. Ce type de perturbation, comparativement aux perturbations partielles, permettrait une accélération dans la croissance des deux espèces en leur conférant une compétitivité équivalente. À l'inverse, dans un régime de perturbation partielle, la compétitivité du FG s'avère supérieure à celle d'AS mais ces perturbations concernent une portion plus restreinte de la superficie du peuplement. Dans l'ensemble, la fertilité des sols des peuplements échantillonnés était faible et si cela nous permet de suggérer que l'envahissement en Outaouais se concentre actuellement sur les sites plus pauvres, il nous est impossible de conclure si la dynamique observée ici entre AS et FG serait la même sur sols plus fertiles.

Dans la deuxième étude, on rapporte des résultats similaires à l'échelle des semis, c'est-à-dire qu'une perturbation sévère de la canopée à permis une bonne réponse de AS en terme de croissance (permettant une compétitivité équivalente à FG), mais pas à un inversement entre la performance des 2 espèces (Obj. 7). Encore une fois, FG a montré une acclimatation efficace peu importe les conditions environnementales. De plus, aucun changement dans la dominance au niveau de la régénération n'a été observé entre les deux espèces en réponse à l'ouverture ou au chaulage (Obj. 4). Ainsi il semble clair que malgré une ouverture sévère et/ou un chaulage, AS tend à dominer la basse régénération alors que FG tend à dominer la haute régénération. Notre étude conclue également qu'il existe très peu de différences, à taille égale, en terme morphologique et physiologique entre AS et FG ce qui laisse supposer des tolérances à l'ombre relativement similaires entre les 2 espèces (mais une gestion et allocation de carbone potentiellement très différente) (Obj. 6). Un résultat particulièrement intéressant de notre étude réside dans le fait que 3 ans après un chaulage de 3t/ha, peu d'effet sur la croissance, la physiologie, la morphologie et l'établissement d'AS sont répertoriés (Obj. 5-6). Seule la perturbation sévère (*i.e.,* CC) combinée avec des sols chaulés ont permis une croissance significativement meilleure en hauteur chez les semis de AS (Obj. 5). Contrairement à ce que l'on aurait cru, l'addition de Ca et de Mg dans les sols aurait eu très peu d'influence sur la performance globale des semis d'espèces tolérantes à l'ombre comme AS et FG, et envisager des dépôts en quantités supérieures afin d'en voir les effets serait très questionnable en terme opérationnel et environnemental.

Ces résultats ont de sérieuses conséquences face à l'aménagement des forêts et plus particulièrement pour la silviculture des érablières qui sont établies sur des sols pauvres. En effet, sur ces sols, plusieurs problèmes pourraient s'intensifier (*i.e.,* le dépérissement généralisé, une hausse de mortalité, une diminution de la densité et du recrutement de AS, etc.) et mèneraient à une modification importante de la composition de ces peuplements. De plus, il semble être extrêmement difficile sur ces sols pauvres d'initier un revirement de situation où AS montrerait une compétitivité significativement supérieure à celle de FG. Ceci soulève d'ailleurs un questionnement important sur le temps, l'argent et les efforts à investir dans les peuplements de faible productivité afin de maintenir la dominance de AS.

Compte tenu des recherches qui ont été conduites sur AS et FG par plusieurs auteurs, une revue de la littérature devrait avoir lieu afin de rassembler tous les aspects importants qui ont été trouvés face à leur autoécologie, leur coexistence, leur régénération dans le but de mieux cibler et diriger de futures recherches. L'un des points importants de cette étude est la capacité du FG de pouvoir produire une banque de gaules alors que AS demeure au stade semis, dans les mêmes conditions environnementales. Il serait important de pousser les recherches dans la compréhension de cette différence fondamentale. Des recherches additionnelles devraient se porter sur le modèle de Nolet et al. (2008a) afin de valider les scénarios sur sols plus riches et donc à plus grande productivité. Ce modèle devrait être étudié dans plusieurs régions puisque la coexistence entre AS et FG pourrait varier topographiquement. De plus, afin de pouvoir réellement discerner des différences au niveau physiologiques et morphologiques, nous croyons que des études devraient être conduites sur la gestion des réserves et sur des individus plus âgés (*i.e.*, gaules) et cela en fonction de la disponibilité en lumière et de la fertilité des sols.

RÉFÉRENCES

Adams, M. C, et al. (1992). Fine-root growth and chemical composition in declining central Ontario sugar maple stands. Ottawa, ON, CANADA, National Research Council of Canada.

Arii, K. and J. Lechowicz, M (2002). "The influence of overstory trees and abiotic factors on the sapling community in an old-growth Fagus-Acer forest." Écoscience 9(3): 386-396.

Beaudet, M. and C. Messier (2008). "Beech regeneration of seed and root sucker origin: A comparison of morphology, growth, survival, and response to defoliation." Forest Ecology and Management 255: 3659-3666.

Beaudet, M., C. Messier, et al. (2000). "Leaf- and plant-level carbon gain in yellow birch, sugar maple, and beech seedlings from contrasting forest light environments." Can. J. For. Res. 30: 390–404.

Beaudet, M., C. Messier, et al. (1999). "Possible mechanisms of sugar maple regeneration failure and replacement by beech in the Boisé-des-Muir old-growth forest, Québec." Écoscience 6(2): 264-271.

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

Bohn, K. K. and R. D. Nyland (2003). "Forecasting development of understory American beech after partial cutting in uneven-aged northern hardwood stands." Forest Ecology and Management 180(1-3): 453-461.

Bouffard, D., F. Doyon, et al. (2003). "Historique et dynamisme écologique de la végétation forestière de la réserve faunique Rouge- Matawin de 1930 à nos jours." Rapport volet II. IQAFF 1-122

Bouliane, A. (1969). "Étude de la transformation de l'érablière à sucre en hêtraie." Mémoire demaîtrise, Faculté de foresterie et de géodésie de l'Université Laval, Québec. 77 p.

Brisson, J. (2001). "Neighborhood competition and crown asymmetry in Acer saccharum." Can. J. For. Res. 31: 2151-2159.

Brisson, J., Y. Bergeron, et al. (1994). "Beech-maple dynamics in an old-growth forest in southern Quebec, Canada." Écoscience 1(1): 40-46.

Canham, D., C. (1990). "Suppression and release during canopy recruitment in Fagus grandifolia." Bulletin of the Torrey Botanical Club 117(1): 1-7.

Canham, D., C. (1988). "Growth and Canopy Architecture of Shade-Tolerant Trees: Response to Canopy Gaps." Ecology 69(3): 786-795.

Canham, D., C. (1985). "Suppression and release during canopy recruitement in Acer saccharum." Torrey Botanical Club 112(2): 134-145.

Canham, D., C, A. Finzi, C, et al. (1994). "Causes and consequences of resource heterogeneity in forests: Interspecific variation in light transmission by canopy trees." Can. J. For. Res. 24: 337-349.

Côté, B. and J. W. Fyles (1993). "Nutrient concentration and acid–base status of leaf litter of tree species characteristic of the hardwood forest of southern Quebec. ." Can. J. For. Res. 24: 192–196.

Delagrange, S., P. Nolet, et al. (2007). "Impact du dégagement et du chaulage sur la régénération en érable à sucre et en hêtre dans les érablières en voie d'hêtrisation soumis à différentes intensités de prélèvements du couvert. Rapport de la phase II." IQAFF: 1-19.

Delagrange, S., C. Messier, et al. (2004). "Physiological, morphological and allocational plasticity in understory deciduous trees: importance of plant size and light availability." Tree Physiology 24: 775–784.

Duchesne, L. and R. Ouimet (2011). "Reply to comment by Messier et al. on "Present-day expansion of American beech in northeastern hardwood forests: Does soil base status matter?"." Can. J. For. Res. 41: 654-659.

Duchesne, L. and R. Ouimet (2009). "Present-day expansion of American beech in northeasthern hardwood forests: Does soil base status matter?" Can. J. For. Res. 39: 2273-2282.

Duchesne, L., J. Moore, D, et al. (2008). "L'importance de la qualité de station pour l'aménagement des forêts feuillues." L'aubelle(153): 14-17

Duchesne, L., J. Moore, D, et al. (2006). "Envahissement du hêtre dans les érablières dépérissantes au Québec." Le naturaliste canadien 130(1): 56-59.

Duchesne, L., R. Ouimet, et al. (2005). "Changes in structure and composition of maple–beech stands following sugar maple decline in Que´bec, Canada." Forest Ecology and Management 208: 223–236.

Duchesne, L., R. Ouimet, et al. (2003). "Diminution de l'abondance de l'érable à sucre au profit du Hêtre à grandes feuilles. *Dans*: Les enjeux de biodiversité relatifs à la composition forestière." Ministère des Ressources naturelles, de la Faune et des Parcs: 191-200.

Duchesne, L., R. Ouimet, et al. (2002). "Basal Area Growth of Sugar Maple in Relation to Acid Deposition, Stand Health, and Soil Nutrients." J. Environ. Qual: 1676–1683.

Dyer, M., J (2001). "Using witness trees to assess forest change in southeastern Ohio." Can. J. For. Res. 31(10): 1708-1718.

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

Forget, E., P. Nolet, et al. (2007). "Ten-year response of northern hardwood stands to commercial selection cutting in southern Quebec, Canada." Forest Ecology and Management 242: 764–775.

Grubb, J. P. (1977). "The Maintenance of Species-Richness in Plant Communities: The Importance of the Regeneration Niche." Biol. Rev 52(4): 107-145.

Hane, N., E (2003). "Indirect effects of beech bark disease on sugar maple seedling survival." Can. J. For. Res. 33: 807–813.

Hane, N., E, P. Hamburg, S, et al. (2003). "Phytotoxicity of American beech leaf leachate to sugar maple seedlings in a greenhouse experiment." Can. J. For. Res. 33: 814–821.

Horsley, S. B. (1994). "Regeneration Success and Plant Species Diversity of Allegheny Hardwood Stands After Roundup Application and Shelterwood Cutting." Northern Journal of Applied Forestry 11: 109-116.

Horsley, S. B., R. P. Long, et al. (2002). "Health of Eastern North American Sugar Maple Forests and Factors Affecting Decline." Northern Journal of Applied Forestry 19: 34-44.

Houle, D., S. Tremblay, et al. (2007). "Foliar and wood chemistry of sugar maple along a gradient of soil acidity and stand health." Plant and Soil 300(1): 173-183.

Kelty, M. J. and R. D. Nyland (1981). "Regenerating Adirondack Northern Hardwoods By Shelterwood Cutting and Control of Deer Density." Journal of Forestry 79: 22-26.

Kobe, K., R, E. Likens, G, et al. (2002). "Tree seedling growth and mortality responses to manipulations of calcium and aluminum in a northern hardwood forest." Can. J. For. Res.: 954-966.

Kobe, K., Richard, S. Pacala, W, et al. (1995). "Juvenile tree survivorship as as component of shade tolerance." Ecological Applications 5(2): 517-532.

Lei, T. T. and M. J. Lechowicz (1990). "Shade adaptation and shade tolerance in saplings of three Acer species from eastern North America." Oecologia: 224-228.

Long, P., R, B. Horsley, S, et al. (1997). "Impact of forest liming on growth and crown vigor of sugar maple and associated hardwoods." Can. J. For. Res. 27: 1560-1573.

Messier, C., N. Bélanger, et al. (2011). "Comment on “Present-day expansion of American beech in northeastern hardwood forests: Does soil base status matter?”." Can. J. For. Res. (41): 1–5.

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

Moore, J., D, C. Camiré, et al. (2000). "Effects of liming on the nutrition, vigor, and growth of sugar maple at the Lake Clair Watershed, Québec, Canada." Can. J. For. Res. 30: 725–732.

Nolet, P., D. Bouffard, et al. (2008). "Relationship between canopy disturbance history and current sapling density of Fagus grandifolia and Acer saccharum in a northern hardwood landscape." Canadian Journal of Forest Research 38: 216-225.

Nolet, P., S. Delagrange, et al. (2008). "The successional status of sugar maple (Acer saccharum), revisited." Ann. For. Sci. 65: 208.

Nolet, P., E. Forget, et al. (2001). "Reconstitution historique du dynamisme du paysage forestier du bassin de La Lièvre au cours du 20ième siècle." IQAFF: 1-122.

Nyland, D., R, A. Bashant, L, et al. (2006). "Interference to Hardwood Regeneration in Northeastern North America: Controlling Effects of American Beech, Striped Maple, and Hobblebush." North. J. Appl. For 23(2): 122–132.

Oliver, D.C., Larson, B. C (1996). "Forest Stand Dynamics." John Willey and Sons, inc. Pages 546

Ouimet, R. and C. Camiré (1995). "Foliar deficiencies of sugar maple stands associated with soil cation imbalances in the Québec Appalachians." Can. J. Soil. Sci. 75: 169-175.

Pothier, D. (1996). "Accroissement d'une érablière à la suite de coupes d'éclaircie: résultats de 20 ans." Can. J. For. Res. 26: 543-549.

Poulson, L., T and J. Platt, W (1996). "Replacement Patterns of Beech and Sugar Maple in Warren Woods, Michigan." Ecology 77(4): 1234-1253.

Ray, D. G., R. D. Nyland, et al. (1999). "Patterns of early cohort development following shelterwood cutting in three Adirondack northern hardwood stands." Forest Ecology and Management 119(1-3): 1-11.

Ricard, J., C. Messier, et al. (2003). "Do understory sapling respond to both light and below-ground competition?: a field experiment in a north-eastern American hardwood forest and a literature review." Ann. For. Sci. 60: 749–756.

Vadeboncoeur, A. M. (2010). "Meta-analysis of fertilization experiments indicates multiple limiting nutrients in northeastern deciduous forests." Can. J. Bot. 40: 1766-1780.

Ward, R. T. (1961). "Some Aspects of Regeneration Habits of the American Beech." Ecology 42(4): 828-832.

Woods, D. K. (2008). "Living long by staying small: stem layering as an adaptive life-history trait in shade-tolerant tree seedlings." Can. J. For. Res. 38: 480-487.