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COMPÉTITION ET COEXISTENCE DE L'ÉRABLE À SUCRE ET DU BOULEAU JAUNE AU STADE JUVÉNILE

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COMME EXIGENCE PARTIELLE

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DODICK GASSER

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RÉSUMÉ

Cette thèse s'intéresse à la compétition et à la coexistence de l'érable à sucre et du bouleau jaune au stade juvénile. Cette thèse s'appuie sur deux modèles conceptuels pour examiner la coexistence de l'érable à sucre et du bouleau jaune : la fluctuation de l'habileté compétitive en fonction de la disponibilité des ressources (différentiation fondamentale des niches) ou la constance dans la performance relative de ces deux espèces (hiérarchie compétitive). J'ai testé ces deux théories selon les gradients les plus susceptibles de mettre en évidence une performance différente de ces deux espèces (taille de la trouée, disponibilité et répartition temporelle de la lumière, la fertilité du sol et la disponibilité en calcium échangeable). Cette thèse comprend trois chapitres.

Le premier chapitre s'intitule *« Effects of gap size, liming, and competition control on the density, growth and survival of sugar maple and yellow birch regeneration following selection cutting »*. L'objectif principal de cette étude est d'examiner comment la performance relative de l'érable à sucre et du bouleau jaune est affectée par la taille de la trouée, la teneur en calcium échangeable du sol et l'environnement compétitive de sous-bois. Une expérience sur le terrain a été établie dans une érablière à bouleau jaune selon un dispositif factoriel avec 12 combinaisons. Trois tailles d'ouverture du couvert ont été créées à l'automne 2006. Le chaulage et le contrôle de la végétation compétitive ont été appliqués selon deux niveaux : présence/ absence. La densité des semis et des gaulis fut déterminée en 2002. La croissance et la mortalité de 1500 individus de chaque espèce furent suivies pendant 36 mois à partir de l'automne 1999. Premièrement, nos résultats démontrent que l'érable à sucre et le bouleau jaune présentent deux stratégies de régénération différentes : la densité de l'érable à sucre est plus élevée que celle du bouleau jaune, tandis que le bouleau jaune se caractérise par une croissance en hauteur plus rapide. Les deux espèces présentent une survie comparable dans la plupart des traitements malgré leur différence de tolérance à l'ombre. Deuxièmement, nous concluons que le bouleau jaune apparaît plus compétitif que l'érable à sucre. De plus, la constance dans la croissance relative de ces deux espèces suggère une hiérarchie compétitive, malgré d'importantes variations de croissance en hauteur et des conditions environnementales contrastantes. Troisièmement, les réponses complexes et inattendues à la suite du chaulage indiquent la nécessité de mener des recherches sur la nutrition minérale et les exigences en calcium échangeable de l'érable à sucre et du bouleau jaune. Finalement, la végétation de sous-bois peut exercer un important effet compétitif sur la croissance du bouleau jaune notamment dans les trouées de taille moyenne et grande en diminuant la disponibilité de la lumière et du nitrate du sol dans les trouées de grande taille. Les effets de la taille de la trouée, du chaulage et du contrôle de la compétition sur le succès

de la régénération de ces deux espèces à haute valeur commerciale sont discutés, et des recommandations sylvicoles sont apportées.

Le deuxième chapitre s'intitule *« Effects of light quantity and variability and soil fertility on the relative competitive ability and dominance of sugar maple and yellow birch seedlings »*. L'objectif principal est de déterminer si un renversement dans l'ordre relatif des espèces évalué en terme d'habileté compétitive peut se produire en fonction du niveau de fertilité du sol, de la disponibilité de la lumière et de la distribution temporelle de la lumière. Les différences interspécifiques et les variations des traits fonctionnels en réponse aux changements de disponibilité de la ressource et à la variabilité de la ressource furent également étudiées pour comprendre leur contribution à l'habileté compétitive et à la dominance relative de ces deux espèces. Des semis d'érable à sucre et de bouleau jaune furent cultivés dans une serre pendant deux saisons de croissance selon un dispositif de série de remplacement le long d'un gradient de fertilité du sol et sous trois environnements lumineux contrastants. Nos résultats montrent que le bouleau jaune est plus compétitif que l'érable à sucre dans la plupart des conditions environnementales (à l'exception du niveau de fertilité du sol riche et de l'environnement lumineux "ombragé hétérogène"), mais l'intensité de la compétition interspécifique est minime, indiquant que la performance compétitive de ces deux espèces est approximativement du même ordre. L'habileté compétitive et la dominance relative ne change pas considérablement selon les conditions environnementales (à l'exception de l'environnement lumineux "ombragé hétérogène"), suggérant qu'il n'existe pas de différenciation des niches le long du gradient de fertilité du sol et de disponibilité de la lumière. L'érable à sucre est relativement plus dominant avec un régime de disponibilité de la lumière plus variable. Nous concluons que le résultat de la compétition interspécifique semble plus constant (hiérarchie compétitive), malgré des conditions environnementales contrastantes. Nos résultats sur les traits fonctionnels corroborent les deux stratégies de croissance contrastantes : la croissance de l'érable à sucre est plus conservatrice, tandis que la croissance du bouleau jaune est plus explosive. Finalement, le degré de similarité de l'habileté compétitive et la faible différence de dominance questionne l'importance de la compétition entre l'érable à sucre et le bouleau jaune pour l'explication de la régénération de ces deux espèces dans les érablières à bouleau jaune.

Le troisième chapitre s'intitule *« Do growth and survival determine the shade tolerance of sugar maple and yellow birch at the juvenile stage? »*. L'objectif principal du troisième chapitre est d'observer si les différences interspécifiques de croissance et de survie peuvent expliquer les différences de tolérance à l'ombre des semis et des jeunes gaulis d'érable à sucre et de bouleau jaune. Plus spécifiquement, les objectifs sont, premièrement, de discriminer les érables à sucre et les bouleaux jaunes morts et vivants selon leur taille, leur taux de croissance et la disponibilité en lumière; deuxièmement, de comparer la réponse de croissance de ces deux espèces à un gradient de disponibilité de la lumière; troisièmement, d'évaluer si la mortalité est principalement liée à une limitation de la croissance causée par de faibles niveaux de lumière; et quatrièmement, de déterminer si les individus de petite taille sont plus vulnérables à la mortalité. Nous avons utilisé le site d'étude et le dispositif expérimental du chapitre 1 car nous avions la possibilité d'étudier la réponse de la croissance

de l'érable à sucre et du bouleau jaune le long d'importants gradients de disponibilité de la lumière et de taille des individus. Par ailleurs, les données sur la croissance et la survie nous permettaient d'établir des relations entre le statut de l'individu (mort/ vivant), la disponibilité de la lumière reçue et les caractéristiques de croissance de l'individu. Premièrement, nos résultats démontrent que l'érable à sucre et le bouleau jaune ne se différencient pas selon leurs patrons de croissance et de survie le long du gradient de disponibilité de la lumière. Deuxièmement, le bouleau jaune semble plus compétitif que l'érable à sucre puisque le bouleau jaune présente un taux de croissance plus élevé que l'érable à sucre sous toutes les conditions de lumière, même pour des disponibilités très faibles. Finalement, les compromis entre le taux de croissance et la survie, et la taille de l'individu et le taux de croissance ne permettent pas d'expliquer clairement la différence de tolérance à l'ombre de ces deux espèces.

En conclusion, les résultats de cette thèse privilégient le modèle de la hiérarchie compétitive comme mécanisme explicatif de la coexistence de l'érable à sucre et du bouleau jaune. Le modèle de la hiérarchie compétitive est en accord avec la stratégie d'exploitation des espèces intolérantes à l'ombre et la stratégie de conservation des espèces tolérantes à l'ombre, la théorie successionnelle des niches, et le mécanisme de l'avantage de la colonisation. Le modèle de la hiérarchie compétitive fournit un outil simple, efficace et puissant pour prédire l'assemblage des espèces forestières.

Mots-clés : érable à sucre, bouleau jaune, régénération, trouée, lumière, sol.

INTRODUCTION

1. Les érablières à bouleau jaune

1.1 Localisation biogéographique

L'érable à sucre (*Acer saccharum* Marsh.) et le bouleau jaune (*Betula alleghaniensis* Britton) sont rencontrés dans une très grande variété de communautés forestières dans l'Est de l'Amérique du Nord (Erdmann 1990, Godman et al. 1990). L'érable à sucre y est dominant ou codominant, et il forme des peuplements purs et mélangés (Tirmenstein 1991). Le bouleau jaune est une espèce dominante, codominante ou une espèce importante dans des peuplements mélangés feuillus et mixtes; des peuplements presque purs de bouleau jaune existent seulement sur de fortes pentes à haute altitude (Sullivan 1994). L'érable à sucre et le bouleau jaune constituent les érablières à bouleau jaune rencontrées dans la région forestière de la pruche de l'Est, du pin blanc et des feuillus nordiques (*« Hemlock-white pine-northern hardwoods forest region »*) (Delcourt and Delcourt 2000), région située au nord de l'aire de répartition de ces deux espèces. Au Québec, les érablières à bouleau jaune sont principalement retrouvées dans le domaine bioclimatique de l'érablière à bouleau jaune, qui couvre une superficie d'environ 65 600 km^2, soit 4 % du territoire québécois. Elles sont également présentes dans l'étage inférieur de certains secteurs du domaine bioclimatique de la sapinière à bouleau jaune. On retrouve trois types d'érablières à bouleau jaune selon la position topographique et le drainage : l'érablière à bouleau jaune et à hêtre à grandes feuilles sur le haut de pente et le sommet, l'érablière à bouleau jaune typique sur le milieu de pente, et l'érablière à bouleau jaune et frêne noir dans les petites dépressions humides. Les érablières à bouleau jaune se situent dans les étages de végétation inférieur et moyen du domaine bioclimatique de l'érablière à bouleau jaune (Bérard and Côté 1996).

1.2 Composition

L'érable à sucre est l'espèce dominante à laquelle est associée le bouleau jaune en proportion variable. D'un point de vue sylvicole, un type forestier porte l'appellation d'érablière à bouleau jaune si les trois conditions suivantes sont respectées :

- la surface terrière du peuplement comprend plus 75 % de feuillus;

- la surface terrière de la partie feuillue est composée de 33 à 66 % par l'érable à sucre, seul ou avec l'érable rouge (en quantité moindre);

- la surface terrière du peuplement est constituée de 33 à 50 % de bouleau jaune (Saucier 1994).

La composition en espèce des érablières à bouleau jaune comprend également du hêtre à grandes feuilles (*Fagus grandifolia* Ehrh.) et certaines espèces conifériennes, telles que le sapin baumier (*Abies balsamea* (L.) Mill.), l'épinette rouge (*Picea rubens* Sarg.), l'épinette blanche (*Picea glauca* (Moench) Voss) et la pruche de l'Est (*Tsuga canadensis* (L.) Carrière). La strate arbustive est composée de semis de certaines espèces arborescentes (principalement l'érable à sucre), d'érable à épis (*Acer spicatum* Lam.), d'érable de Pennsylvanie (*Acer pensylvanicum* L.), de noisetier à long bec (*Corylus cornuta*), de sureau rouge (*Sambucus pubens*), de chèvrefeuille du Canada (*Lonicera canadensis*), de viorne à feuilles d'aulne (*Viburnum alnifolium* L.) et d'if du Canada (*Taxus Canadensis* Marsh.). Les érablières à bouleau jaune sont des communautés forestières de fin de succession (Delcourt and Delcourt 2000). L'érablière à bouleau jaune typique croît sur des dépôts de till de drainage modéré et sur des podzols humo-ferriques ou ferro-humiques recouverts d'un humus de type moder (Bérard and Côté 1996).

1.3 Dynamique forestière naturelle

Le régime de perturbations naturelles représentatif du domaine bioclimatique de l'érablière à bouleau jaune donne lieu à une dynamique de trouées (Bérard and Côté 1996). Un large gradient de taille des perturbations naturelles existe dans la forêt décidue du nord-est américain (Lorimer 1989, Seymour et al. 2002), mais les perturbations de faibles étendues sont les plus fréquentes (Runkle 1985, Lorimer 1989, Delcourt and Delcourt 2000, Seymour et al. 2002). Le temps écoulé entre deux perturbations catastrophiques (causant la destruction et le remplacement d'un peuplement entier) était généralement long ($\geq$1000 ans) (Lorimer 1989, Seymour et al. 2002). Bien que certains éléments suggèrent que les feux d'origine naturelle auraient pu être une perturbation relativement importante dans certains secteurs, l'historique des feux demeure peu documenté dans le domaine bioclimatique de l'érablière à bouleau jaune (Bérard and Côté 1996). Le chablis était la perturbation naturelle prédominante dans la forêt tempérée décidue de l'Est de l'Amérique du Nord (Delcourt and Delcourt 2000). La plupart des arbres meurent et sont remplacés individuellement ou par petits groupes. La mort d'un ou de plusieurs arbres peut être causée par différents facteurs agissant individuellement ou en interaction (Beaudet and Messier 1997). Les facteurs de mortalité sont par exemple, la sénescence, le bris de branches provoqué par le verglas, la défoliation du houppier par des insectes, les agents pathogènes et le phénomène de dépérissement. Le vent peut aussi provoquer le bris du tronc ou le déracinement d'arbres affaiblis par des agents pathogènes ou ayant un enracinement superficiel (Beaudet and Messier 1997, Seymour et al. 2002). La taille moyenne de l'ouverture du couvert forestier est petite avec une superficie de 53 m^2, et varie de 4 à 1135 m^2. L'intervalle de retour du régime de trouées est habituellement de l'ordre de 50 à 200 ans (Seymour et al. 2002). Dans une érablière à bouleau jaune au Québec, l'analyse dendrochronologique des patrons de surcimage et de détente a permis de déterminer que la dynamique de l'érablière a été contrôlée au cours des deux derniers siècles par de petites perturbations associées à une succession de chablis simples et multiples, chevauchants et de petite taille. La superficie des trouées variait de 9 à 385 m^2, la majorité des trouées mesurant moins de 200 m^2 (Payette et al. 1990). La formation périodique de trouées conduit à un peuplement de structure inéquienne (Lorimer 1989, Payette et al. 1990). La structure inéquienne de l'érablière à bouleau jaune

démontre la capacité de l'érable à sucre et du bouleau jaune à profiter des trouées pour se régénérer ou accélérer leur croissance (Bérard and Côté 1996). Le régime de trouées est aujourd'hui peu actif puisque les gros arbres ont été prélevés lors des coupes forestières (Bérard and Côté 1996).

1.4 Aménagement

Les érablières à bouleau jaune font l'objet d'utilisations très diverses telles que l'exploitation forestière, l'acériculture, les aires de récréation et de conservation. Ces différentes vocations du territoire reflètent l'attribution par la société, de valeurs économiques, sociales, culturelles et écologiques à ces écosystèmes forestiers. Les érablières à bouleau jaune sont exploitées depuis plus de 200 ans (Bérard and Côté 1996). Généralement, seules les tiges de plus fort diamètre et de meilleure qualité ont été récoltées. Ces coupes d'écrémage ont laissé des peuplements dégradés où la qualité des tiges est pauvre et/ou la surface terrière résiduelle est faible. Actuellement, l'utilisation de la régénération naturelle et la volonté de conserver la structure inéquienne des peuplements sont deux tendances observées en matière de gestion et d'aménagement forestier au Québec. L'importance accordée à la régénération naturelle s'est traduite par l'abandon des coupes à blanc qui ont été remplacées par les coupes avec protection de la régénération et des sols (CPRS). L'aménagement inéquienne s'est traduit par un certain essor de la coupe de jardinage (Beaudet and Messier 1997).

2. Effet des trouées sur la compétition pour les ressources, et sur la disponibilité et l'hétérogénéité des ressources et des conditions environnementales

2.1 Effet des trouées sur la compétition pour les ressources

La mort ou la chute de branches, d'un seul arbre ou d'un petit groupe d'arbres créent un "trou" dans le couvert forestier libérant ainsi de l'espace disponible pour la croissance (Oliver

and Larson 1990). Une trouée correspond à une ouverture temporaire dans la végétation qui se caractérise par une diminution de la compétition pour une certaine période de temps. Selon la nature de la compétition, une trouée peut se subdiviser en trois types d'ouverture :

- au niveau de la canopée qui réduit la compétition pour la lumière (*« Canopy gaps »*);

- au niveau du système racinaire qui diminue la compétition pour les ressources du sol (*« Root gaps »*);

- au niveau des tiges qui procure un espace pour l'établissement, la croissance et le développement des semis (*« Stem gaps »*) (Bullock 2000).

La formation d'une trouée influence donc la compétition pour les ressources (White and Jentsch 2001).

2.2 Effet des trouées sur l'hétérogénéité des ressources et des conditions environnementales

La formation d'une trouée influence grandement l'hétérogénéité spatiale et temporelle des ressources, des conditions environnementales et des signaux pour la croissance et le développement. L'hétérogénéité spatiale et temporelle d'une ressource ou d'un facteur environnemental peut être décrite selon sa quantité cumulative ou moyenne (disponibilité de la ressource); sa fréquence de distribution; la durée, le moment, l'étendue et la localisation de valeurs critiques (seuil de tolérance; par exemple, des extrêmes microclimatiques); sa variabilité; et sa simultanéité avec d'autres ressources ou facteurs (Bazzaz and Wayne 1994). En comparaison avec le sous-couvert, les ouvertures du couvert forestier créent des lits de germination variables (Payette et al. 1990), augmentent localement et temporairement la disponibilité des ressources et l'hétérogénéité environnementale, et modifient considérablement les conditions environnementales locales. Les trouées forment une mosaïque complexe de conditions environnementales (Collins et al. 1985, Payette et al. 1990, Bazzaz and Wayne 1994).

Par exemple, à la suite d'un chablis, différentes zones peuvent être reconnues :

- la zone où les racines de l'arbre sont exposées;
- la zone occupée par le tronc;
- la zone occupée par le houppier;
- et la zone non-perturbée.

Ces différentes zones se distinguent par la perturbation du sol, l'accumulation de biomasse en voie de décomposition, et la présence d'obstructions physiques à la croissance des semis.

La zone exposée des racines peut se subdiviser également en dépressions, plan vertical et monticules de terre. Ces zones sont différentes du point de vue de la température et de l'humidité du sol, et de l'intensité de la lumière (Bullock 2000).

La formation de trouées provoque un changement dans le microclimat. Malgré la diminution de la transpiration et de l'interception des précipitations, l'humidité du sol est plus faible dans les trouées que sous le couvert forestier (Linteau 1948, Walters and Reich 1997) ou est comparable entre les deux milieux (Mladenoff 1987, Finzi and Canham 2000). L'évaporation, la température moyenne de l'air et du sol et l'amplitude thermique sont plus élevées dans les trouées (Linteau 1948, Sipe and Bazzaz 1995).

Le régime de lumière est affecté par la formation d'une trouée tant du point de vue de la disponibilité, que de la répartition temporelle et spatiale, et de la qualité de la lumière reçue au niveau du sol (Messier and Bellefleur 1988, Messier 1994). La qualité de la lumière fait référence à sa composition spectrale et au type de lumière (lumière directe ou diffuse, transmise ou réfléchie). Par exemple, les trouées résultant de la coupe de jardinage par pied d'arbre reçoivent une disponibilité en lumière d'environ 17 % de la lumière incidente deux ans après l'intervention sylvicole (Beaudet and Messier 2002). Dans les trouées, il existe une très grande variabilité spatiale et verticale de la lumière au cours de la journée et des saisons (Canham et al. 1990) : par exemple, la partie ouest de la trouée est exposée le matin, tandis

que la partie est reçoit le soleil de l'après-midi. La durée moyenne de lumière directe augmente avec la taille de la trouée : par exemple, une trouée de 200 m^2 reçoit environ deux heures de lumière directe, alors qu'une trouée de 1000 m^2 en reçoit environ pendant 4 heures; le reste de la journée étant composé de lumière diffuse (Canham et al. 1990).

Les perturbations du couvert forestier interviennent également sur la fertilité des sols. Au-delà d'une taille minimale de perturbation, il devrait y avoir une augmentation temporaire de la disponibilité en éléments nutritifs à cause d'une réduction de la compétition et d'une augmentation de la décomposition et de la minéralisation de la matière organique. Des pertes en éléments nutritifs seraient éventuellement possibles (Vitousek 1985). Dans la réalité, on observe soit une diminution de la concentration en nitrate dans les trouées (Mladenoff 1987) ou aucune différence dans les concentrations d'ammonium et de nitrate entre les trouées et le couvert forestier (Walters and Reich 1997, Finzi and Canham 2000).

3. Régénération par trouée et stratégies de régénération de l'érable à sucre et du bouleau jaune

3.1 Régénération par trouée

À cause de la diminution de compétition et de l'augmentation de la disponibilité des ressources, une trouée offre une opportunité pour l'établissement et le recrutement des espèces forestières (Watt 1947, Pickett and White 1985, Bullock 2000). La perturbation initie ainsi une nouvelle cohorte d'individus si la perturbation est suffisamment sévère et étendue (Forcier 1975, Oliver and Larson 1990). La végétation forestière répond à l'ouverture du couvert forestier par une réorganisation de la végétation établie avant la perturbation et par l'établissement de la végétation à la suite de la perturbation. La réorganisation de la végétation comprend l'empiètement latéral des houppiers et des racines des arbres entourant la trouée, la production de branches épicormiques par les arbres non-endommagés entourant ou à l'intérieur de la trouée, la production de rejets de souches et de

drageons par les individus endommagés à l'intérieur de la trouée, et le dégagement de la régénération avancée de semis et de gaulis établis à l'intérieur de l'ouverture. Les graines dormantes et enfouies, et les graines dispersées germent (Marks 1974). Les petites trouées favorisent la réorganisation de la végétation établie avant la perturbation, notamment la régénération avancée des espèces tolérantes à l'ombre, tandis que les grandes trouées favorisent l'établissement de la végétation à la suite de la perturbation, notamment la colonisation des espèces intolérantes à l'ombre grâce à la germination des graines et le rejet de souches (McCarthy 2001, White and Jentsch 2001).

La création d'une trouée dans le couvert forestier initie un processus de succession. Deux modèles conceptuels décrivent la succession secondaire dans les forêts tempérées nordiques. Le modèle de Bormann et Likens (1979) établit une relation entre la dominance des espèces formant la régénération cinq ans après la perturbation et la taille de l'ouverture du couvert forestier : plus l'ouverture est importante, plus la régénération est composée d'espèces intolérantes, et vice et versa. Le modèle de Forcier (1975) représente la dynamique naturelle d'une érablière à bouleau jaune et à hêtre à grandes feuilles selon une microsuccession à la suite de la formation d'une trouée dans un couvert forestier dominé par le hêtre à grandes feuilles. Le bouleau jaune, espèce semi-tolérante, domine la régénération à la suite de la perturbation. Puis l'érable à sucre, espèce tolérante à l'ombre, remplace graduellement le bouleau jaune. Finalement, le hêtre à grandes feuilles, espèce très tolérante à l'ombre, domine la fin de la succession. Le remplacement des espèces se fait de façon cyclique dans le temps en fonction de leur tolérance à l'ombre. Dans les deux cas, le phénomène de tolérance à l'ombre apparaît comme le trait d'histoire de vie responsable du remplacement des espèces.

3.2 Stratégies de régénération de l'érable à sucre et du bouleau jaune

L'érable à sucre et le bouleau jaune présentent deux stratégies de régénération très différentes (Sutherland et al. 2000).

L'érable à sucre appartient à la guilde des « persistants » et au groupe des « tolérants de sous-bois à faible croissance » (Sutherland et al. 2000). L'érable à sucre se régénère par graines et végétativement par rejets (semis, gaulis, souche et racines) (Tirmenstein 1991, Sutherland et al. 2000, Anderson et al. 2001). L'érable à sucre présente de grosses graines avec des réserves en énergie suffisantes pour permettre l'établissement de semis à l'ombre. Les bonnes années semencières sont produites à intervalles réguliers et les lits de germination sont très variés. De larges cohortes de semis se mettent en place à la suite d'années semencières ou d'autres événements occasionnels (Sutherland et al. 2000). L'érable à sucre est une espèce très tolérante à l'ombre (Baker 1949, Barnes et al. 1998) puisque les semis peuvent survivre de longues périodes en conditions ombragées (Godman et al. 1990, Marks and Gardescu 1998, Sutherland et al. 2000). Cette tolérance à l'ombre permet le développement et le maintien en sous-bois d'une importante banque de semis et de gaulis à l'état opprimé à laquelle s'ajoutent les rejets de souche (Tirmenstein 1991, Sutherland et al. 2000). Toutefois, les semis et les gaulis d'érable à sucre conservent une très forte capacité de croissance leur permettant de répondre à une augmentation de la lumière à la suite de l'ouverture du couvert forestier (Canham 1985, 1988b, Payette et al. 1990), de dépasser les espèces compétitives et d'occuper rapidement la trouée (Tirmenstein 1991). L'érable à sucre peut ainsi tolérer plusieurs périodes de suppression avant d'atteindre la canopée (Canham 1985, Payette et al. 1990) et est donc recruté graduellement dans la canopée à la suite de la formation de petites trouées (Sutherland et al. 2000). La croissance radiale et en hauteur sont généralement assez faibles comparativement à celles des espèces compagnes (Godman et al. 1990, Sutherland et al. 2000). Finalement, l'érable à sucre présente plusieurs caractéristiques de la stratégie conservatrice (Bormann and Likens 1979). L'érable à sucre est qualifié de spécialiste des petites trouées (Canham 1988b).

Le bouleau jaune appartient à la guilde des « opportunistes » et au groupe des « semi-tolérants à longue longévité ». Le bouleau peut se régénérer à la suite de plusieurs types de perturbations (Sutherland et al. 2000). Le bouleau se régénère principalement par graines (Sullivan 1994) et rarement par rejets de souche (au stade de semis et de gaulis) (Erdmann 1990, Bazzaz and Wayne 1994, Anderson et al. 2001). Un ensemencement fréquent et une viabilité relativement longue des graines assurent que des graines sont continuellement

disponibles. Les grandes ouvertures de la canopée et la perturbation du sol favorisent la germination (Sutherland et al. 2000). Le bouleau jaune est une espèce semi-tolérante à l'ombre (Baker 1949) puisqu'il ne peut pas se régénérer sous une canopée fermée (Erdmann 1990). Il ne tolère pas les périodes de suppression (Payette et al. 1990) et très peu de régénération avancée est présente (Sullivan 1994, McClure et al. 2000). Il présente une capacité de croissance faible à moyenne après une période de suppression (Bérard and Côté 1996, Anderson et al. 2001). Le bouleau jaune doit rapidement devenir dominant pour survivre jusqu'à maturité (Beaudet and Messier 1997) et nécessite un niveau de lumière élevé et continu pour un recrutement dans la canopée. Le bouleau jaune est une des espèces présentant la croissance la plus rapide et est très compétitive lorsqu'elle domine la canopée (Sutherland et al. 2000). Sa stratégie de régénération est qualifiée d'opportuniste à cause d'une production abondante de petites graines (Sullivan 1994) et du patron de croissance des semis et des gaulis (Beaudet and Messier 1998). Le bouleau jaune est une composante majeure de la phase « régénération dans la trouée » dans les érablières à bouleau jaune et à hêtre à grandes feuilles (Erdmann 1990).

Les traits d'histoire de vie importants pour la reproduction sexuée sont présentés en annexe (appendice A).

4. Quels sont les mécanismes et les facteurs écologiques susceptibles d'expliquer la coexistence de l'érable à sucre et du bouleau jaune dans les érablières à bouleau jaune ?

Par définition, l'érable à sucre domine et le bouleau jaune codomine dans une érablière à bouleau jaune. L'érable à sucre est une espèce climacique ou de fin de succession (très tolérant à l'ombre) (Marks 1974, Tirmenstein 1991, Bazzaz and Wayne 1994, McLaughlin 2000). Par conséquent, il présente une fécondité, une dispersion et une croissance relativement plus faible, et une survie élevée dans des conditions pauvres en ressources (Rees et al. 2001). Le bouleau jaune est présent à tous les stades de la succession forestière (Erdmann 1990) et persiste même jusqu'en fin de succession (semi-tolérant à l'ombre)

(Marks 1974, Bazzaz and Wayne 1994, Sullivan 1994). Par conséquent, il présente une fécondité plus élevée, une dispersion plus étendue, une croissance plus rapide lorsque les ressources sont abondantes, et une survie relativement plus faible lorsque les ressources se font rares (Rees et al. 2001). Basé sur leur statut successionnel respectif, l'érable à sucre devrait graduellement exclure le bouleau jaune en absence de perturbations parce que l'érable à sucre réduit les ressources en-deça du niveau requis par le bouleau jaune (Iverson et al. 1999, Rees et al. 2001).

Actuellement, il n'existe pas de consensus définitif sur le(s) mécanismes et le(s) facteurs écologiques responsables de la coexistence de l'érable à sucre et du bouleau jaune.

4.1 Quels sont les mécanismes et les facteurs écologiques qui permettent au bouleau jaune de persister dans les érablières ?

Les mécanismes suivants ont été proposés pour expliquer au moins partiellement la persistance du bouleau jaune :

- L'hypothèse de la perturbation intermédiaire;
- L'hypothèse de la différentiation des espèces selon la taille de la trouée (*« The gap-size partitioning hypothesis »*) et la localisation à l'intérieur de la trouée;
- L'avantage de la colonisation et la théorie de la niche successionnelle.

4.1.1 L'hypothèse de la perturbation intermédiaire

Le régime de perturbations peut retarder l'exclusion compétitive du bouleau jaune par l'érable à sucre si la fréquence et l'intensité des perturbations conviennent car les perturbations créent des opportunités pour l'établissement et le recrutement. Un taux de perturbations élevé favorisera le bouleau jaune et un faible taux de perturbation permettra à la

compétition interspécifique d'évincer le bouleau jaune. Selon Payette et al. (1990), le régime de perturbations permet d'expliquer en partie la composition, la structure et la dynamique d'une vieille érablière à bouleau jaune. Woods (2000a, 2000b) a observé dans un peuplement de fin de succession un déclin et peu de régénération du bouleau jaune, mais peu de changement d'abondance pour les populations d'érables à sucre. Cette observation suggère que la persistance du bouleau jaune dépend de l'ouverture sporadique du couvert forestier.

4.1.2 L'hypothèse de la différentiation des espèces selon la taille de la trouée et la localisation à l'intérieur de la trouée

Si l'érable à sucre et le bouleau jaune sont deux espèces suffisamment spécialisées dans leur utilisation des ressources, le partage des ressources réduit la compétition interspécifique et permettrait leur coexistence (théorie de la différentiation fondamentale des niches) (Townsend et al. 2003). Puisque les arbres semblent occuper des niches similaires, la séparation des niches peut se limiter au stade de la régénération où de nombreuses différences interspécifiques sont possibles en terme d'exigences pour la régénération. L'érable à sucre et le bouleau jaune présenteraient des préférences pour des habitats différents, et donc une performance différente selon la taille de la trouée ou leur localisation dans la trouée. En d'autres termes, ces deux espèces auraient le potentiel de se partager le gradient de taille d'ouverture du couvert forestier.

La taille de l'ouverture du couvert forestier est généralement l'axe de différentiation le plus souvent évoqué (*« The « gap-size partitioning hypothesis »*). La taille de l'ouverture de la canopée est considérée être un élément important influençant la composition et l'abondance relative des espèces selon le niveau de tolérance à l'ombre (McCarthy 2001). Les espèces tolérantes à l'ombre survivent mieux dans les petites trouées (elles croissent dans toutes les tailles de trouées, mais présentent leur taux de croissance le plus élevé en pleine lumière). Les espèces intolérantes à l'ombre ne peuvent pas survivre longtemps dans les petites trouées, mais elles croissent plus vite que les espèces tolérantes dans les grandes trouées.

Une corrélation positive existe donc entre la taille minimale de l'ouverture nécessaire à leur survie et leur taux de croissance maximum (en pleine lumière) (White and Jentsch 2001). Les modèles conceptuels de Forcier (1975) et de Bormann et Likens (1979) reposent sur la différentiation des espèces forestières selon la taille de la trouée. L'érable à sucre est considéré comme un spécialiste des petites trouées (Canham 1988b), tandis que le bouleau jaune est qualifié d'espèce caractéristique de la régénération dans les trouées (Erdmann 1990). La coupe de jardinage par pied d'arbre permet la régénération d'espèces tolérantes à l'ombre, telles que l'érable à sucre, tandis que la coupe de jardinage par trouée favorise la régénération d'espèces semi-tolérantes, telles que le bouleau jaune (Leak and Filip 1977, Hornbeck and Leak 1992, Majcen 1995, Anderson et al. 2001).

Toutefois, certaines observations semblent contredire l'hypothèse de la différentiation des espèces forestières selon la taille de la trouée. Premièrement, Willis et Johnson (1978) ont observé que le degré d'ouverture du couvert forestier (par des coupes de jardinage de différentes intensités) avait peu d'effet sur la densité de semis de bouleau jaune. Deuxièmement, dans des érablières à bouleau jaune au New Hampshire, le suivi à long terme des coupes de jardinage de différentes superficies (324-2400 m^2) a permis de montrer que le bouleau est moins abondant dans la forêt mature que dans les trouées, tandis que l'érable à sucre est plus abondant dans la forêt mature que dans les trouées. Toutefois dans les trouées, l'abondance de l'érable à sucre et du bouleau jaune, exprimée soit en surface terrière ou en densité, ne présente pas de relations significatives ni avec la taille et ni avec l'âge des trouées (le bouleau jaune est relativement plus abondant au centre des trouées que sur les bordures, tandis que l'abondance de l'érable à sucre est indifférente à la localisation dans les trouées (McClure and Lee 1993). Troisièmement, la croissance et la survie de l'érable à sucre sont peu influencées par un gradient d'ouverture de la canopée (conditions ombragées de sous-bois, 75 m^2; 300 m^2) (Sipe and Bazzaz 1994). Busing et White (1997) ont observé peu de variations de l'abondance de l'érable à sucre et du bouleau jaune le long d'un gradient d'ouverture du couvert. Ces auteurs concluent que la différentiation des espèces selon la taille de la trouée est un mécanisme peu important. Les trouées fourniraient seulement une meilleure niche de régénération que le couvert forestier, car elles permettent une augmentation de la disponibilité des ressources.

Le manque de différentiation de l'érable à sucre et du bouleau jaune selon le degré d'ouverture de la canopée permettrait donc d'expliquer la coexistence de ces deux espèces selon la théorie de la neutralité (Brokaw and Busing 2000). Selon cette théorie, l'érable à sucre et le bouleau jaune auraient des exigences similaires pour la régénération, et le recrutement serait un processus stochastique. La création des trouées est imprévisible. De plus, l'abondance des graines et des semis présents dans la trouée varie grandement selon les aléas et les limites à la dispersion des graines et à l'établissement des semis dans l'espace et dans le temps (sans considération de l'effet des caractéristiques des trouées). À cause de la limitation du recrutement (c'est-à-dire l'échec pour une espèce de se régénérer dans tous les sites favorables à sa croissance et à sa survie), les trouées ne sont pas occupées par le meilleur compétiteur, mais par un ensemble d'espèces qui par chance étaient présentes au bon moment.

4.1.3 L'avantage de la colonisation et la théorie de la niche successionnelle

L'avantage de la colonisation repose sur le compromis entre la capacité de dispersion et l'habileté compétitive. La fécondité et la dispersion élevées des espèces de début de succession leur permettent de coloniser des sites récemment perturbés, avant que les espèces compétitrices de fin de succession arrivent.

La théorie de la niche successionnelle se définit par le compromis entre la croissance et la survie. Une croissance rapide dans des conditions de disponibilité élevée en ressources (lumière) permet aux espèces pionnières (intolérantes à l'ombre) de surpasser temporairement les espèces de fin de succession (tolérantes à l'ombre), même si les espèces de début et de fin de succession se retrouvent simultanément dans un site récemment perturbé. Par contre, les espèces pionnières ne peuvent pas survivre dans des conditions de faible lumière, contrairement aux espèces de fin de succession (Pacala and Rees 1998, Rees et al. 2001).

Selon Pacala et al. (1996), la co-dominance du bouleau jaune dans les peuplements en milieu et fin de succession est déterminée par la combinaison d'une croissance en hauteur relativement forte dans des conditions élevées de lumière, une croissance en hauteur rapide dans des conditions ombragées (observation inattendue si l'on considère son degré de tolérance à l'ombre) et une distance moyenne de dispersion des semences la plus grande. Ces caractéristiques devraient contribuer à la persistance du bouleau jaune dans les forêts surannées : la grande distance de dispersion des semences permet de coloniser des trouées et la croissance rapide à tous les niveaux de lumière permet de rattraper et de dépasser la régénération avancée d'espèces plus tolérantes à l'ombre, comme l'érable à sucre.

4.2 Quels sont les mécanismes et les facteurs écologiques qui permettent à l'érable à sucre de dominer dans les érablières ?

Plusieurs hypothèses sont généralement avancées pour expliquer la dominance de l'érable à sucre observée au niveau de la régénération, mais aussi par prolongement au niveau de la strate arborescente :

- La tolérance à l'ombre de l'érable à sucre et du bouleau jaune, et le rôle de la disponibilité de la lumière;
- La nature des lits de germination;
- L'inhibition allélopathique de l'érable à sucre envers le bouleau jaune;
- L'effet compétitif de la régénération avancée d'érable à sucre sur le bouleau jaune (Erdmann 1990);
- La susceptibilité à l'herbivorie du bouleau jaune.

4.2.1 La tolérance à l'ombre de l'érable à sucre et du bouleau jaune, et le rôle de la disponibilité de la lumière

La plus grande tolérance à l'ombre de l'érable à sucre lui permettrait de dominer le bouleau jaune (Forcier 1975). Une régénération avancée abondante d'érable à sucre est généralement présente en sous-couvert (Houle and Payette 1991a) et les semis d'érables à sucre (< 1 m) peuvent survivre plus de 30 ans dans des conditions ombragées (Marks and Gardescu 1998). Le bouleau jaune présente une régénération avancée plus ou moins abondante (Houle and Payette 1991a), mais sa régénération avancée est généralement inférieure à cinq ans (McClure et al. 2000).

L'érable à sucre et le bouleau jaune se différencieraient en fonction de leur environnement lumineux selon un compromis entre la croissance sous des conditions élevées de lumière et la survie sous de faibles conditions de lumière (théorie de la niche successionnelle) : le bouleau jaune présente un taux de croissance plus élevé que l'érable à sucre dans des conditions élevées de lumière, mais possiblement une survie plus faible que l'érable à sucre dans des conditions ombragées (et inversement pour l'érable à sucre) (Kobe et al. 1995).

La plus forte mortalité du bouleau jaune dans de faibles conditions de lumière s'expliquerait par son patron de croissance et d'allocation des ressources. La stratégie de croissance en hauteur « plus explosive » du bouleau jaune le placerait dans une situation précaire vis-à-vis de sa survie à cause d'une augmentation des coûts de respiration. À l'opposé, la croissance lente de l'érable à sucre dans conditions ombragées expliquerait sa capacité de survie plus importante. Il y aurait donc un compromis entre la croissance en hauteur et la taille (Messier et al. 1999, Messier and Nikinmaa 2000). Dans des conditions de faible lumière, les semis d'érables à sucre présentent une concentration en sucres plus élevée que les semis de bouleau jaune et allouent plus de sucre pour la mise en réserve dans les racines que dans la croissance de la tige. Ce patron d'allocation fournirait un tampon contre les stress et les dommages mécaniques (Gaucher et al. 2005).

Toutefois le rôle de la disponibilité de la lumière dans l'explication de la tolérance à l'ombre de l'érable à sucre et du bouleau jaune est à nuancer par les observations suivantes. Premièrement, la quantité de lumière optimale pour la croissance des semis d'érable à sucre et de bouleau jaune est relativement comparable entre les deux espèces (Logan 1965, Perala and Alm 1990a, Nyland 1998). Deuxièmement, la croissance juvénile du bouleau jaune est généralement plus élevée que celle de l'érable à sucre (Logan 1965, Sutherland et al. 2000), et même à l'ombrage (Beaudet and Messier 1998, Ricard et al. 2003). Néanmoins, si l'effet de la taille est pris en considération dans l'analyse de la réponse de la croissance à la disponibilité de la lumière, le bouleau jaune présente une plus forte croissance en hauteur et en diamètre que l'érable à sucre tout le long des gradients de disponibilité en lumière et de taille, mais les différences entre les deux espèces ne sont pas significatives (Delagrange et al. 2004). Troisièmement, la réponse de la croissance du bouleau jaune à l'augmentation de la disponibilité de la lumière est plus forte (Logan 1965, Walters and Reich 1996, Beaudet and Messier 1998), plus faible (Messier and Nikinmaa 2000), ou similaire (Pacala et al. 1993, Pacala et al. 1994a, Pacala et al. 1996, Delagrange et al. 2004). Quatrièmement, plusieurs études montrent que le bouleau jaune présente un taux de mortalité plus élevé que celui de l'érable à sucre dans des conditions ombragées (McClure et al. 2000, Kobe et al. 2002), mais également en pleine lumière (Bellefleur and Pétillon 1983, Cogliastro et al. 1997). Par ailleurs, les relations modélisées décrivant la probabilité de mortalité en fonction de la disponibilité de la lumière ne démontrent aucune différence significative entre ces deux espèces (Kobe et al. 2002). L'explication d'une meilleure survie de l'érable à sucre dans des conditions ombragées est également à nuancer. Premièrement, le rapport des tissus photosynthétiques / non-photosynthétiques n'est pas significativement différent entre l'érable à sucre et le bouleau jaune (Gaucher et al. 2005). Delagrange et al. (2004) ont observé que la proportion de tissus photosynthétiques était différente entre les deux espèces, mais ne l'était pas en fonction du gradient de taille (semis et gaulis) et de disponibilité en lumière. Deuxièmement, Delagrange et al. (2004) proposent que la survie de l'érable à sucre et du bouleau jaune pendant quatre années dans des conditions de faible lumière est causée par une plasticité phénotypique élevée chez les semis et l'utilisation des réserves chez les gaulis. Troisièmement, la survie de petits semis semble dépendre relativement peu de la disponibilité

de la lumière, mais est plutôt affectée par des facteurs biotiques ou abiotiques qui causent la défoliation ou la perte de tissus et donc de réserves (Canham et al. 1999).

4.2.2 La nature des lits de germination

La germination de l'érable à sucre se fait sur un substrat de nature variable mais nécessite un milieu ombragé, tandis que la germination du bouleau jaune s'effectue préférentiellement sur des substrats particuliers, tels qu'un substrat perturbé, le bois pourri, la mousse, les monticules de terre, et les fissures dans les roches (Erdmann 1990, Sullivan 1994). La perturbation du substrat améliore la régénération du bouleau jaune, indépendamment du degré d'ouverture de la canopée (Houle 1992a, Roberts and Dong 1993). Certaines observations nuancent l'hypothèse du microsite. Premièrement, même si le bouleau jaune présente une certaine spécificité vis-à-vis des lits de germination (Houle and Payette 1990a, Houle 1992b), les lits de germination sont de nature variée. Deuxièmement, la perturbation du substrat ne représente pas une condition obligatoire pour la régénération du bouleau jaune (Roberts and Dong 1993, Busing and White 1997).

4.2.3 L'inhibition allélopathique de l'érable à sucre envers le bouleau jaune

Le phénomène d'allélopathie a été mis en cause pour expliquer la faible régénération du bouleau jaune. Tubbs (1973) a observé avec des cultures en pot que la croissance des semis de bouleau jaune était réduite par la présence des semis d'érable à sucre malgré l'absence de compétition. Lors de leur croissance, les racines d'érable exudent un inhibiteur qui diminue la croissance racinaire du bouleau jaune. Il jugea que l'allélopathie pouvait représenter un mécanisme écologique important qui augmenterait probablement l'effet compétitif de l'érable à sucre exercé sur le bouleau jaune. Toutefois, l'existence d'une interaction allélopathique est extrêmement difficile à démontrer en conditions naturelles (Kruse et al. 2000, Gurevitch et al. 2002). Par ailleurs, il est intéressant de noter que la dominance du bouleau jaune et

l'absence de régénération de l'érable à sucre observées une vingtaine d'année après l'utilisation du feu comme traitement sylvicole sont expliquées par l'effet allélopathique du bouleau jaune sur l'érable à sucre (Cole et al. 2003).

4.2.4 La susceptibilité à l'herbivorie du bouleau jaune

Le bouleau jaune est particulièrement brouté par un certains rongeurs et mammifères. Si le broutage est sévère au stade du semis, il peut diminuer la régénération du bouleau jaune (Godman and Krefting 1960) et placer le bouleau jaune dans une situation défavorable face à la compétition de l'érable à sucre (Cole et al. 2003).

4.3 Synthèse

Malgré la controverse entourant l'opposition entre la théorie de la différentiation fondamentale des niches et la théorie de la neutralité (Brokaw and Busing 2000), il semble que la distribution et l'abondance des arbres de sous-bois dans les forêts tempérées nordiques soit principalement déterminée par les conditions environnementales, et secondairement par la dispersion des semences (Gilbert and Lechowicz 2004), ce qui privilégie le modèle de la différentiation fondamentale des niches (Silvertown 2004). De plus, l'établissement des semis d'érable à sucre et de bouleau jaune ne semble pas être limité par la disponibilité des graines (Godman and Krefting 1960, Houle and Payette 1990a, Clark et al. 1998, Caspersen and Saprunoff 2005). Par conséquent, la variabilité dans la taille des trouées (McCarthy 2001) et l'hétérogénéité à l'intérieur de la trouée (Bazzaz and Wayne 1994) seraient suffisantes pour permettre la différentiation entre l'érable à sucre et le bouleau jaune, qui se manifesterait principalement au stade de la régénération. La niche de régénération (Grubb 1977) est fonction de l'espèce et comprend tous les processus de la régénération (la production de graines viables, le patron de dispersion des graines dans l'espace et le temps,

les exigences de la germination, de l'établissement des semis et pour le développement des juvéniles).

Parmi les différents mécanismes écologiques susceptibles de contribuer à la coexistence de l'érable à sucre et du bouleau jaune, la théorie de la niche successionnelle et l'avantage de la colonisation sont actuellement les plus privilégiés (Rees et al. 2001). L'avantage de la colonisation est probablement peu important car les espèces tolérantes à l'ombre sont abondantes et colonisent donc facilement les petites trouées (Rees et al. 2001). La coexistence de l'érable à sucre et du bouleau jaune serait donc possiblement maintenue grâce à leur performance relative le long d'un gradient de disponibilité de la lumière (compromis entre la croissance et la survie).

5. Selon les conditions environnementales, l'habileté compétitive de l'érable à sucre et du bouleau jaune est-elle uniforme, ou bien y-a-t-il un changement d'hiérarchie ?

Puisque le phénomène de la compétition intervient dans les deux compromis permettant d'expliquer la coexistence de l'érable à sucre et du bouleau jaune (croissance / survie; compétition / dispersion), il est important de déterminer si la hiérarchie compétitive entre l'érable à sucre et le bouleau jaune est uniforme, ou bien si la performance relative entre ces deux espèces fluctue selon les conditions environnementales (Goldberg 1996, Gurevitch et al. 2002).

Deux modèles conceptuels sont proposés pour expliquer la distribution des espèces selon les gradients environnementaux et pour expliquer comment les différentes adaptations des espèces peuvent influencer le résultat de la compétition pour les ressources : le modèle de la différentiation fondamentale des niches et le modèle de la hiérarchie compétitive (Keddy 1989, Latham 1992). Selon le modèle de la différentiation fondamentale des niches, les espèces se séparent le long d'un gradient de ressources parce qu'elles présentent une performance optimale (optimum physiologique) sur une ou différentes portion de ce gradient

(Townsend et al. 2003). Par conséquent, la performance relative entre les espèces dépend des conditions environnementales puisque l'habileté compétitive des espèces change le long du gradient. D'après le modèle de la hiérarchie compétitive, toutes les espèces présentent leur optimum physiologique dans la partie riche du gradient de disponibilité de la ressource, mais l'habileté compétitive des espèces est différente, créant ainsi une hiérarchie. Les niches sont inclusives. Par conséquent, il n'y a pas de renversement de la performance compétitive entre les espèces. La théorie de la hiérarchie suppose un compromis entre la tolérance des espèces dans des conditions de faible ressource et l'habileté compétitive dans des conditions élevées de ressources, et que ces caractéristiques soient inhérentes et spécifiques à chaque espèce. Les espèces les moins compétitives, mais les plus tolérantes sont déplacées vers la partie pauvre du gradient (Keddy 1989, Keddy and Shipley 1989, Latham 1992).

Aucun de ces deux modèles ne semble actuellement être privilégié (Goldberg 1996, Sack and Grubb 2001) et les deux modèles semblent s'appliquer aux espèces forestières (Latham 1992, Bigelow and Canham 2002).

6. Facteurs écologiques potentiellement discriminants entre la performance de l'érable à sucre et du bouleau jaune

Pour tenter d'expliquer la coexistence de l'érable à sucre et du bouleau jaune, il est important de choisir judicieusement les axes de différentiation les plus probables d'après notre connaissance autécologique de ces deux espèces. Sinon, il devient délicat de réfuter l'hypothèse de la différentiation fondamentale des niches (Silvertown and Charlesworth 2001).

Cinq facteurs écologiques potentiellement discriminants peuvent expliquer la performance de l'érable à sucre et du bouleau jaune :

- La taille de la trouée à cause de la différence de tolérance à l'ombre de l'érable à sucre et du bouleau jaune et de l'importance de la disponibilité de la lumière. La nécessité d'améliorer les pratiques sylvicoles motive également le choix de ce facteur;

- La disponibilité de la lumière : la disponibilité de la lumière est le facteur limitant prépondérant (Ricard et al. 2003, Gilbert and Lechowicz 2004) la croissance de l'érable à sucre et du bouleau jaune en sous-bois, du moins jusqu'au stade de gaulis et jusqu'à 50 % de pleine lumière (Pacala et al. 1994a, Beaudet and Messier 1998, Beaudet et al. 2000, Finzi and Canham 2000, Messier and Nikinmaa 2000) et leur survie (Kobe et al. 1995, Kobe 1996);

- La répartition temporelle de la lumière : la répartition temporelle de la lumière (indépendamment de la disponibilité de la lumière) peut affecter la croissance de l'érable à sucre (Sipe and Bazzaz 1995) et du bouleau jaune (Wayne and Bazzaz 1993);

- Malgré l'importance de la disponibilité de la lumière, la disponibilité en éléments nutritifs est un facteur potentiellement important (Taylor and Aarssen 1989, Latham 1992, McClure and Lee 1993, Sipe and Bazzaz 1995, Finzi and Canham 2000, McCarthy 2001, Bigelow and Canham 2002, Gilbert and Lechowicz 2004, Schreeg et al. 2005) surtout dans des conditions de lumière modérées ou élevées (Canham et al. 1996, Coomes and Grubb 2000). L'érable à sucre présente des exigences relativement élevées en éléments nutritifs, tandis que les exigences du bouleau jaune sont moins clairement définies (Hornbeck and Leak 1992, Cogliastro et al. 1997, Iverson et al. 1999, Anderson et al. 2001). Par ailleurs, une forte affinité de l'érable à sucre pour la disponibilité en calcium échangeable du sol (Kobe et al. 1995, Kobe 1996, Arii and Lechowicz 2002, Kobe et al. 2002) suggère un axe de différentiation potentiel;

- L'environnement compétitif de sous-bois à cause de l'importance de la compétition dans l'organisation des communautés végétales (Gurevitch et al. 2002).

Dans le but de mieux définir la niche écologique de l'érable à sucre et du bouleau jaune, les exigences écologiques de ces deux espèces sont comparées en annexe (appendice B).

7. La thèse

7.1 Problématique générale

La problématique générale de cette thèse consiste à comprendre la compétition et la coexistence de l'érable à sucre et du bouleau jaune à l'échelle du peuplement et se concentre sur la régénération de ces deux espèces.

La présente thèse a pour objet d'étude uniquement le stade juvénile de l'érable à sucre et du bouleau jaune après l'établissement des semis. Malgré leur rôle important pour la régénération, les processus de production, de dispersion et de germination des graines, et d'établissement des semis n'ont pas été examinés dans le cadre de cette thèse puisque ces aspects ont déjà été largement étudiés (Houle and Payette 1990a, 1991a, Houle 1992a, 1994, 1995a, 1998, 1999).

Voici un certain nombre de questions sur lesquelles mon projet de recherche s'est articulé :

- Une inhibition allélopathique de l'érable à sucre envers le bouleau jaune est-elle observée ? Le bouleau jaune est-il plus compétitif que l'érable à sucre ?

- L'habileté compétitive de l'érable à sucre et du bouleau jaune varient-elles selon les conditions environnementales ? Ou bien est-elle constante ?

- Observe-t-on une différentiation de l'érable à sucre et du bouleau jaune selon la taille de l'ouverture du couvert forestier ? Selon la disponibilité de certaines ressources (fertilité du sol, lumière, calcium échangeable) ? Selon la répartition temporelle de certaines ressources (lumière) ?

- Quels sont les traits écophysiologiques responsables de l'habileté compétitive, de la tolérance et de la dominance relative de l'érable à sucre et du bouleau jaune ?

- Est-ce-que la végétation compétitive de sous-bois peut changer la hiérarchie compétitive entre l'érable à sucre et le bouleau jaune ?

- La végétation compétitive affecte-t-elle la relation entre la taille de la trouée et la performance du bouleau jaune ?

- Que signifie la tolérance à l'ombre pour l'érable à sucre et le bouleau jaune en terme d'abondance, de croissance et de survie ?

- Existe-t-il une taille minimale nécessaire pour la régénération du bouleau jaune ?

- Le chaulage des érablières est-il nécessaire pour contrebalancer la perte de calcium échangeable du sol et maintenir une bonne régénération de l'érable à sucre ?

7.2 Objectifs spécifiques

Les objectifs du premier chapitre sont, premièrement, d'examiner l'effet de la taille des trouées, de la végétation de sous-bois et l'apport de calcium sur la densité, la croissance et la survie de jeunes érables à sucre et bouleaux jaunes; et deuxièmement, d'évaluer les effets et l'intérêt de la coupe de jardinage, du dégagement mécanique de la végétation compétitrice de sous-bois et du chaulage pour augmenter le succès de régénération de ces deux espèces à haute valeur commerciale. Le premier chapitre s'intitule *« Effects of gap size, liming, and competition control on the density, growth and survival of sugar maple and yellow birch regeneration following selection cutting »*.

Les objectifs du deuxième chapitre sont d'examiner l'interaction compétitive entre les semis d'érable à sucre et de bouleau jaune croissant sous des environnements lumineux contrastants et le long d'un gradient de fertilité. Plus précisément, l'objectif est de déterminer si un renversement dans l'ordre des espèces en terme d'habileté compétitive pourrait se produire en fonction de la disponibilité et de la distribution temporelle de la lumière, et de la fertilité du sol. De plus, un certain nombre de traits écophysiologiques sont étudiés afin d'évaluer leur contribution à l'habileté compétitive et à la dominance de ces deux espèces. Le deuxième chapitre s'intitule *« Effects of light quantity and variability and soil fertility on the relative competitive ability and dominance of sugar maple and yellow birch seedlings »*.

L'objectif du troisième chapitre est d'observer si les différences interspécifiques de croissance et de survie peuvent expliquer les différences de tolérance à l'ombre des semis et des jeunes gaulis d'érable à sucre et de bouleau jaune. Plus spécifiquement, les objectifs sont, premièrement, de discriminer les érables à sucre et les bouleaux jaunes morts et vivants selon leur taille, leur taux de croissance et la disponibilité en lumière; deuxièmement, de comparer la réponse de croissance de ces deux espèces à un gradient de disponibilité de la lumière; troisièmement, d'évaluer si la mortalité est principalement liée à une limitation de la croissance causée par de faibles niveaux de lumière; et quatrièmement, de déterminer si les individus de petite taille sont plus vulnérables à la mortalité. Le troisième chapitre s'intitule *« Do growth and survival determine the shade tolerance of sugar maple and yellow birch at the juvenile stage? »*.

7.3 Approches méthodologiques

L'étude de la compétition et de la coexistence de l'érable à sucre et du bouleau jaune a porté sur les premiers stades de croissance et de développement, soient les stades de semis (< 50 cm) et de gaulis de petite taille (50 < < 450 cm) à cause des raisons suivantes :

- La tolérance à l'ombre s'exprime dans les premiers stades de croissance et de développement (Sutherland et al. 2000, Delagrange et al. 2004);

- La niche de régénération est importante pour expliquer la coexistence des espèces végétales (Grubb 1977, Kobe 1996, Pacala et al. 1996);

- La production, la dispersion et la germination de graines, ainsi que l'établissement des semis ont déjà été largement étudiés par (Houle and Payette 1990a, 1991a, Houle 1992a, 1994, 1995a, 1998, 1999);

- Il est beaucoup plus aisé d'étudier l'effet des variations des conditions environnementales sur des semis et des gaulis que sur des arbres matures si l'on doit appliquer les traitements dans la forêt.

Deux approches méthodologiques complémentaires ont été privilégiées. La première approche consiste à évaluer la performance relative de l'érable à sucre et du bouleau jaune soumis à différents niveaux de fertilité et de régime de lumière à l'aide d'une expérience de compétition menée pendant deux saisons de croissance dans une serre. La deuxième approche s'est appuyée sur un suivi à long terme de la régénération naturelle de l'érable à sucre et du bouleau jaune à la suite de coupes de jardinage, d'un chaulage et d'un dégagement de la végétation compétitive dans une érablière à bouleau jaune.

CHAPITRE I

EFFECTS OF GAP SIZE, LIMING AND COMPETITION CONTROL ON THE DENSITY, GROWTH AND SURVIVAL OF SUGAR MAPLE AND YELLOW BIRCH REGENERATION FOLLOWING SELECTION CUTTING

1.1 Avant-propos

Ce chapitre sera soumis à la revue « Forest Ecology and Management » ou « Revue Canadienne de la Recherche Forestière » avec les co-auteurs suivants : Dodick Gasser, Christian Messier, Marilou Beaudet et Martin Lechowicz.

1.2 Introduction

Variation in the size of canopy openings is thought to favor the coexistence of species with contrasting shade tolerance (Forcier 1975, Bormann and Likens 1979, McCarthy 2001). For instance, the single-tree selection cutting allows for the natural regeneration of shade tolerant tree species, whereas the group selection cutting is believed to favor the regeneration of mid-shade tolerant tree species (Leak and Filip 1977, Hornbeck and Leak 1992, Majcen 1995, Anderson et al. 2001). The coexistence of sugar maple (*Acer saccharum* Marsh.) and yellow birch (*Betula alleghaniensis* Britton) in northern hardwoods may be due to their regeneration strategy, with sugar maple being a shade tolerant, small-gap specialist (Canham 1988b), and yellow birch a mid-tolerant, gap-phase species (Erdmann 1990). Nonetheless, the gap-size effect on the distribution of sugar maple and yellow birch is not always clearly reported,

providing little evidence for the gap-size partitioning hypothesis (Willis and Johnson 1978, McClure and Lee 1993, Sipe and Bazzaz 1994, Busing and White 1997). Gap size being a complex environmental gradient (Bazzaz and Wayne 1994), the lack of a clear relationship between gap size and the relative performance of these two species may be related to our poor mechanistic understanding of the ecological factors and processes contributing to their regeneration success. Other factors such as soil fertility and understory competitive environment may intervene.

Soil fertility may segregate the performance of sugar maple and yellow birch (Taylor and Aarssen 1989, Latham 1992, McClure and Lee 1993, Sipe and Bazzaz 1995, Walters and Reich 1997, Finzi and Canham 2000, McCarthy 2001, Bigelow and Canham 2002, Gilbert and Lechowicz 2004, Schreeg et al. 2005) particularly in medium and large gaps (Canham et al. 1996, Coomes and Grubb 2000, Ricard et al. 2003). Sugar maple requires relatively high soil nutrients availability, while yellow birch requirements are less clearly defined (Hornbeck and Leak 1992, Cogliastro et al. 1997, Anderson et al. 2001). Among soil nutrients, calcium availability may play an important role (Jenkins et al. 1998). A strong positive influence of high Ca availability (and pH) on the abundance of sugar maple has been found (van breemen et al. 1997, Long et al. 1998, Woods 2000a, Arii and Lechowicz 2002, Bigelow and Canham 2002). However, the responses of the growth and survival of these two species to soil exchangeable Ca availability (and pH) are less conclusive (Perala and Alm 1990a, Kobe et al. 1995, Kobe 1996, Long et al. 1998, Bigelow and Canham 2002, Kobe et al. 2002). The divergent observations among studies prompt for more research on the relationship between Ca availability (and soil pH) and the performance of sugar maple and yellow birch, especially in consideration of the substantial losses of calcium from forested ecosystems (Huntington 2005).

Understory vegetation may interfere on the relationship between gap size and the relative performance of sugar maple and yellow birch. Light availability can be drastically diminished particularly in large gaps (Beaudet et al. 2004) because of the invasion and growth of shade intolerant competitors such as pin cherry and raspberry (Marks 1974,

Majcen and Richard 1992, Ricard and Messier 1996). The greater shade tolerance and early establishment should confer to sugar maple a competitive advantage, but its slow growth would make it to be overtopped by the surrounding vegetation. The faster growth may possibly enable yellow birch to outgrow understory vegetation, but its mid-shade tolerance gives it an intermediate competitive ability (Erdmann 1990). Previous observations suggest that understory competition may possibly be one reason explaining the high mortality of yellow birch (Hatcher 1966, Perala and Alm 1990b) whereas sugar maple may be less affected because of its ability to persist in the understory (Marks and Gardescu 1998). Finally, though understory vegetation compete with the regeneration of desired species for limiting resources (Oliver and Larson 1990, Bérard and Côté 1996), it can shelter seedlings against damaging agents (Silvertown and Charlesworth 2001), such as browsing (Perala and Alm 1990b), and therefore increase the survival of sugar maple and yellow birch (Bellefleur and Pétillon 1983, Berkowitz et al. 1995).

The main objective of this study was to examine how the relative performance of sugar maple and yellow birch is influenced by gap size, soil exchangeable calcium and understory competitive environment. We anticipated that small gaps will allow for the natural regeneration of sugar maple, whereas large gaps will favour the regeneration of yellow birch. We also expected that liming and competition control will promote the regeneration of both species. Finally, possible interactive effects between gap size, liming and competition control may play a significant role on the competitive success of sugar maple and yellow birch. The effects of gap size, liming and competition control on the regeneration success of these two commercially valuable species are discussed and silvicultural recommandations are presented.

1.3 Materials and methods

1.3.1 Study site

The study site is located in Quebec in the transition zone between the sugar maple-yellow birch and balsam fir-yellow birch bioclimatic domains (Bérard and Côté 1996), in the Réserve faunique de Portneuf near Rivière-à-Pierre, Québec, Canada (47°04'N, 72°15'W). The study site covers 60 ha and is at an altitude ranging from 320 and 430 m a.s.l., on the north-facing side of a small hill, where the slope varies from 9 to 16% (Ricard 1999). The average annual precipitation totals 1146 mm, mean monthly temperatures range from - 21°C in January to 24°C in July, and the frost-free season lasts 164 days (Anonymous 2005). The surface deposit is an undifferentiated till approximately 1 m deep overlaying a granitic bedrock. Soils are well to moderately-well drained and range from brunisols to podzols across the study site (Anonymous 1998, Ricard 1999). The humus is a moder or mor according to the location. Stoniness is low (< 13 %) and the maximal root depth varies from 7 to 45 cm. The pH averages 5.3. The overstory is dominated by sugar maple, yellow birch and American beech (*Fagus grandifolia* Ehrh.) (54%, 23% and 11% of the stand basal area, respectively [before harvesting]). Red maple (*Acer rubrum* L.), red spruce (*Picea rubens* Sarg.), balsam fir (*Abies balsamea* (L.) Mill.) and paper birch (*Betula papyrifera* Marsh.) were found in smaller amounts. Before harvesting, the basal area averaged 23.3 m^2 ha^{-1}, and the density was 710 stems per hectare (DBH > 10 cm). The mean height of co-dominant and dominant trees ranges from 17 to 22 m. The stand structure is uneven-aged. In terms of logging history, the forest map of the Ministry of Natural Resources of Quebec indicated some old partial cuttings, which was confirmed by the presence of stumps and rotten logs at the study site. This forest was not damaged by the 1998 ice-storm. The understory vegetation is mainly composed of sugar maple, yellow birch, American beech, pin cherry (*Prunus pensylvanica* L. f.) and red maple seedlings and saplings, in addition to striped maple (*Acer pensylvanicum* L.), mountain maple (*Acer spicatum* Lam.), common hobblebush (*Viburnum alnifolium* L.) and ground hemlock (*Taxus Canadensis* Marsh.), in the shrub layer (Ricard 1999).

1.3.2 Experimental design

A group selection cut was performed in November and December 1996. Fifty large gaps (700 to 1200 m^2) were created with 50 m from gap border to gap border (Fig. 1.1). Between these large gaps, approximately 20 % of the basal area was harvested, creating smaller gaps (50 to 300 m^2). Trees were harvested whatever their species and diameter, but defective stems were removed in priority. Logging was done manually (i.e. with a chain-saw and a cable skidder). Trimming and topping of broadleaf tree species were carried out on the felling site (coniferous species were lopped near the road). Most branches were therefore left on site. Except for the traffic of machinery, understory vegetation was not intentionally destroyed, and no specific scarification had been applied. Soil had likely started to freeze and some snow was probably present at the time of harvest, but probably not enough deep to protect soil and vegetation from the disturbance created by machinery (A. Rouleau (personal communication 2005)).

The experimental design is a factorial with three factors: gap size (3 levels: small, medium, large), liming (2 levels: with or without) and competition control (2 levels: with or without). Each of the 12 resulting combinations of treatments was replicated 12 times, for a total of 144 quadrats of 49 m^2 area each.

Three gap sizes were selected: small (approximately 50 m^2), medium (100 to 300 m^2) and large gaps (700 to 1200 m^2). A number of small, medium and large gaps were randomly selected across the 60 ha of the study area (n = 36, 23, and 12, respectively). Forty-eight 49 m^2 quadrats were set up for each gap size (48 x 3 = 144 quadrats in total). However, the number of quadrats established per gap varied depending on the gap size: only one quadrat was installed in each of 24 small and in one of the medium gaps; two quadrats were installed in each of 12 small and 19 medium gaps; three quadrats were installed in each of three medium gaps; and four quadrats in each of the 12 large gaps.

The four combined treatments of liming and competition control were randomly assigned to the 49 m^2 quadrats. Liming was done by applying lime powder composed of at least 92% calcium carbonate ($CaCO_3$, Ca: 36%) and 0.76% magnesium carbonate ($MgCO_3$, Mg: 0.35%) at 500 kg ha^{-1}. We did not expect to raise significantly the soil pH of limed quadrats with this moderate application rate. Amounts of lime required to bring soil pH of acid forest soil around neutrality are usually in the order of several tons (Burke and Raynal 1998). Our intent was only to increase the availability of soil exchangeable calcium because calcium intervenes in most common nutritional deficiencies of sugar maple (Côté 1998b). Lime application was carried out in early July 1997 (first growing season after harvest). It was uniformly spread by hand in each of the treated quadrats (as well as in a 0.5 m wide buffer strip around these quadrats). In addition to the above-mentioned soil amendment, potassium chloride (KCL) was also applied (at 25 kg ha^{-1}) to mitigate the potentially negative impact that liming can have on sugar maple potassium nutrition (Moore et al. 2000) and to alleviate potential deficiency of soil exchangeable potassium which has been shown to be relatively common (Côté 1998b).

Competition control was performed by weeding by hand on all species of herbs, shrubs and trees (except sugar maple and yellow birch seedlings and saplings of seed origin) in the treated quadrats (and in a 0.5 m wide surrounding buffer strip). Ferns were left in place, as well as graminoïds and club-mosses, except when they were very abundant (in which case they were removed). Small plants were pulled up gently not to disturb too much the soil. Larger plants were cut at the root collar. This procedure was repeated twice a year (early June and early August) for the first three growing seasons after harvesting (1997-1999).

In autumn 1999, nearly 1500 seedlings of sugar maple and 1500 seedlings of yellow birch were tagged, i.e. roughly 10 seedlings of each species per quadrat. All tagged seedlings were from seed origin. For yellow birch, most of the selected seedlings had established after the cut. For sugar maple, however, which is abundantly present as advance regeneration, we selected a maximum height of 50 cm as our selection criteria.

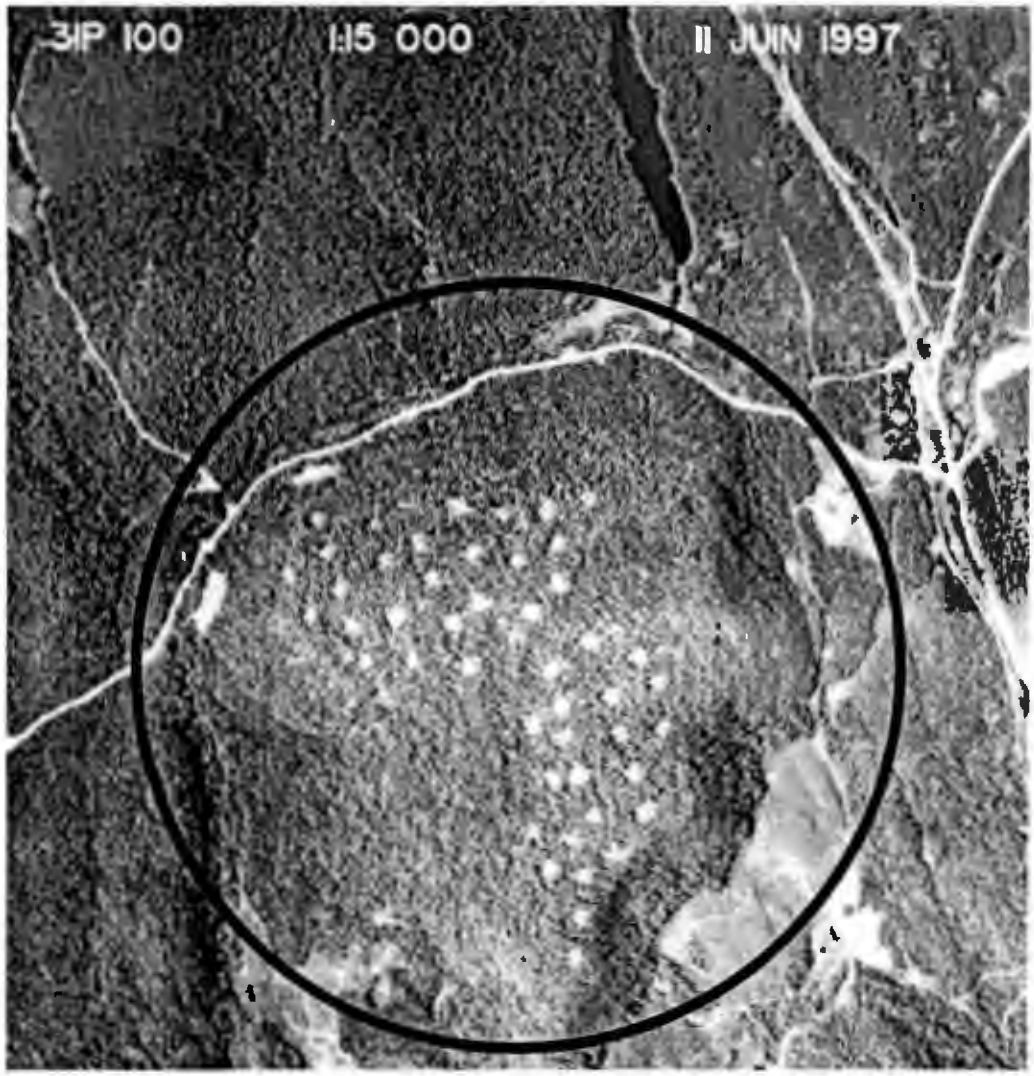

Figure 1.1 Aerial photograph of the study site taken in June 1997, six months after a selection cutting was performed (large gaps of approximately 1000 m^2) (Ministry of Natural Resources of Quebec).

1.3.3 Measurement of environmental conditions

1.3.3.1 Cover of understory vegetation

To assess the efficiency of competition control three years after the last weeding, we measured (end of July to Mid-August 2002) the cover of understory vegetation around a randomly selected set of tagged sugar maple and yellow birch equally distributed among the treatments (300 individuals of each species). The stem length of each targeted individual was measured and used to define the radius of observation for estimation of vegetation cover. Only the cover of understory woody and shrubby vegetation (But also raspberry (*Rubus idaeus* L.)) was considered because of the dynamic nature of the herbaceous layer. We visually estimated the percent cover of each competing species from above the tip of the leader of each targeted individual up to 4 m above-ground. The cover classes were 0-1%, 1-5%, 5-10%, followed by 10% cover class. The percent cover of each species measured individually was summed, thereby allowing us to take into account potential overlap among species.

1.3.3.2 Light availability

The understory light availability was evaluated in July 2002 from instantaneous measurements of the diffuse non-interceptance (DIFN) obtained under completely overcast sky conditions with a LAI-2000 Plant Canopy Analyser (LI-COR, Inc., Lincoln, NE, USA). Such measurements provide a good estimate of the mean growing season percent photosynthetic photon flux density (PPFD, μmol photon m^{-2} s^{-1}; 400-700 nm) transmitted under the forest canopy (Parent and Messier 1996, Gendron et al. 1998). Measurements were taken at the centre of each 49 m^2 quadrat near the forest floor (< 0.3 m) and at 1 and 2.5 m above-ground (Q_o). Above–canopy DIFN (Q_i) was estimated by placing a second device (LAI-2000) on a tripod in a large adjacent clearing. Both devices were synchronized and programmed to compute and record for every 1 min period the mean DIFN from

measurements taken at 5 s interval. The percent transmission of above canopy DIFN was calculated as: % DIFN = (Q_o / Q_i) X 100. Results were averaged across measurement heights within each quadrat before proceeding to statistical analysis.

1.3.3.3 Soil disturbance

In summer 1997, soil disturbance (% area) was evaluated visually in four 1 m^2 plots, evenly spaced out along the diagonal in each 49 m^2 quadrat. Two classes of soil disturbance were defined: 1) "undisturbed" (typically covered with leaf litter, rocks and wood); and 2) "disturbed" (when the forest floor was mixed with the mineral horizon or scraped away from the soil surface); and the % area with "disturbed" soil was evaluated. Results were averaged across plots within each quadrat.

1.3.3.4 Soil pH and nutrient availability

Soil pH was measured from soil samples collected in 2000 in each 49 m^2 quadrat at three evenly spaced locations along the steepest slope. At each location, two soil cores were extracted with a soil-borer, divided in two fractions (organic and mineral). The corresponding fractions from the two cores were then bulked into one sample. Sometimes, the humus layer had been mixed with the mineral soil due to soil disturbance, and the organic and mineral fractions could not be separated. Otherwise, the organic fraction was usually composed of the F-layer alone or in association with the subjacent H-layer. The mineral fraction typically comprised the A and B horizons. Soil samples were sieved (5 mm mesh) to remove roots and coarse debris and the pH of the soil solution (soil:water = 1:10) was determined for each soil sample. Results were averaged across fractions and locations within each quadrat.

Soil nutrient availability was assessed from exchange resins bags placed under the forest floor at three evenly spaced locations along the steepest slope in each quadrat. Exchange resins were left on site for one growing season (early June to early October 1999). Cations and anions were extracted. NH_4^+ and NO_3^- concentrations and exchangeable cations concentrations (K^+, Ca^{2+}, Mg^{2+}) were determined. Results were averaged across locations within each quadrat.

1.3.4 Density, growth and survival of juvenile sugar maple and yellow birch

The density of sugar maple and yellow birch juveniles was assessed in 2002 by recording the number of individuals (< 4 m high) of each species in four 1 m^2 plots, evenly spaced out along the diagonal of the 49 m^2 quadrats. For this census, we did not distinguish between seed- and stump sprout-origin individuals: both were taken into account, but stump sprouts were much less frequent than seed origin individuals (personal observation). When stump sprouts were present, each sprout was considered as an individual. Results were averaged across plots within each quadrat before proceeding to statistical analysis.

The survival and height growth of sugar maple and yellow birch juveniles were monitored on the 1500 tagged seedlings which were censused twice a year (between mid-May and mid-June, and between mid-August and early November) from autumn 1999 to 2002. The stem length (from the root collar to the tip of the leader) of all tagged individuals was measured every year during the autumn survey. The leader was defined as the shoot that reached the highest point of the crown. We assumed that sugar maple and yellow birch had completed the bulk of their height growth by this time of the growing season (Anderson et al. 2001).

1.3.5 Statistical analyses

Variations in the cover of understory vegetation, light availability, soil pH and soil nutrients availability as a function of gap size, competition control and liming were analyzed with a full factorial ANOVA with fixed factors. A one-way ANOVA was carried out to test for the effect of gap size on soil disturbance. The experimental unit was the 49 m^2 quadrat, except for the cover of understory vegetation. In the latter case, the experimental unit was each randomly selected sugar maple and yellow birch.

A full factorial ANOVA with fixed factors was performed to test for the effects of gap size, liming, competition control and their interactions on the density of sugar maple and yellow birch in 2002. The experimental unit was the 49 m^2 quadrat.

The annual leader increment of each tagged individual was calculated as the difference in the stem length between two subsequent years for the growing season of 2000, 2001 and 2002. We then calculated the mean annual leader increment over the three years and used it to test for the effects of gap size, liming and competition control and their interactions with a full factorial ANOVA with fixed factors for each species. Each tagged individual represented an experimental unit.

Following ANOVA's, *post-hoc* means comparisons tests were done to detect significant differences. For each significant main effect, Student's t-test was used to make comparison between two levels of one factor, or Tukey's HSD test was used to make comparisons between all levels of one factor. For each significant interaction effect, an analysis of contrasts was performed to make comparisons among all the levels of one factor in the interaction for each level of each factor in the interaction.

A Wilcoxon rank sums test was carried out to compare the interspecific difference in density and mean annual leader increment for each of the 12 combinations of treatments.

Prior to survival analysis, the right-censoring of survival data was done. Survival data contain duration times until the occurrence of the mortality of an individual and are sometimes referred to as event-time response data. If mortality did not occur before the end of the study for an observation, the individual was said to be censored (coded 1). Lost individuals (6.56% for sugar maple, 5.24% for yellow birch), harvested individuals (5.31% for sugar maple, 5.39% for yellow birch [for a companion study]), and individuals with an unknown status (i.e. still alive or dead; 0.23% for sugar maple, 0.90% for yellow birch) at the end of the survey were censored with the duration until the event occurred, and surviving individuals (74.94% for sugar maple, 72.73% for yellow birch) at the end of the survey were censored for a survival time of 36 months. A dead individual (12.96% for sugar maple, 15.73% for yellow birch) was noncensored (coded 0) with the duration until it died. The time step was set to 6 months. The mortality survey included therefore 6 periods for a total duration of 36 months. Since survival times can have specialized non-normal distributions, we checked graphically for each species the appropriateness of using either the exponential, Weibull, or lognormal distribution before parametric regression. The exponential distribution of survival time was found to fit closely the empirical distribution for both species. Parametric regression was used to test separately for each species the effects of gap size, liming, competition control and their interactions on survival, with survival time as the dependent variable. The univariate survival analysis (Kaplan-Meier procedure) was used firstly to compute product-limit survival estimates of each group for each effect found significant in order to build graphs, and secondly to test significant differences between groups. The relationship in the frequency of mortality between species' identity and the nature of the season (growing *versus* dormant) was examined by contingency table analysis. Finally, differences in survival among sugar maple and yellow birch individuals were analyzed for each of the 12 combined treatments by using the univariate survival analysis. Each tagged individual was an experimental unit.

Data transformations were used when necessary to approach the normality and homoscedasticity assumptions. Significance level was set at $p = 0.05$. Statistical analyses were carried out with JMP software, version 6 (SAS institute Inc. 2006).

1.4 Results

1.4.1 Environmental conditions

1.4.1.1 Understory vegetation cover

The cover of understory vegetation above the tip of the leader of sugar maple and yellow birch increased significantly with gap size from 25% ± 2 in small gaps to 33% ± 2 in medium gaps and 59% ± 3 in large gaps (Table 1.1; $p < 0.001$; values differed significantly from each other). Competition control decreased considerably the cover of understory vegetation from 52% ± 3 to 24% ± 2 (Table 1.1; $p < 0.001$).

Table 1

Effects of gap size (G), liming (L) and competition control (C) on understory vegetation cover in 2002, light availability in 2002 and soil nutrient availability in 1999. Significant effects were detected by ANOVA

Environmental variables	G	L	C	G X L	G X C	L X C	G X L X C
Understory vegetation cover[a] (2002)	**< 0.001**	0.598	**< 0.001**	0.136	0.159	0.609	0.552
Light availability[b] (2002)	**< 0.001**	0.141	**< 0.001**	0.941	**< 0.001**	0.990	0.204
Nutrient availability[c] (1999)							
NO_3^-	**< 0.001**	0.219	**0.046**	0.807	**0.002**	0.334	0.305
Mg^{2+}	**0.009**	**< 0.001**	0.235	0.721	0.350	0.762	0.621

a) %, square root transformed (SQRT (x)); b) % diffuse non-interceptance, arcsine transformed (Arcsine [SQRT (x / 100)]); c) ppm, logarithm transformed (Log_{10} (x)).

1.4.1.2 Light availability in 2002

Light availability increased with gap size, but was also dependent on competition control. Competition control augmented light availability in small and large gaps, but not in medium gaps (Table 1.1; $p < 0.001$; Fig. 1.2).

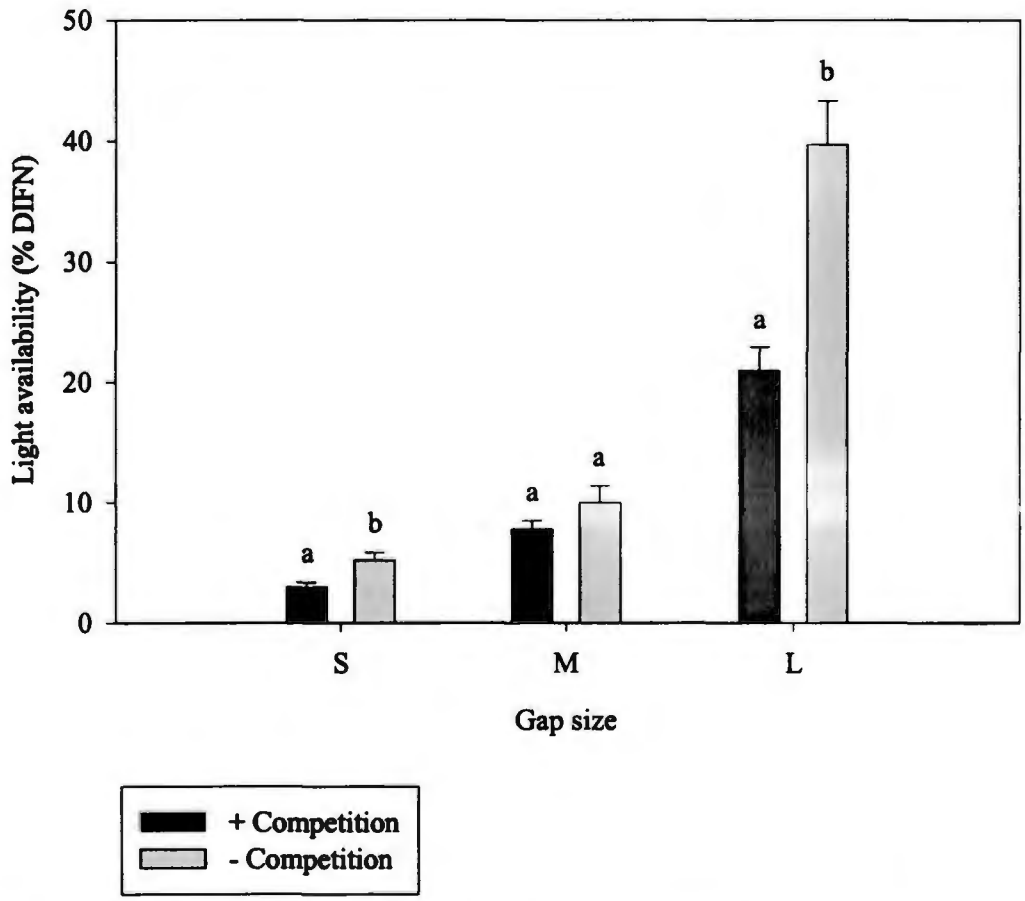

Figure 1.2 Interactive effect of gap size and competition control on mean light availability (± 1 standard error of mean) measured in 2002 in the center of the quadrats. % DIFN stands for the percentage of diffuse noninterceptance; S, small; M, medium; L, large gaps. Different letters within each gap size indicate significant differences between understory competitive environments.

1.4.1.3 Soil disturbance

The percentage of area with disturbed soil varied with gap size ($p = 0.001$). Values were significantly different one another, with the greatest value in medium gaps (18.3% ± 2.4), an intermediate value in large gaps (13.8% ± 2.8), and the smallest value in small gaps (8.7% ± 1.7).

1.4.1.4 Soil pH and nutrient availability

In general, soil was acidic with a pH of 4.2. Soil pH did not vary among treatments ($p = 0.480$), nor did ammonium and potassium availability (NH_4^+; $p = 0.678$; K^+; $p = 0.731$). In the case of nitrate, a significant interaction was found between gap size and competition control, showing that nitrate availability increased markedly with competition control only in large gaps (Table 1.1; $p = 0.002$; Fig. 1.3). Calcium availability was not affected by any treatments including liming ($p = 0.215$). Magnesium availability increased with gap size from 7.2 ± 0.7 ppm in small gaps to 8.6 ± 1.0 ppm in medium gaps and 11.8 ± 1.5 ppm in large gaps (Table 1.1; $p = 0.009$; values differed significantly from each other). Liming increased magnesium availability from 7.1 ± 0.7 ppm to 11.0 ± 1.0 (Table 1.1; $p < 0.001$).

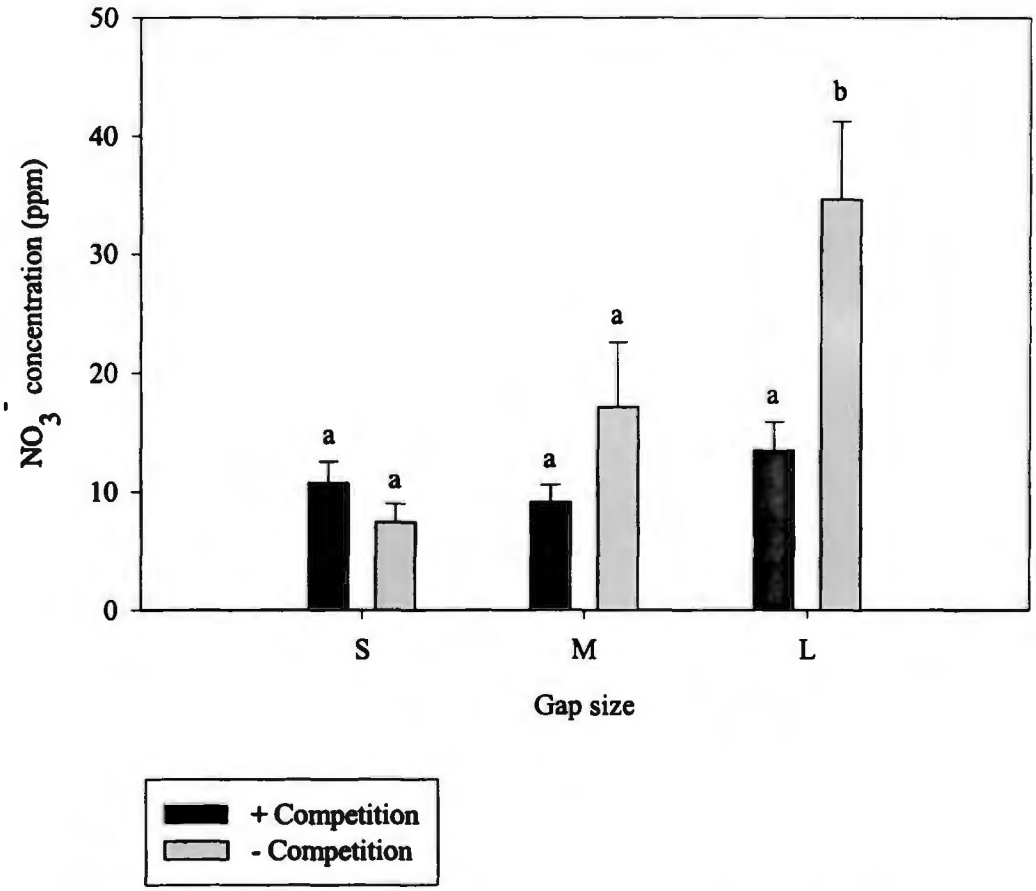

Figure 1.3 Interactive effect of gap size and competition control on mean soil nitrate availability (± 1 standard error of mean) during the growing season of 1999. Different letters within each gap size indicate significant differences between understory competitive environments.

1.4.2 Responses of juvenile sugar maple and yellow birch

1.4.2.1 Density in 2002

The density of sugar maple was affected by gap size (Table 1.2; $p < 0.001$). The density of sugar maple in large gaps (10.4 ± 1.6 individuals.m^{-2}) was significantly lower than the

density in small (32.5 ± 3.4 individuals.m^{-2}) and medium (29.9 ± 2.5 individuals.m^{-2}) gaps. Competition control increased significantly the density of sugar maple from 19.8 ± 2.1 individuals.m^{-2} in unweeded quadrats to 29.5 ± 2.7 individuals.m^{-2} in weeded quadrats (Table 1.2; $p < 0.001$).

The density of yellow birch was affected by gap size (Table 1.2; $p = 0.001$). Its density was significantly lower in small gaps (1.1 ± 0.2 individuals.m^{-2}) in comparison with medium (3.4 ± 0.6 individuals.m^{-2}) and large (4.0 ± 0.6 individuals.m^{-2}) gaps. Liming decreased the density of yellow birch from 3.6 ± 0.5 individuals.m^{-2} in unlimed quadrats to 2.1 ± 0.4 individuals.m^{-2} in limed quadrats (Table 1.2; $p < 0.001$), while competition control increased the density of yellow birch from 1.4 ± 0.2 individuals.m^{-2} in unweeded quadrats to 4.3 ± 0.5 individuals.m^{-2} in weeded quadrats, (Table 1.2; $p < 0.001$).

Although the density of sugar maple was always superior to that of yellow birch ($p < 0.05$) (except in large gaps with liming ($p = 0.065$) / without liming ($p = 0.217$), but with competition control), the magnitude of the difference between the two species varied among treatments (Fig. 1.4a). The smallest differences were observed in large gaps because of the combined tendency for sugar maple density to decrease with increasing gap size, and for yellow birch density to increase with increasing gap size.

Table 2

Responses of sugar maple and yellow birch in terms of density, height growth and survival to gap size (G), liming (L) and competition control (C). ANOVAs were used to analyze data of density and height growth of each species, and parametric regression was performed to analyze data of survival of each species. Density data were analyzed at the quadrat scale; height growth and survival at the individual scale

Responses	G	L	C	GXL	GXC	LXC	GXLXC
Density[a] (2002)							
Sugar maple	**< 0.001**	0.092	**< 0.001**	0.087	0.244	0.859	0.968
Yellow birch	**< 0.001**	**< 0.001**	**< 0.001**	0.114	0.642	0.088	0.772
Mean annual leader increment[b] (2000-2002)							
Sugar maple	**< 0.001**	0.553	**< 0.001**	0.998	**< 0.001**	0.424	**0.007**
Yellow birch	**< 0.001**	0.388	**< 0.001**	**0.038**	**< 0.001**	0.560	0.130
Survival[c] (1999-2002)							
Sugar maple	**< 0.001**	0.939	**0.006**	**0.003**	**0.013**	0.978	0.234
Yellow birch	**0.009**	0.108	**< 0.001**	**0.020**	0.704	0.146	**0.018**

a) Number of individuals/m^2, SM: fourth root transformed ($\sqrt[4]{x}$); YB: cubic root transformed ($\sqrt[3]{x}$); b) cm, SM: logarithm transformed ($\log_{10}(x + 4)$); YB: logarithm transformed ($\log_{10}(x + 20)$); c) Censored data.

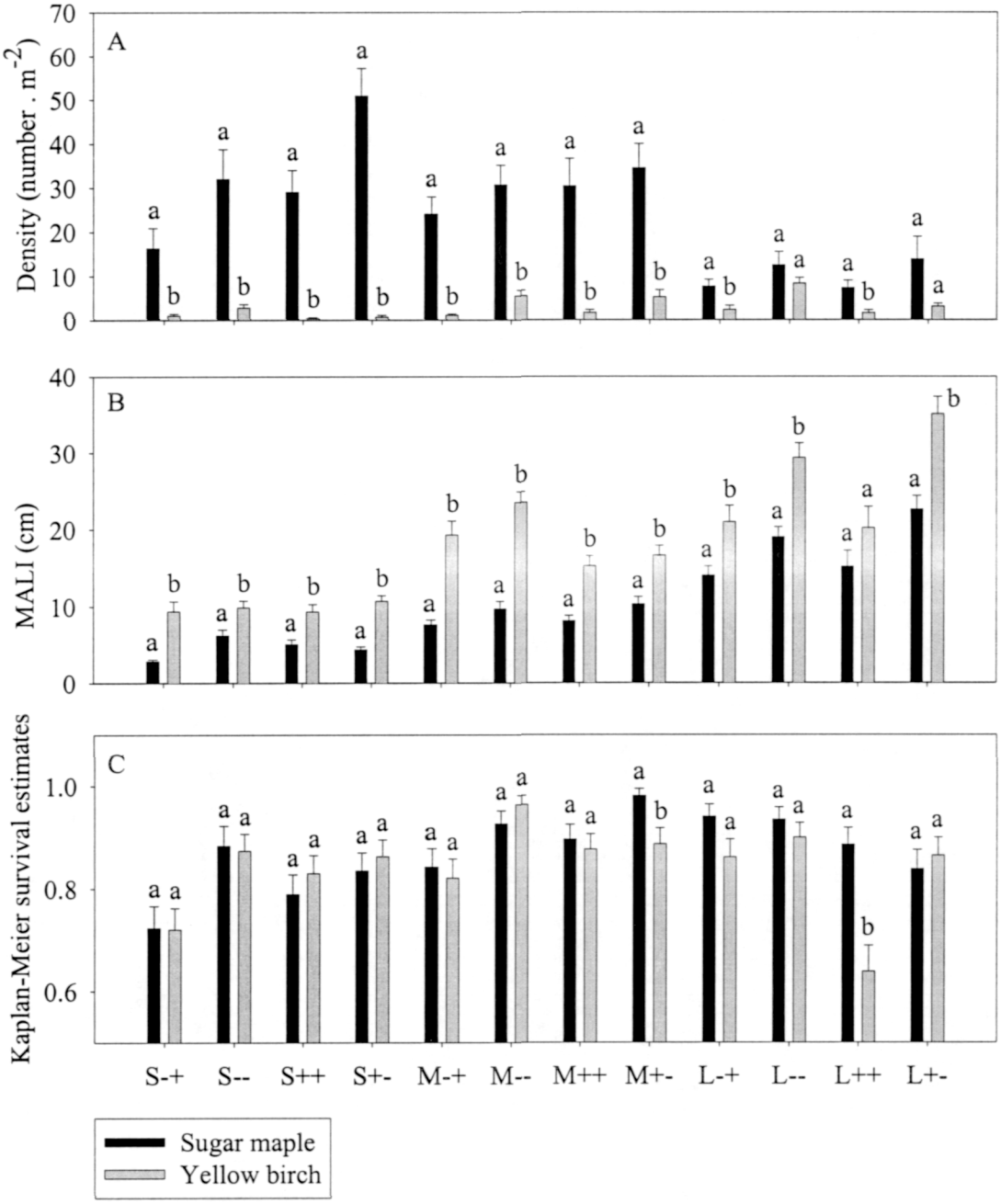

Figure 1.4 Comparison of A) the mean density, B) mean annual leader increment, and C) product-limit survival estimates (± 1 standard error of mean) between sugar maple and yellow birch within the twelve combinations of treatments. S, M, L stand for small, medium and large gap, respectively; the first sign represents the liming treatment (+: with; –: without); the second sign represents understory competition (+: with; -: without). Different letters within each combination of treatments indicate significant differences between species.

1.4.2.2 Mean annual leader increment

The mean annual leader increment of sugar maple increased with gap size (Table 1.2; $p < 0.001$) and competition control (Table 1.2; $p < 0.001$), but was also affected by liming (Table 1.2; $p = 0.007$): liming increased growth uniquely in small gaps with competition (Fig. 1.5a and 1.5b).

The mean annual leader increment of yellow birch increased with increasing gap size, but this increase varied with liming. Liming reduced significantly the leader increment in medium gaps but not in small and large gaps (Table 1.2; $p = 0.038$; Fig. 1.5c). Competition control increased the leader increment of yellow birch, but this effect depended on gap size. This positive effect of competition control was only observed in medium and large gaps (Table 1.2; $p = 0.001$; Fig. 1.5d).

The mean annual leader increment of yellow birch was greater than that of sugar maple in all treatments ($p < 0.05$), except in large gaps with liming and competition, in which case the two species did not differ ($p = 0.150$; Fig. 1.4b).

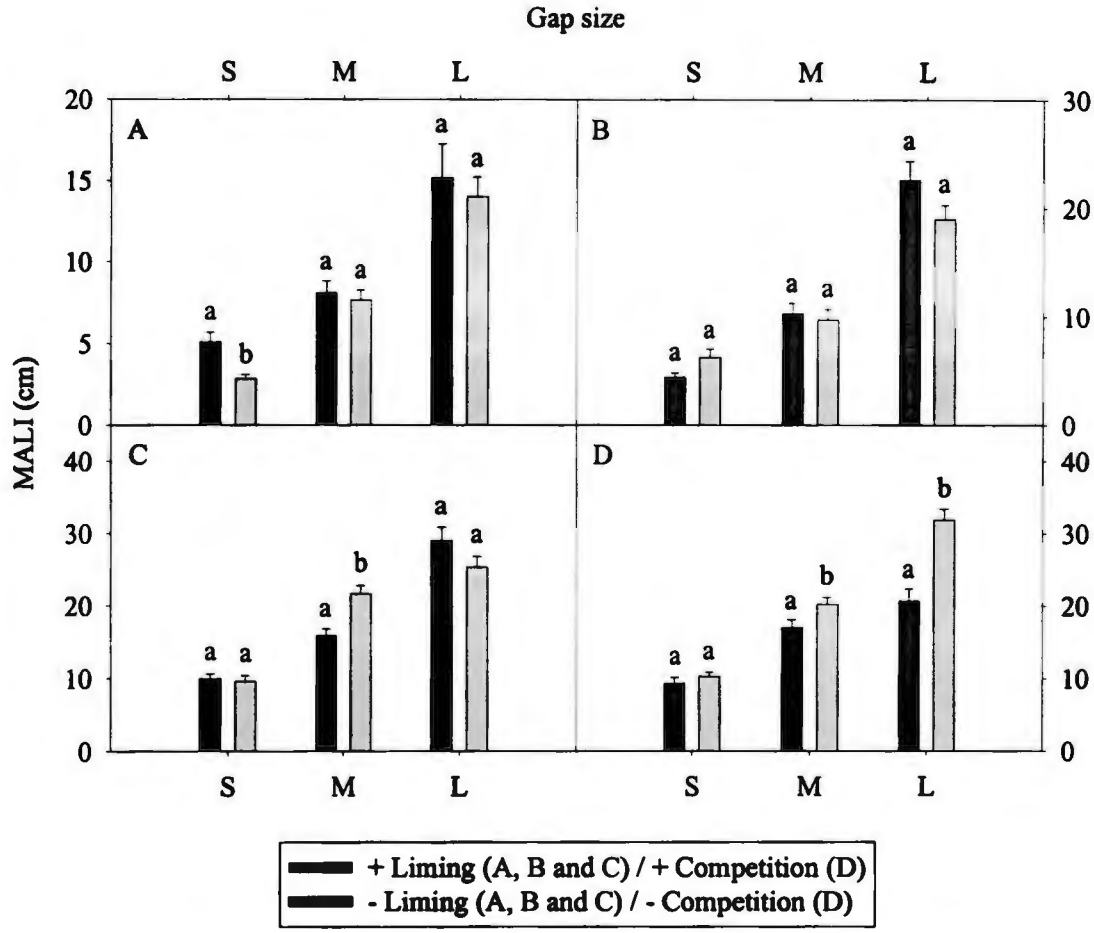

Figure 1.5 Interactive effect of gap size, liming and competition control on the mean (2000-2002) annual leader increment (± 1 standard error of mean) of sugar maple with competition (A) and without competition (B). Interactive effect of gap size and liming on the mean annual leader increment (± 1 SEM) of yellow birch (C). Interactive effect of gap size and competition control on the mean annual leader increment (± 1 SEM) of yellow birch (D). Different letters within each gap size indicate significant differences between liming treatments (A, B and C) or understory competitive environments (D).

1.4.2.3 Survival

The survival of sugar maple was generally lower in small gaps in comparison with medium and large gaps ($p < 0.001$), but the effect of gap size varied somewhat depending on liming and competition control. Liming decreased very slightly the survival of sugar maple in large

gaps but did not cause any effect in small and medium gaps (Table 1.2; $p = 0.003$; Fig. 1.6a). Competition control showed a positive effect on the survival of sugar maple in small and medium gaps, but no effect in large gaps (Table 1.2; $p = 0.013$; Fig. 1.6b).

The survival of yellow birch was greater in medium gaps in comparison with small and large gaps (Table 1.2; $p = 0.009$), but the effect of gap size differed as a function of competition control and liming (Table 1.2; $p = 0.018$). In presence of competition, liming augmented survival in small gaps, did not have any effect in medium gaps and decreased it in large gaps (Fig. 1.6c). With competition control, liming did not change survival in small and large gaps, but reduced it slightly in medium gaps (Fig. 1.6d).

In general, survival was high, ranging from 0.64 to 0.98, and did not differ significantly between sugar maple and yellow birch except in two treatments where the survival of yellow birch was significantly lower than that of sugar maple (Fig. 1.4c): in limed medium gaps with competition control ($p = 0.006$) and in limed large gaps with competition ($p < 0.001$).

A significant relationship between species and the period of mortality was noticed ($p < 0.001$). The mortality of sugar maple occurred more during the dormant season than the growing season (73% of dead sugar maple *versus* 27%), while the mortality of yellow birch was roughly divided between the two periods (56% during the dormant season *versus* 44% during the growing season).

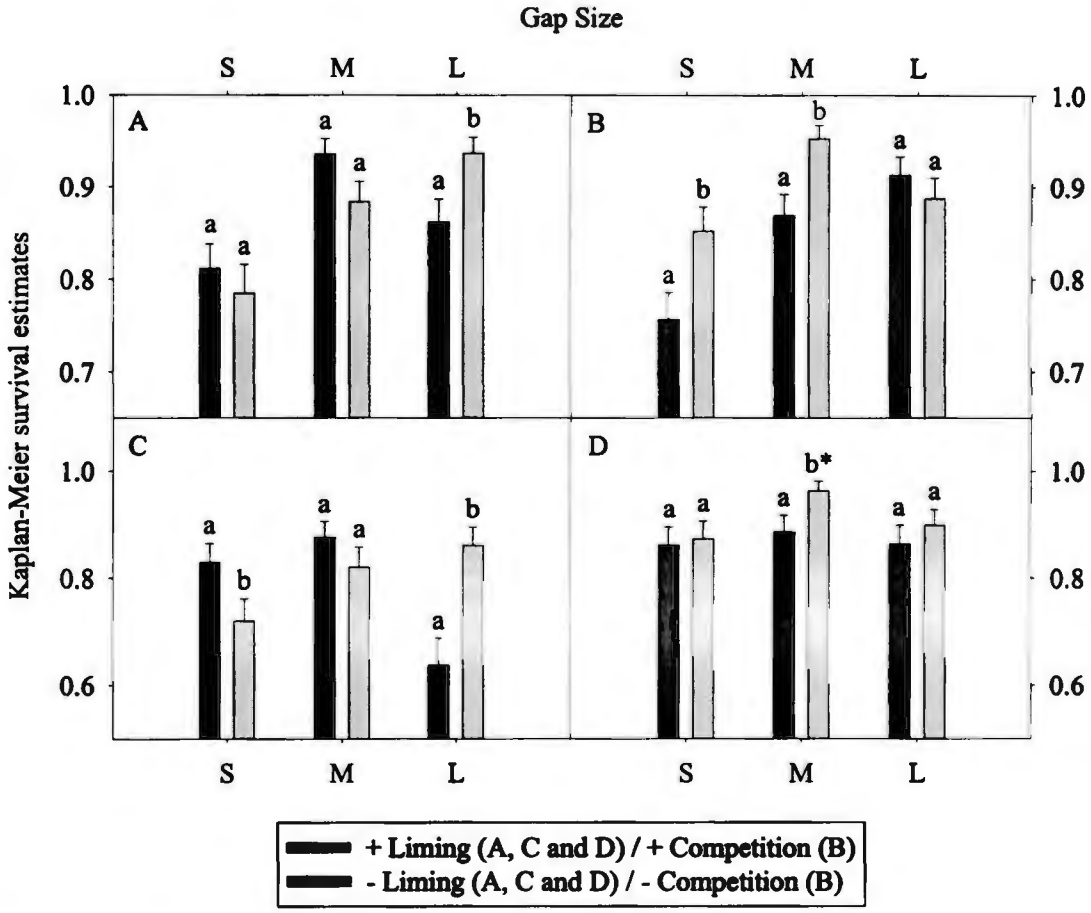

Figure 1.6 Survival of sugar maple and yellow birch from fall 1999 to fall 2002. Interactive effect of gap size and liming on the survival of sugar maple (A). Interactive effect of gap size and competition control on the survival of sugar maple (B). Interactive effect of gap size, liming and competition control on the survival of yellow birch with competition (C) and without competition (D) * significant ($p < 0.05$) or marginally significant depending on the statistical test used: Log-Rank or Wilcoxon. Product-limit survival estimates (± 1 standard error of mean). Different letters within each gap size indicate significant differences between liming treatments (A, C and D) or understory competitive environments (B).

1.5 Discussion

1.5.1 Density

Sugar maple and yellow birch are two species with the ability to regenerate well naturally. Overall, sugar maple was ubiquitous (from 7.3 ± 1.7 to 51.0 ± 6.2 individuals.m^{-2}) and yellow birch was relatively abundant (from 0.4 ± 0.2 to 8.3 ± 1.3 individuals.m^{-2}). The important density of sugar maple suggests a continuous establishment which leads progressively to the formation of a persistent seedling bank (Marks and Gardescu 1998, Sutherland et al. 2000). Sugar maple and yellow birch showed two opposite patterns of density along the gradient of gap size; while sugar maple was most abundant in small and medium gaps, yellow birch was more abundant in medium and large gaps. Although the proportion of soil disturbance was lower in large gaps than in medium gaps, we think that disturbances of understory vegetation caused by machinery operations could have been more important in large gaps and lowered the initial density of already established sugar maple in large gaps. We do not think that seed availability has limited the abundance of sugar maple in large gaps since most sugar maple seeds are dispersed from a forest edge to a distance of 15-20 m (Tirmenstein 1991, Pacala et al. 1996), comparable to the radius of the large gaps. The lower density of yellow birch in small gaps probably resulted from both a lower establishment of seedlings and a higher mortality rate. Litter acts as a restrictive barrier in small gaps (Anderson et al. 2001) and the percentage of disturbed soil, following harvest operations, was lower in small gaps therefore creating less favourable conditions for yellow birch establishment than in larger gaps (Erdmann 1990, Houle 1992a, Roberts and Dong 1993). The higher mortality of yellow birch observed in small gaps is associated with the smothering effect of litterfall on newly established seedlings (Anderson et al. 2001) and the extremely low light availability.

The effect of liming on regeneration density varied as a function of species. Unlike for sugar maple, liming reduced by 42% the density of yellow birch. This negative effect may be related to the negative effect of liming on growth and survival of yellow birch in some environmental conditions. In comparison, greater density of yellow birch has been observed

following a relatively important application of calcium carbonate (6.9 $t.ha^{-1}$) (Smallidge and Leopold 1995). Surprisingly, the density of sugar maple did not respond positively to liming even in small gaps. This observation contrasts with previous studies which showed a positive relationship between the availability of soil exchangeable calcium and the abundance of sugar maple seedlings and saplings growing in the understory (Jenkins et al. 1998, Long et al. 1998, Arii and Lechowicz 2002, Bigelow and Canham 2002).

Understory vegetation was well-developed to exert a competitive effect by diminishing the abundance of sugar maple and yellow birch. Nevertheless, competition did not affect sugar maple and yellow birch similarly: sugar maple showed a moderate reduction of density (33%), whereas the density of yellow birch dropped by 67% in presence of understory vegetation. The density response to understory vegetation may be related to the difference in shade tolerance between these two species. In comparison Bellefleur et Pétillon (1983) found a positive effect of competition removal on the abundance of yellow birch but a small negative effect on the abundance of sugar maple in a recent clearcut in a sugar maple-beech-yellow birch stand.

1.5.2 Mean annual leader increment

The early height growth rate of yellow birch is relatively greater than that of sugar maple, in spite of its lower shade tolerance (Hornbeck and Leak 1992, Beaudet and Messier 1998, Sutherland et al. 2000, Ricard et al. 2003, Delagrange et al. 2004), conferring to yellow birch its competitive superiority. Since most yellow birch established after gap formation (McClure et al. 2000), faster growth of newly established yellow birch seedlings gives them the ability to catch up and outgrow sugar maple in few years even under relatively low light conditions in small gaps where sugar maple was most likely present as advance regeneration (Marks and Gardescu 1998, McClure et al. 2000).

Sugar maple and yellow birch both increased their mean annual leader increment with increasing gap size, and this growth response is associated with the concomitant increase in light availability (Ricard et al. 2003) and soil nutrient availability (nitrate and magnesium) observed in this study. Competition for water has been rejected as a possible competitive mechanism of understory vegetation on the growth of these two species in the region (Bellefleur and Pétillon 1983, Ricard et al. 2003). Competition control increased significantly light availability in small gaps, but probably not enough to affect the height growth of yellow birch. Competition release of yellow birch was sufficiently important to be significant in medium and large gaps. In large gaps, the increase of light and nitrate availability following competition control may explain the greater growth of yellow birch. Finally, even if understory vegetation affected negatively growth, it should be noted that sugar maple and yellow birch were apparently less targeted by browsing in presence of understory vegetation. Understory vegetation cover could also have sheltered sugar maple and yellow birch by mitigating extreme microclimatic events occurring in large gaps (pers. obs.).

We expected that liming would increase the growth of sugar maple and yellow birch by improving soil fertility and increasing soil exchangeable calcium availability in particular. In fact, our study detected an important increase in the height growth of sugar maple (78%), but only in small gaps with competition. Otherwise, liming did not generate any other positive effect on growth and even caused a decrease of the height growth of yellow birch in medium gaps (27%). These results revealed the importance of environmental conditions, such as canopy opening and understory vegetation in the response of tree species to liming and may contribute to explain the divergent observations among previous studies. Our results agree to some extent with the finding of Kobe et al. (2002) who noticed a significant increase in the mean relative diameter growth of sugar maple seedlings with an addition of 10 g m^{-2} of calcium (100 kg ha^{-1}), but no effect for yellow birch. In contrast, Bigelow et Canham (2002) found that the growth of sugar maple saplings was unrelated to soil chemistry. Sugar maple is a relatively nutrient-demanding species (Ouimet et al. 1996b, Anderson et al. 2001) and the absence of liming effect in the other combined treatments may be explained by an insufficient addition of lime. We spread an equivalent of 500 kg ha^{-1} of lime, which provided

an equivalent of 180 kg ha^{-1} of calcium in amended quadrats. Although typical application rates ranges from 400 to 800 kg ha^{-1} (Côté 1998b) and moderate application of lime (< 1500 kg ha^{-1}) have been recommended by Pagé et al. (1990), the granitic nature of the bedrock and the significant net losses of exchangeable calcium and magnesium observed in a nearby mature sugar maple-American beech-yellow birch stand (about 50 km) (Houle et al. 1997) suggest that the soil at our study site would be badly provided with exchangeable cations. In addition liming did not raise soil pH and exchangeable calcium availability, suggesting that the amount of lime spread was probably too low to generate enough differences in soil chemistry. On such poor soil, calcium has probably been pumped out very quickly by the vegetation, notably by the potentially nutritionally-stressed overstorey trees (Long et al. 1997, Moore et al. 2000). The lower leader increment of yellow birch following liming in medium gaps may possibly due to nutritional imbalances.

1.5.3 Survival

Overall, sugar maple and yellow birch had relatively high survival rates. In comparison, lower survival rates have been found for transplanted seedlings of sugar maple and yellow birch (Sipe and Bazzaz 1995, Cogliastro et al. 1997, Kobe et al. 2002). Moreover, despite their contrasting shade tolerance, survival rates of these two species were often similar. The relative success in survival may depend on habitat factors. For example, Cogliastro et al. (1997) attributed the high mortality of yellow birch seedlings to drought which was unlikely the case at our study site (Linteau 1948, Bellefleur and Pétillon 1983, Ricard et al. 2003).

The absence of interspecific difference in survival in small gaps agreed with the observed relationship between mortality and the availability of light in previous studies. The juvenile survivorship functions modelled by Kobe et al. (1995) described only a higher probability of mortality for yellow birch, compared to sugar maple, below 2 or 3 % of light availability. Above this threshold, the probability of mortality was similar between the two species. In our study, the lowest light level (measured near the forest floor in small gaps with

competition) averaged 2.5% of full sunlight during the 2002 growing season. Walters et Reich (1996) also showed that yellow birch survival was consistently inferior to that of sugar maple at 2 %, but similar or superior at 8 % of light availability. Delagrange et al. (2004) also observed that understory trees of both species survived for 4 years under low light levels (0.5 to 16% of full sunlight). Our study suggests thus that yellow birch (mainly at the seedling stage in small gaps), a mid-tolerant species, can persist like sugar maple, a shade tolerant species, under low-light level for at least 3 years. Beside it is interesting to note that the survival of sugar maple, unlike yellow birch, responded positively to competition control in small and medium gaps, despite its greater degree of shade tolerance. The small increase in light availability in small gaps may explain the higher survival of sugar maple. Nonetheless our observations do not exclude the hypothesis that yellow birch seedlings could be physiologically stressed (Delagrange et al. 2004). Indeed Gaucher et al. (2005) found that sugar maple seedlings had higher carbohydrate concentration than yellow birch seedlings under low light conditions (1-18% full sunlight) and suggested that allocation of carbohydrates to storage in roots instead of stem growth may play an important role in seedling survival by providing a buffer against agents of stress and physical damage. We expect therefore that a higher mortality rate will be observed for yellow birch in small canopy gaps because of progressive gap closure (i.e. decrease in light availability) (Delagrange et al. 2004) or stronger effect of biotic or abiotic factors that cause defoliation or loss of root or shoot tissues (and the reserves stored in those tissues) (Canham et al. 1999). Such prediction would comply with the low mortality of sugar maple seedlings (Marks and Gardescu 1998) and the low survival of yellow birch under closed canopy (Willis and Johnson 1978, McClure et al. 2000, Anderson et al. 2001).

In our study, the moderate application of calcium (18 g m^{-2}) was sufficient to influence the survival of sugar maple and yellow birch. Sugar maple displayed unexpectedly lower survival in large gaps following liming. Liming effect on the survival of yellow birch was very variable according to gap size and understory competition. Unfortunately, a possible explanation of these observations can be difficult to bring for the two following reasons. First of all, no parallel could be drawn between survival responses of sugar maple and yellow birch on one hand and variations in the surrounding vegetation, resources availability or soil

acidity on the other hand. Secondly, several damaging agents came into play (Erdmann 1990, Godman et al. 1990) and consequently a multitude of causes of mortality can be hypothesized. For example, mechanical injuries, deer browsing and hot air temperatures in large canopy gaps were noticed during the survey, but the identification of the most probable mortality agents for each individual was beyond the scope of this study. Nonetheless, we think that the negative influence of liming on survival can be attributable to nutritional imbalances and/or deficiencies. Burke et Raynal (1998) suggested that surface liming of acidic forest soils could intensify nutrient deficiencies and affect the potassium nutrition of sugar maple seedlings, which in turn would potentially result in increased susceptibility to frost injury, drought and pathogens. In our study, the addition of potassium was probably not sufficient to limit the negative impact of liming on sugar maple potassium nutrition (Moore et al. 2000). In comparison Long et al. (1998) observed a higher survival rate of sugar maple seedlings in the understory after a very high application of dolomitic lime (22.4 tonnes ha^{-1}).

Finally, sugar maple died more frequently during the dormant season whereas yellow birch mortality occurred likewise among the growing and the dormant season. Based on the differential range of sugar maple and yellow birch at the northern limit of their geographic distribution, we supposed that frost tolerance would be a key determinant of the ability of yellow birch to survive and frost would be a possible killing agent explaining the higher mortality rate of sugar maple during the dormant season. Nonetheless, no clear conclusion about the relative frost tolerance of these species appears in the literature. Calme et al. (1994) found that sugar maple was less frost tolerant than yellow birch while Trimble (1975) found the reverse. Late spring frost was found to be the main cause of the mortality of seedlings of yellow birch (Linteau 1948). In the latter case, other damaging agents during the growing season (for example: herbivory) must have been equally important to compensate for the mortality of yellow birch during the dormant season.

1.6 Conclusions and silvicultural implications

This paper documents the interactive influence of three important ecological factors, namely, gap size, soil fertility (calcium) and understory competition, on the regeneration of sugar maple and yellow birch over a relatively long time period (almost 6 years post-treatment). The density, height growth and survival of the regeneration were compared among these two species. Possible mechanisms were proposed to explain observed variations by relating the regeneration pattern of sugar maple and yellow birch with key environmental variables (Understory vegetation cover, light availability, soil disturbance, soil pH and nutrient availability). Firstly, our results show that sugar maple and yellow birch exhibited two different regeneration strategies: the density of sugar maple was greater than that of yellow birch, while yellow birch was characterized by a faster height growth. Interestingly, both species displayed similar survival in most treatments despite their contrasting shade tolerance. Secondly, we conclude that yellow birch appeared more competitive than sugar maple. Furthermore the consistency of the relative rank order for growth (Goldberg 1996) suggests a competitive hierarchy (Keddy 1989), though observed variations in height growth were considerable and environmental conditions were contrasting. This observations suggests that the shifting competitive hierarchy model may be a powerful mean of explaining forest community organization (Bigelow and Canham 2002, Canham et al. 2006). Thirdly, the unexpected and complex responses following liming prompts for more research on the mineral nutrition and soil calcium requirements of sugar maple and yellow birch. Finally, understory vegetation can exert an important competitive effect on the growth of yellow birch in particular growing in medium and large gaps by decreasing light and soil nitrate availability in large gaps.

Our study also has some management implications. First of all, selection cutting system can provide favourable conditions for regenerating two silviculturally valuable species. Small and medium gaps showed the highest density of sugar maple, while medium and large gaps showed the highest density of yellow birch; the growth of both species increased with increasing gap size; medium gaps favoured the survival of yellow birch, while small gaps

decreased the survival of sugar maple. Medium-size gaps represent thus a good trade-off to regenerate both species as it optimized survival without sacrificing too much growth. Since yellow birch is more affected physiologically by the closure of canopy gaps (Delagrange et al. 2004), it is difficult to predict if small and medium gaps will provide enough light until the next entry to sustain the growth, or even allow the survival of yellow birch. A mixture of single-tree and group selection cutting may be needed to maintain the composition of the sugar maple-yellow birch-American beech forest community by creating conditions that allow regeneration of both shade-tolerant and mid-shade tolerant species (Leak and Filip 1977). Even on soil badly provided with exchangeable cations, liming can have a negative impact on the regeneration of sugar maple and yellow birch under certain conditions and should be applied carefully. The control of non-commercial species by mechanical weeding should focus on large canopy gaps to be relevant and should not be performed in forest densely inhabited by white-tailed deer. Otherwise seedlings will be exposed to browsing. To conclude, we have discussed about the impacts of recently introduced silvicultural treatments by paying attention only to the two major commercial species. Elements such as biodiversity conservation should be addressed and taken into consideration if we want to pursue the paradigm of emulation silviculture.

CHAPITRE II

EFFECTS OF LIGHT QUANTITY AND VARIABILITY AND SOIL FERTILITY ON THE RELATIVE COMPETITIVE ABILITY AND DOMINANCE OF SUGAR MAPLE AND YELLOW BIRCH SEEDLINGS

2.1 Avant-propos

Ce chapitre sera soumis à la revue « Écoscience » ou « Revue Canadienne de la Recherche Forestière » avec les co-auteurs suivants : Dodick Gasser, Christian Messier et Yves Mauffette.

2.2 Introduction

Sugar maple (*Acer saccharum* Marsh) and yellow birch (*Betula alleghaniensis* Britton) are two major sympatric tree species growing in a wide variety of forest communities in eastern North America (Erdmann 1990, Godman et al. 1990). After gap formation, many characteristics of the understory environment are profoundly altered: a growing space is released and the availability of resources is temporarily increased (Pickett and White 1985). For instance, increased decomposition of organic matter and nitrogen mineralization can lead to higher soil nutrient availability (Vitousek 1985 but see, Mladenoff 1987). Significant temporal and spatial variation in understory light levels can also be created within gaps (Canham et al. 1990). As a result, different combinations of resources could be produced within gaps (Bazzaz and Wayne 1994). Tree species respond to these new environmental

conditions, and intense intra- and interspecific resource competition follows, which eliminates most individuals through time.

Recently, three alternate models have been applied to understand tree species distribution along environmental gradients (Bigelow and Canham 2002, Canham et al. 2006). Under fundamental niche differentiation, species segregate because they are specialized and have optimal performance at different points along a gradient. The relative dominance is thus contingent on environmental conditions since the relative competitive abilities change along the resource gradient. Under Keddy's (1989) shifting competitive hierarchy (SCH), all species have physiological optima at the upper end of resource gradients, but may be displaced to suboptimal locations by competition. SCH supposes that competitive ability is an inherent and species-specific characteristic, and predicts no reversals in competitive dominance. The continuum concept (CC) of Austin and Smith (1989) combines elements of both FND and SCH, depending on the nature of the gradients (whether a depletable resource or a non-depletable environmental factor). Growth responses show some evidence for the three models of community organization depending on the studied species (Bigelow and Canham 2002, Canham et al. 2006). Furthermore, Goldberg (1996) concluded based on a literature review that « No simple answer to whether competitive ability is consistent among environments or hierarchies change ». As proposed by Keddy et al. (2000), the outcome of competitive interactions may be relatively predictable and independent of the environmental conditions at the broad community scale (*i.e.* competitive hierarchy), but at a finer scale, it is more contingent. In the last case, variation in the environmental conditions can have a major influence on dominance, particularly for pairs of species that are similar in their competitive performance.

The nature of the interaction between sugar maple and yellow birch seedlings is not clearly defined. Although resource competition is recognized to play a major role in structuring plant communities and considered to be intense in productive nutrient-rich environments (Tilman 1982, Keddy 1989, Gurevitch et al. 2002), Tubbs (1973) observed that the growth of yellow birch seedlings was suppressed in the presence of sugar maple seedlings despite the

absence of competition and considered allelopathy as an ecological significant mechanism which would probably augment the competition exerted by sugar maple on yellow birch. Moreover, an unambiguous description of the competitive ability of each species is also lacking. Erdmann (1990) evaluated the competitive ability of yellow birch as intermediate and noted that yellow birch seedlings cannot compete successfully with advance regeneration of sugar maple, while Bellefleur et Villeneuve (1984) concluded that yellow birch was relatively more competitive than sugar maple.

The recent literature review of Ricard et al. (2003) demonstrated the overriding importance of light availability on the growth of understory sugar maple and yellow birch, at least up to the sapling stage and up to 50 % light availability. However, seedlings become generally more sensitive to soil nutrient availability as light availability increases with gap size (Canham et al. 1996, Coomes and Grubb 2000), and the response could be more marked in more light-demanding species (Coomes and Grubb 2000). Beside, competitive hierarchies among tree species can vary with soil fertility (Latham 1992, Fahey et al. 1998a). Finally, several studies suggested that soil resources may also play a significant role in structuring tree species composition in understory communities. McClure et Lee (1993) suggested that soil conditions and root competition may play an important role in the distribution of yellow birch within a gap. Taylor et Aarssen (1989) found that variation in the height of two-year-old sugar maple seedlings was unaffected by light intensity but was to some extent accounted for by soil variables. Lastly Bigelow et Canham (2002) found that tree species are already segregated along gradients of soil nutrients at the sapling stage.

Because understory species differ in their abilities to capture sunflecks and light patches, temporal heterogeneity of light availability may play a significant role on species composition in understory communities (Chazdon 1988, Ellsworth and Reich 1992, Wayne and Bazzaz 1993). In forest gaps, sugar maple seedlings receiving similar mean daily density of photosynthetic photon flux, but with differing daily time courses of availability exhibited variations in growth (Sipe and Bazzaz 1995). Sugar maple seedlings can also gain a large part of its carbon during sunflecks (Weber et al. 1985). Moreover, a photoprotective

mechanism against high-irrradiance confers to sugar maple a relative tolerance to high irradiance (Veeranjaneyulu and Leblanc 1998). In contrast, Wayne et Bazzaz (1993) demonstrated that light variability may affect the performance of yellow birch since for a similar level of light availability, growth was reduced in variable light environments compared to uniform ones.

The general objective of this study was to examine the competitive interaction between seedlings of sugar maple and yellow birch under contrasting light environments and along a gradient of soil fertility. More specifically, we wanted to determine if a shift in the ranking of species could occur under gradients of light regimes defined by their availability and temporal distribution, and different levels of soil fertility. Moreover, interspecific differences and variations in functional traits to changes in resource availability and distribution were investigated to explore their role in shaping the competitive ability and relative dominance of sugar maple and yellow birch seedlings. To this end, a competition experiment between sugar maple and yellow birch seedlings was conducted over two growing seasons in a greenhouse along a gradient of soil fertility and under three light environments.

2.3 Materials and methods

2.3.1 Experimental design and seedlings' growth conditions

The competition experiment was set up in a greenhouse situated at the Agriculture and Agrifood Canada experimental station in Lennoxville, Quebec (45° 22' N; 71°49' O; 181 m) and conducted over 2 growing seasons (2000 and 2001). The greenhouse was located in an open-field and thus was well-exposed to full sun from dawn to dusk. The space inside the greenhouse was divided into three sections, each section with one replicate. For each replicate, nine experimental treatments were created by the combination of three light environments and three levels of soil fertility. Each treatment was randomly assigned a 1 m^2 space within each section. Within each treatment, the relative competitive ability of sugar

maple and yellow birch was tested with an initial biomass replacement series (Connolly et al. 2001).

Three light environments were defined according to mean light availability and daily time course of light availability: "full sunlight", "homogeneous shade" and "heterogeneous shade". Light availability was 100 % of incident light for the "full sunlight" environment. Both "shaded" understories provided 20 % of incident light, but the daily time course of light availability differed: beneath the "homogeneous shade" environment, seedlings received no midday direct sunlight and an overall more uniform distribution of light availability, whereas under the "heterogeneous shade" environment, seedlings were exposed to a relatively more heterogeneous diurnal light regime, with a midday full sun peak and low light availability in the mornings and afternoons. The "homogeneous shade" light environment was created by suspending a neutral density shade cloth (Industries Harnois, Qc) on a wooden frame. The shade cloth was chosen to filter 80 % of incident light. For the "heterogeneous shade" environment, two layers of 20 %-transmittance shade cloth were superposed and installed laterally on the wooden frame. The frame top was covered with a black plastic film with a 0.2 m^2 circular opening in the middle in order to give the same light amount as the "homogeneous shade" environment (20 % full sunlight). The adjustment of light availability between the "homogeneous shade" and "heterogeneous shade" environments was obtained empirically. During the first growing season, a black plastic film with a circular opening of various sizes (0, 0.2, 0.4, 0.6 and 1 m^2) were randomly installed on the frame top of each of the 9 "heterogeneous shade" environments (3 levels of soil fertility X 3 replicates) for one day long. The photosynthetic photons flux density (PPFD) was measured in both "shaded" environments every hour with a quantum sensor at the centre of gravity of each experimental unit. The regression between the sum of hourly PPFD and opening size allowed the determination of the appropriate opening size. The opening size was then applied to all "heterogeneous shade" environments. This procedure was repeated periodically (approximately every two weeks) to achieve similar light amounts. From the results of the first year, a circular opening of 0.2 m^2 was found to provide an amount of incident light comparable to the "homogeneous shade" environment. A 15 cm gap between the ground and the shade cloth allowed air circulation for both "shade" light environments. Wooden frames

were progressively raised during the course of the experiment to follow the growth of seedlings.

A gradient of soil fertility was created with three relative levels (poor, medium and rich). The soil from a sugar maple and yellow birch dominated forest was used as growth medium since mycorrhizae may influence the growth of sugar maple (Ouimet et al. 1996a) and play a role in interspecific competition (Allen and Allen 1990). The poor soil fertility level was produced by the addition of commercial sand to the forest soil in a proportion of 3 / 4 of sand for 1 / 4 of forest soil. The rich soil fertility level was obtained with the addition of a nutrient solution to the basic growing medium. The soil belonged to the brunisolic order (Anonymous 1998) and was a fine-textured sandy loam. This soil is typical of those on which birch and maple grow naturally (Erdmann 1990, Godman et al. 1990). The upper leaf litter layer was removed before excavation and the upper 15 to 20 cm of soil was utilised for the experiment. It was composed of the H, A and upper B soil horizons. Stones and coarse woody debris were removed by sieving the soil through a 6 mm mesh sieve. Before seedlings establishment, the soil was thoroughly mixed to uniform moisture and soil fertility. The nutrient solution was prepared by diluting a mixture of complete fertilizer (20/20/20 N/P/K [w/w/w] with micro-nutrients, Plants Products) with calcium chloride and magnesium sulfate in deionized water. The addition of Ca and Mg respected the proportion of a modified Hoagland solution. The fertilization treatment resulted in the addition of an equivalent to: 300 /N, 300 /P, 300 /K, 171 /Ca and 102 /Mg in $kg.ha^{-1}.y^{-1}$. The nutrient solution was added four times from mid-May to mid-July during each of the two growing seasons. A complete nutrient solution was preferred over an addition of nitrogen alone for two reasons. First, sugar maple and yellow birch probably differ in their nutrients requirements. Second, the balance of the nutrition is as important as the amount of nutrients (Ouimet and Camire 1995a).

Replacement series design was chosen because it is valuable for determining the relative severities of inter- and intraspecific competition (Goldberg 1996) and comparing the outcome of competition between plant species under different environmental conditions. The

replacement series consisted of two monocultures and a mixture in a proportion of 50 % of each species, expressed in fresh initial biomass. We used biomass instead of density at the start of the experiment because individual seedlings of both species did not have a similar biomass at the start of the experiment, because we anticipated a low mortality rate and because the competitive interaction was evaluated on biomass. The monoculture of sugar maple or yellow birch was composed of an assortment of seedlings of different size (sugar maple: n = 3.3 ± 0.1 (mean ± SE); yellow birch: n = 4.4 ± 0.3), randomly sampled to give a fresh total biomass of 40.0 g ± 5 % at the beginning of the experiment. The mixture was composed of 20 g ± 10 % of fresh total biomass for each species (sugar maple: n = 1.6 ± 0.1; yellow birch: n = 2.1 ± 0.1). A monoculture and a mixture of both species were set up for each of the 9 treatments. The unit of observation is defined as the pot for the monoculture and the species within the pot for the mixture.

Sugar maple and yellow birch seedlings were obtained from the governmental nursery of the Ministry of Natural Resources, Quebec, Berthierville. Sugar maple was two-years old bare roots seedlings, while yellow birch were one-year old plug seedlings. Before establishment, sugar maple roots were rinsed with tape water and the soil of the yellow birch roots were removed under water pressure. Seedlings were planted at the end of May 2000 in 15 cm diameter plastic pots (volume = 3 L) filled with 1.6 kg (on fresh basis) of the two soil fertility levels (i.e. impoverished or basic growing medium). For the mixture, seedlings of each species were planted on each side of the pot. Seedlings were regularly watered to field capacity. No diseases were observed. Pots were shifted randomly every two weeks within each treatment and replicate, in order to avoid possible position effects. Seedlings were brought into a cold chamber in mid-November for the dormant season. The experiment was pursued for a second growing season from mid-May until harvest.

2.3.2 Seedlings' measurements

In mid-August 2001, potted seedlings were brought into laboratory and harvested. We assumed that growth would have been completed by this time of the growing season for the two species (Anderson et al. 2001). To determine the competitive ability and relative dominance of sugar maple and yellow birch seedlings, dry total woody biomass was measured for each observation unit. Leaves were clipped, shoots were then cut at root collar, and roots were delicately removed from the soil and washed under water. Roots were not pot bound. Woody structures (root, stem and branches) and leaves (except for chlorophylls analysis) were placed separately by observation unit in paper bags and then oven dried at 65 °C until constant mass and weighed. Live seedlings were also censored to determine the survival rate at the end of the experiment.

Several growth-related, architectural, biomass allocation, morphological and physiological traits were measured with the idea that each one captures different aspects of the species performance and gives different insights into how they relate to the competitive ability and dominance of sugar maple and yellow birch. Seedlings architecture was investigated for the root system and the crown. Root volume of each observation unit was determined as the amount of water being displaced in a graduated cylinder. The total number of primary lateral branches, the live crown ratio, the crown profile, the height: basal diameter ratio, the leaf area index and the crown volume were determined to describe crown architecture. The live crown ratio and the crown profile were calculated as the ratio of crown length to leader length, and of crown length to mean crown diameter, respectively. Crown length was measured for each observation unit from the base of the crown, the lowest leaf, to the tip of the leader with the leader defined as the shoot that reached the highest point of the crown. Leader length was measured from the root collar to the tip of the leader. Mean crown diameter was determined for each observation unit and was calculated as the mean of two perpendicular diameter measurements, one of which was the maximum crown diameter. Total height, basal diameter and the annual leader increment for the second growing season were measured for each seedling within each observation unit. The annual leader increment was measured from the

bud scar to the tip of the leader. The leaf area index described the leaf display and is defined as the ratio of total leaf area to projected crown area. The total leaf area per observation unit was estimated from the product of the total number of leaves with the leaf area. The projected crown area was determined with the formula of ellipse area. The product of the projected crown area with crown length estimated the crown volume.

The biomass allocation pattern was estimated by the root: shoot ratio, the leaf area ratio and the leaf mass ratio. Leaf area ratio and leaf mass ratio were calculated as the ratio of total leaf area to dry total woody biomass, and of total leaf biomass to dry total woody biomass, respectively.

Leaf morphology was examined by measuring specific leaf area and leaf dry matter content. During leaf sampling, three leaves per observation unit were randomly subsampled. These leaves were placed in a Ziploc bag with moist tissue paper and kept in the dark at 4 °C for 24 hours for hydration according to the precautions proposed by Garnier et al. (2001). After rehydration, leaves were dried with tissue paper to remove any surface water, and immediately weighed to determine their saturated fresh mass. Their leaf area was obtained by analysing a digital picture with WinFolia (Régent Instruments Inc., Québec, Qc). Samples were then dried at 65 °C until constant mass and weighed. Specific leaf area was calculated as the ratio of leaf area to leaf dry mass, and leaf dry matter content as the ratio between leaf dry mass and saturated fresh mass.

Three to five other leaves were also randomly selected for chlorophylls analysis. Leaf extracts for chlorophylls analysis was performed on about 0.5 g (fresh weight) of leaf tissue. Being under cover from light, leaf material was ground in 20 ml volume of cold 80 % (v/v) acetone and then centrifuged at 7 g for 20 min at 4°C. The absorbance of the supernatant was read at wave length of 643 and 660 nm with a spectrophotometer. Concentrations of chlorophyll a and b were determined using the following formulas:

$$\text{Chl a} = 12.21 * DO_{643} - 2.81 * DO_{660}$$

$Chl\ b = 20.13 * DO_{660} - 5.03 * DO_{643}$

Chlorophylls concentrations were expressed on a tissue dry mass basis and chlorophyll a: b ratio was calculated. Total chlorophylls were calculated as the sum of chlorophyll a and b.

2.3.3 Indices, graphs and statistical analyses

To assess the competitive ability of each study species, relative yield (RY) was determined from total woody biomass data, as follows:

$RY_i = Y_{mix\,i} / Y_{mono\,i}$

where $Y_{mix\,i}$ represents the yield of species i in mixture, and $Y_{mono\,i}$ the yield of species i in monoculture. The relative yield total (RYT) was calculated as the sum of the RY of each species to examine the nature of the interaction between sugar maple and yellow birch.

Replacement series diagrams were constructed to examine visually the nature of interference and the competitive ability. In replacement diagrams, observed RY of each species is plotted against the appropriate planting proportion (i.e. 0, 50 and 100 %). Expected RY for a species occurs when plants of this species grow equally well in mixture than in monoculture (i.e. diagonal line). Comparisons of observed RY of each species with their expected RY indicate (1) competition if the observed RY curve of one species is concave and that of the second convex, (2) niche differentiation if observed RY curves of both species are convex, or (3) mutual antagonism if observed RY curves of both species are concave. If observed RY curves are linear (i.e. do not differ from expected), the ability of one species to interfere with the other is equivalent. Values of RYT of 1.0 imply that there is competition, > 1.0 imply niche differentiation, and < 1.0 imply mutual antagonism (Harper 1977). Replacement diagrams may therefore reveal (in)equality of intra- and interspecific interference, and may indicate the directions of imbalances (Jolliffe 2000).

Total woody biomass data were also used to calculate an index of aggression (A) in order to evaluate the relative dominance among the two species:

$A_i = [Y_{mix\,i} / (Y_{mix\,i} + Y_{mix\,j})] * 100$

where $Y_{mix\,i}$ represents the yield of species i in mixture (Weigelt and Jolliffe 2003) and $Y_{mix\,j}$, the yield of species j in mixture.

Mean comparison tests with Wilcoxon Signed-Rank non-parametric test were also carried out to test our hypothesizes: (i) the observed value of RYT for the mixture was not significantly different to the expected RYT value of 1.0, implying a competitive interaction between the two study species, and (ii) the observed values of RY and A were significantly inferior to the expected value of 0.5 and 50 %, respectively, for sugar maple. For yellow birch, the inverse prediction was expected.

The relative performance of the two study species was also analysed on absolute basis with a full factorial ANOVA of the total woody biomass data to test for any main treatment effects and interaction effects of light environments, levels of soil fertility, type of interaction (intra-*versus* interspecific) and species. Prior to analysis, the values of total woody biomass measured in monoculture were divided per 2 to standardize the response with mixture. Following ANOVA, ***post-hoc*** means comparisons tests were done to detect significant differences. For each significant interaction effect, an analysis of contrasts was performed to make comparisons among all the levels of one factor in the interaction for each level of each factor in the interaction. Survival was analyzed with multiple logistic regression to examine the effects of light environments, levels of soil fertility, type of interaction and species, and their interactions.

A one-way nonparametric ANOVA (Welch ANOVA) was carried out to detect significant species-specific differences in ecophysiological traits. Prior to ANOVA, the values of crown volume, root volume and the total number of primary lateral branches measured in monoculture were divided per 2 to standardize the response with mixture.

The index of the relative performance of ecophysiological traits was calculated for each species as follows:

$RP_i = P_{mix\,i} / P_{mono\,i}$

where $P_{mix\,i}$ is the value of species i in mixture and $P_{mono\,i}$ is the value of species i in monoculture (Weigelt and Jolliffe 2003). Spearman's rank correlations of the relative performance of ecophysiological traits with the relative yield were performed for the whole dataset because no major shift in the relative competitive ability was noticed. Spearman's rank correlations of the relative performance of ecophysiological traits with the index of aggression were examined separately for seedlings grown under "heterogeneous shade" and other treatments (except "heterogeneous shade") because of the reversal in the relative dominance.

All statistical analyses were performed with JMP software (SAS Institute Inc., version 4.0.2, 2000). Data transformations were used when necessary to meet the normality and homoscedasticity assumptions for the parametric analyses. Following ANOVA's, *post-hoc* multiple comparisons tests were then performed using Tukey's HSD method to detect significant differences. Significance level was set at $p = 0.05$.

2.4 Results

2.4.1 Nature of interference, relative competitive ability and dominance

When data were analyzed at the species level (i.e. including all 9 treatments), the Wilcoxon sign-rank non-parametric test indicated that the observed value of RYT for the mixture was close to the expected RYT value of 1.0 (RYT = 0.98 ± 0.03 (Mean ± SE); $p = 0.088$), meaning that the two species competed for the same limiting resources. The observed RY value of sugar maple was significantly inferior to the expected RY value of 0.5 ($RY_{sm} = 0.43 \pm 0.02$; $p = 0.001$), while the observed RY value of yellow birch was significantly superior

(RY_{yb} = 0.55 ± 0.03; p = 0.012). The concave RY curve of sugar maple indicates the effect of interspecific competition on seedlings of this species was greater than that of intraspecific competition. On the other hand, the convex RY curve of yellow birch reveals the effect of interspecific competition on seedlings of this species was less than that of intraspecific competition (Fig. 2.1). The observed value of A was not significantly different from the expected value of 50 % for both species (A_{sm} = 50.34 ± 1.80, p = 0.628; A_{yb} = 49.66 ± 1.80, p = 0.628).

Mean comparison tests of RYT and RY for each main treatment showed some significant differences (Fig. 2.2). In nutrient-rich conditions, the observed value of RYT for the mixed culture was significantly different to the expected RYT value of 1.0 (RYT = 0.93 ± 0.02, p = 0.039), suggesting a possible mutual antagonism between sugar maple and yellow birch. The observed value of RYT for the mixed culture was close to the expected RYT value of 1.0 in other treatments (p > 0.05), indicating a competitive interaction between the two study species. The observed RY value of sugar maple was significantly lower than the expected RY value of 0.5 in "full sunlight" (RY_{sm} = 0.43 ± 0.03, p = 0.025), under "homogeneous shade" (RY_{sm} = 0.40 ± 0.03, p = 0.004), in the poor and medium levels of soil fertility (RY_{sm} = 0.43 ± 0.04, p = 0.029; RY_{sm} = 0.42 ± 0.02, p = 0.010, respectively); whereas the observed RY value of yellow birch was significantly greater than the expected RY value of 0.5 under "homogeneous shade" (RY_{yb} = 0.64 ± 0.06, p = 0.020) and in the medium level of soil fertility (RY_{yb} = 0.65 ± 0.06, p = 0.004). The observed RY values of sugar maple and yellow birch were close to the expected RY value of 0.5 under "heterogeneous shade" and in the rich level of soil fertility (p > 0.05), indicating that intra- and interspecific competition were in balance. The observed A value of sugar maple was significantly lower than the expected A value of 50% (A_{sm} = 44.14 ± 3.23, p = 0.027), and the observed A value of yellow birch was significantly greater than the expected A value of 50% under "homogeneous shade" (A_{yb} = 55.86 ± 3.23, p = 0.027). Contrary to our hypothesis, the observed A value of sugar maple was significantly greater than the expected A value of 50% (A_{sm} = 55.00 ± 2.79, p = 0.049), and the observed A value of yellow birch was significantly lower than the expected A value of 50% under "heterogeneous shade" (A_{yb} = 45.00 ± 2.79, p = 0.049). The observed A value

was not significantly different from the expected A value of 50 % in other environmental conditions for both species ($p > 0.05$).

The observed values of RYT, RY and A were not significantly different to their expected values for any combinations of treatment ($p > 0.05$; figures not shown).

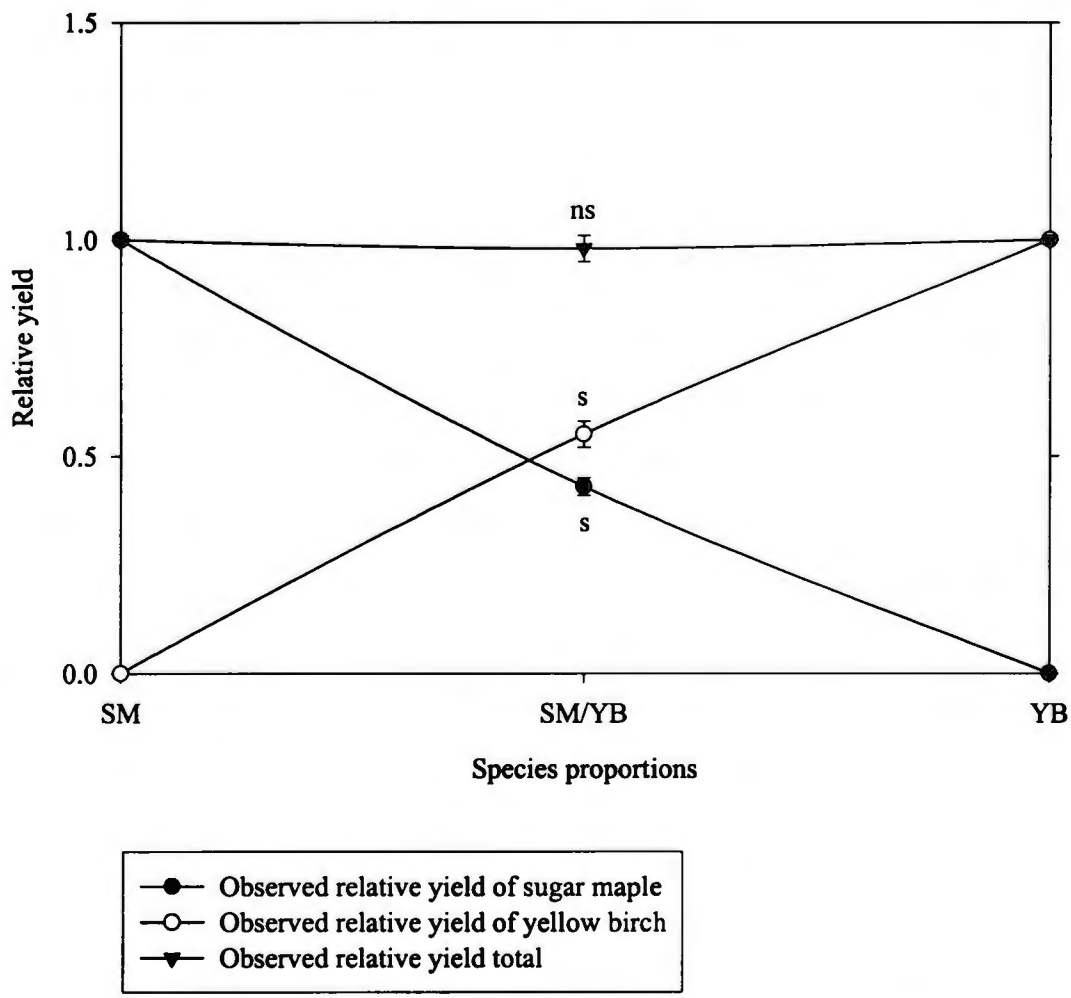

Figure 2.1 Replacement series diagram at the species level (i.e. including the nine treatments). SM: monoculture of sugar maple; SM/YB: mixture; YB: monoculture of yellow birch. ns: non-significant; s: significant. Values represent means (± SE).

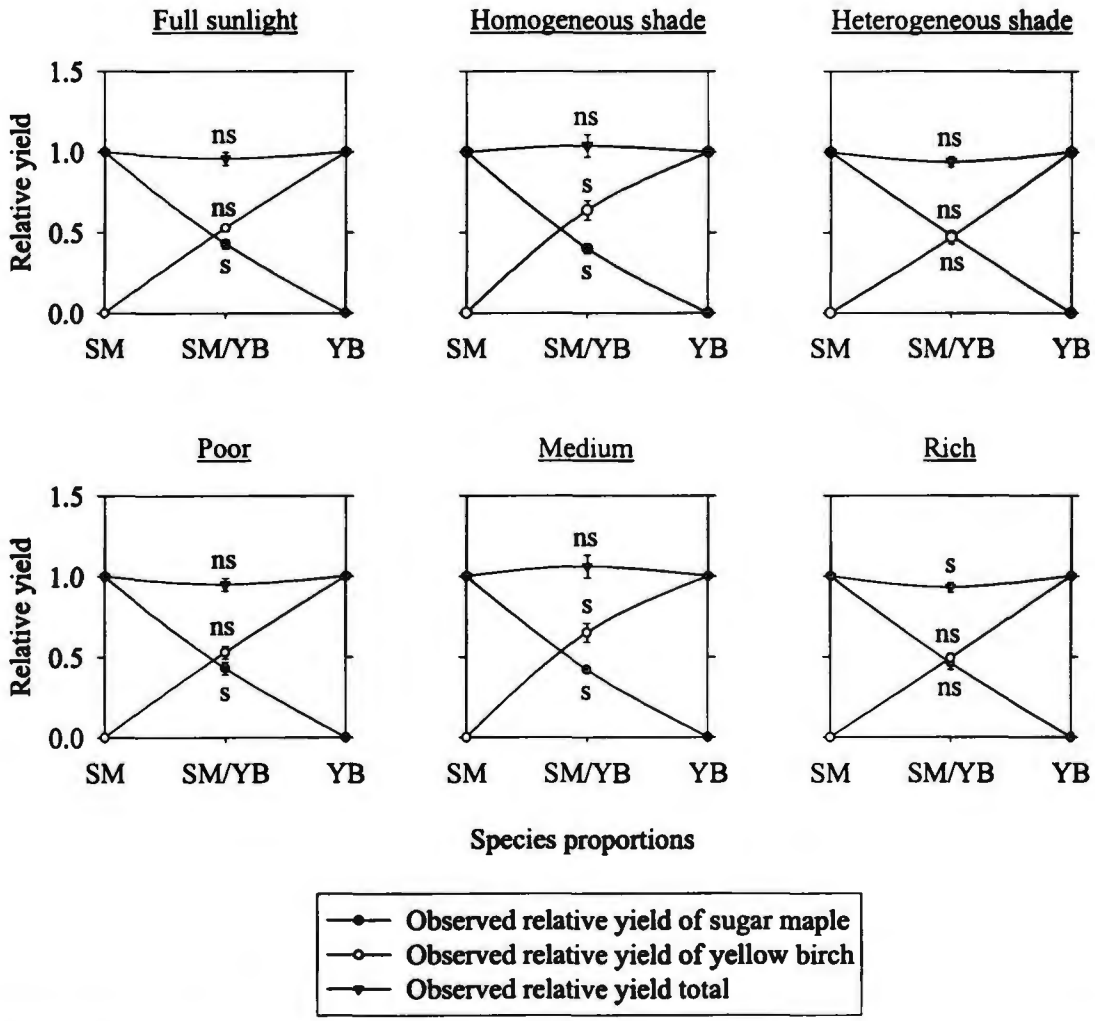

Figure 2.2 Replacement series diagram for each of the three light environments and the three levels of soil fertility. Abbreviations are identical to those of figure 1. Values represent means (± SE).

2.4.2 Interactions effects on total woody biomass and survival

Two significant triple interactions explained the variation in total woody biomass measured at the end of the competition experiment (Table 2.1). Firstly, the total woody biomass was affected by the light environments, types of competition and species (LE X C X S: $p = 0.033$). When grown in monoculture, the total woody biomass of sugar maple was reduced

with decreasing light availability, but also by a more temporally variable distribution of light availability. When grown in mixture, its biomass was only reduced by a decrease in light availability (Fig. 2.3a). By contrast, the total woody biomass of yellow birch diminished only with decreasing light availability when grown in monoculture. Its biomass was reduced only by a more variable distribution of light availability when grown in mixture (Fig. 2.3b). The total woody biomass of sugar maple was significantly greater in monoculture than in mixture in "homogeneous shade" (Fig. 2.3a). The opposite was observed for yellow birch (Fig. 2.3b). Otherwise the total woody biomass of sugar maple and yellow birch did not differ significantly between the types of competition in "full sunlight" and "heterogeneous shade".

Secondly, woody biomass was affected by the light environments, levels of fertility and species (LE X F X S: $p = 0.030$). The total woody biomass of sugar maple grown in poor- and medium-nutrient conditions was reduced only by the combination of a decrease and a more variable distribution in light availability. When grown in rich-nutrient conditions, its biomass was reduced with decreasing light availability, but also by a more variable distribution of light availability (Fig. 2.4a). In comparison, the total woody biomass of yellow birch grown in poor-nutrient conditions diminished with a more variable distribution of light availability. When grown in medium- and rich-nutrient conditions, its biomass was reduced by a decrease in light availability, but also a more variable distribution in light availability (Fig. 2.4b). Additionally, the total woody biomass of sugar maple grown in "full sunlight" was significantly greater in the rich level of soil fertility in comparison with the poor and medium levels of soil fertility. The gradient of soil fertility did not affect the total woody biomass of sugar maple in "homogeneous shade" and in "heterogeneous shade" (Fig. 2.4a). The total woody biomass of yellow birch grown in "full sunlight" was similar but significantly greater in the medium and rich levels in comparison with the poor level of soil fertility. The total woody biomass of yellow birch did not vary with soil fertility when grown in "homogeneous shade", but increased with increasing soil nutrient conditions when grown in "heterogeneous shade" (Fig. 2.4b).

Survival was not affected by any main treatments and their interactions (light environments, levels of soil fertility, type of interaction and species) ($p = 0.268$).

Table 2.1
Analysis of variance of final total woody biomass

Source	Final total woody biomass[1]		
	DF	F ratio	p > F
Light environment (LE)	2	58.539	**< 0.001**
Fertility (F)	2	22.234	**< 0.001**
Competition (C)	1	2.301	0.134
Species (S)	1	8.475	**0.005**
LE x F	4	3.621	**0.010**
LE x C	2	0.225	0.799
LE x S	2	3.005	0.056
F x C	2	0.234	0.792
F x S	2	0.036	0.965
C x S	1	7.145	**0.009**
LE x F x C	4	0.386	0.818
LE x F x S	4	2.841	**0.030**
LE x C x S	2	3.578	**0.033**
F x C x S	2	1.130	0.329
LE x F x C x S	4	0.292	0.883

[1]: ln-transformed.

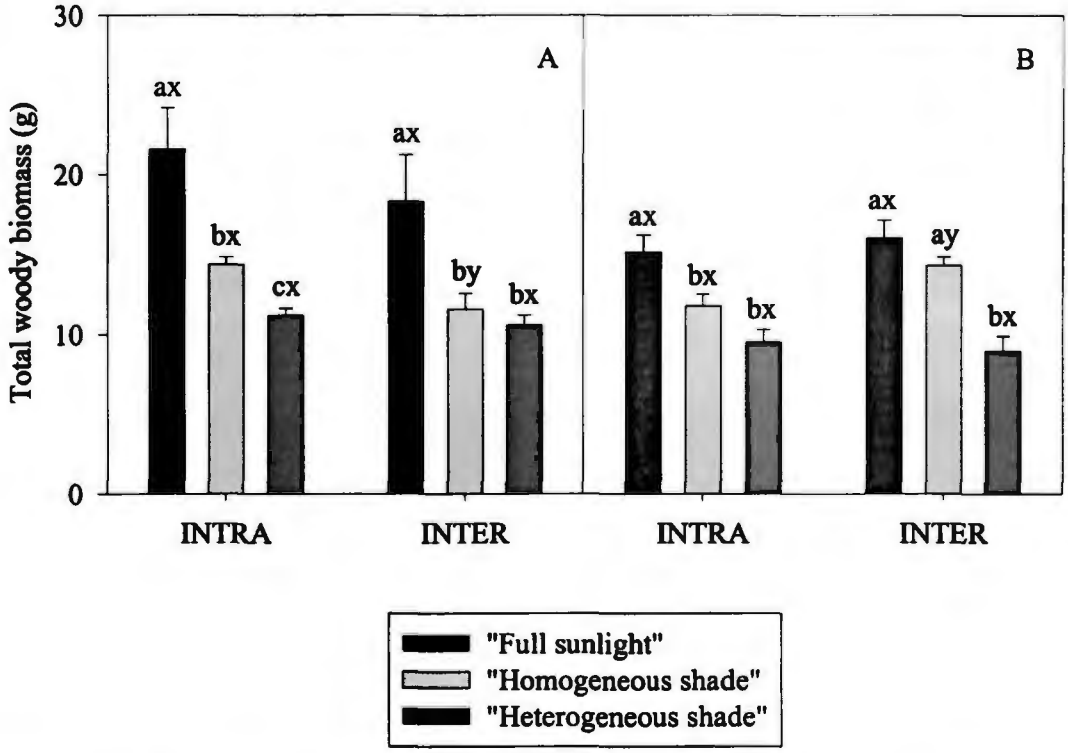

Figure 2.3 Interactive effect of light environments and the nature of competition on the total woody biomass of sugar maple (a) and yellow birch (b) (LE x C x S). Different letters (a and b) indicate significant differences between light environments within each type of competition and species. Different letters (x and y) indicate significant differences between the types of competition within each light environment and species. INTRA: intraspecific competition; INTER: interspecific competition. Values represent means (± SE).

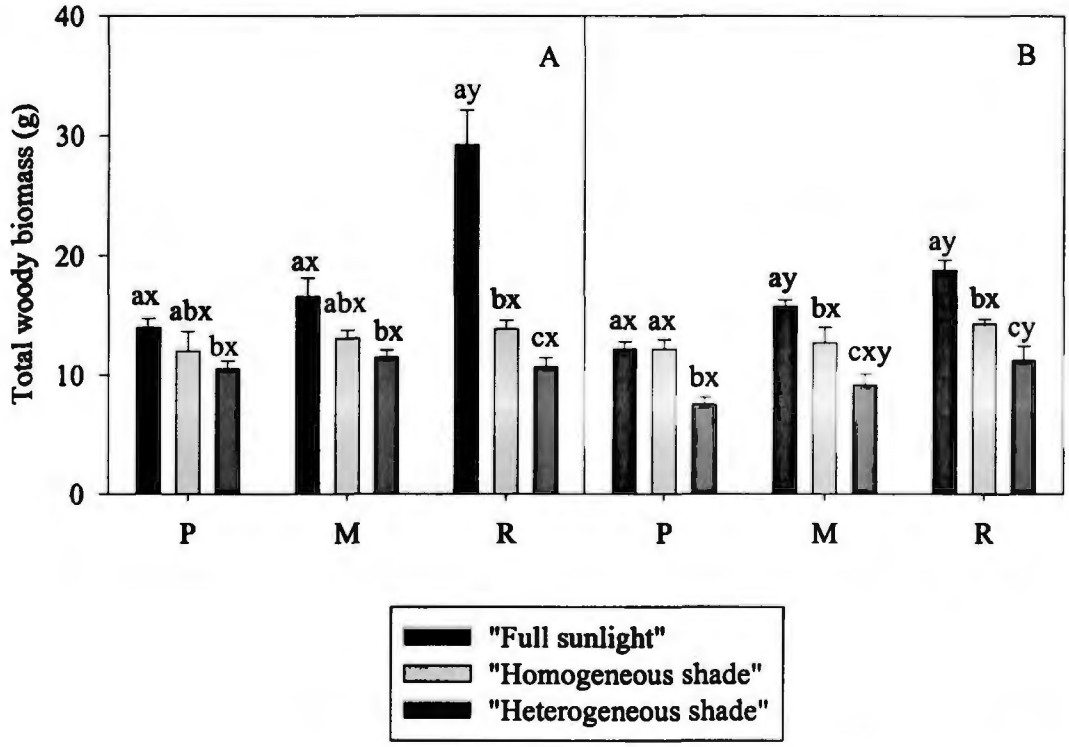

Figure 2.4 Interactive effect of light environments and soil fertility on the total woody biomass of sugar maple (a) and yellow birch (b) (LE x F x S). Different letters (a and b) indicate significant differences between light environments within each level of soil fertility and species. Different letters (x and y) indicate significant differences between levels of soil fertility within each light environment and species. P: poor; M: medium; R: rich. Values represent means (± SE).

2.4.3 Interspecific differences and phenotypic plasticity in ecophysiological traits

Species-specific differences in ecophysiological traits were noted at the end of the competition experiment (Table 2.2). Sugar maple presented a greater crown profile, root: shoot ratio and leaf dry matter content ($p < 0.001$). In contrast, yellow birch had a greater total height, annual leader increment, crown volume, live crown ratio, height: basal diameter ratio, leaf area ratio and specific leaf area ($p < 0.05$). The values of other ecophysiological traits were similar between the two study species ($p > 0.05$) (Table 2.2).

For most ecophysiological traits, the range of values for yellow birch was larger than that of sugar maple: total height, annual leader increment, crown volume, height: basal diameter ratio, leaf area index, leaf area ratio, leaf mass ratio, specific leaf area, leaf dry matter content and chlorophylls total. Otherwise, the range of values was similar (total number of primary lateral branches and live crown ratio) or larger for sugar maple than yellow birch (root volume, crown profile, root: shoot ratio and chlorophyll a: b ratio) (Table 2.2).

Table 2.2
Comparison of ecophysiological traits between sugar maple and yellow birch

Ecophysiological traits	Sugar maple		Yellow birch	
	Mean (± SE)	Range	Mean (± SE)	Range
Growth				
Total height (cm)	55.4 (1.1) **a**	40.0	69.2 (1.9) **b**	62.0
Annual leader increment (cm)	9.2 (0.7) **a**	25.0	11.4 (0.9) **b**	31.5
Architecture				
Crown volume (cm3)	26970 (1587) **a**	47810	82683 (8101) **b**	258133
Root volume (cm3)	28.8 (2.1) **a**	70.0	27.6 (1.2) **a**	35.0
Total number of primary lateral branches	3.46 (0.25) **a**	7.00	3.77 (0.27) **a**	7.50
Live crown ratio (cm.cm-1)	0.61 (0.03) **a**	0.90	1.02 (0.02) **b**	0.89
Crown profile (cm.cm-1)	1.32 (0.06) **a**	2.04	0.65 (0.02) **b**	0.81
Height: basal diameter ratio (cm.mm-1)	12.16 (0.40) **a**	12.28	17.47 (0.61) **b**	17.47
Leaf area index (cm2.cm-2)	1.58 (0.07) **a**	2.43	1.63 (0.09) **a**	2.92
Biomass allocation				
Root: shoot ratio (g.g-1)	1.14 (0.09) **a**	2.95	0.68 (0.03) **b**	1.20
Leaf area ratio (cm2.g-1)	93.25 (5.26) **a**	161.77	137.73 (9.53) **b**	294.83
Leaf mass ratio (g.g-1)	0.18 (0.00) **a**	0.14	0.18 (0.01) **a**	0.19
Leaf morphology				
Specific leaf area (cm2.g-1)	350.45 (10.71) **a**	302.07	418.93 (19.86) **b**	626.24
Leaf dry matter content (g.g-1)	0.38 (0.01) **a**	0.17	0.24 (0.01) **b**	0.22
Leaf physiology				
Chlorophylls total (mg.g-1)	86.87 (6.75) **a**	174.97	109.58 (9.97) **a**	249.63
Chlorophyll a: b ratio	0.11 (0.00) **a**	0.08	0.11 (0.00) **a**	0.06

Different letters indicate significant differences between sugar maple and yellow birch.

2.4.4 Relationships of ecophysiological traits with the competitive ability and dominance

RY_{sm} was positively related to the relative performance of root volume ($\rho = 0.572$, $p = 0.002$). A_{sm} grown under "heterogeneous shade" was positively associated with the relative performance of live crown ratio ($\rho = 0.667$, $p = 0.050$), and to a certain extent, with that of annual leader increment ($\rho = 0.650$, $p = 0.058$). Positive relationships were found between RY_{yb} and the relative performance of crown volume ($\rho = 0.455$, $p = 0.022$), root volume ($\rho = 0.506$, $p = 0.010$) and leaf area index ($\rho = 0.411$, $p = 0.041$). RY_{yb} was negatively correlated with the relative performance of specific leaf area ($\rho = -0.435$, $p = 0.030$) and chlorophylls total ($\rho = -0.450$, $p = 0.024$). A_{yb} was positively associated with the relative performance of crown volume ($\rho = 0.641$, $p = 0.004$) and root volume ($\rho = 0.670$, $p = 0.002$), and negatively related to that of chlorophylls total ($\rho = -0.494$, $p = 0.037$) in all environmental conditions, except "heterogeneous shade". A negative correlation between A_{yb} and root: shoot ratio was observed when grown under "heterogeneous shade" ($\rho = -0.857$, $p = 0.014$).

2.5 Discussion

2.5.1 Competitive interaction between sugar maple and yellow birch seedlings

The results obtained at the species level revealed that the two species overall competed for the same limiting resources when grown together. This first result contrasts clearly with Tubbs' findings (1973), which showed that the growth of yellow birch seedlings was suppressed in the presence of sugar maple seedlings despite the absence of competition. Tubbs suggested that growing maple roots reduced the growth of yellow birch roots by the exudation of an inhibitor and proposed that allelopathy would probably augment the competition exerted by sugar maple on yellow birch. Our results did not detect this allelopathic inhibition. On the contrary, seedlings of yellow birch displayed an overall greater competitive ability than seedlings of sugar maple despite a lower total woody biomass for yellow birch at the establishment of the competition experiment. The discrepancy

between the two studies can lie in the differences in experimental conditions, especially the density, the duration of the experiment and the abiotic factors experienced by seedlings. Factors such as light and nutrient availability can influence the production of allelochemicals in plants and are considered to play an important role in the expression of allelopathy (Kruse et al. 2000). The competitive interaction between sugar maple and yellow birch was slightly asymmetric, like most pairwise interactions, meaning that one species grew better in mixture than in monoculture while the other species grew poorer in mixture than in monoculture (Shipley 1993). The asymmetry of interspecific competition was small however, and no competitive exclusion was observed. The intensity of the interspecific competition was therefore minimal, indicating that the competitive performance of the two species was approximately of the same order. Finally we think that the superior competitive ability of advanced regeneration of sugar maple (Erdmann 1990) is associated with its early establishment and the relative size than the identity of species.

Light environment and soil fertility did not modify the competitive nature of the interference between sugar maple and yellow birch. Even in rich-nutrient conditions, we preferred to conclude to a competitive interaction over a possible mutual antagonism since the observed RY curves of both species were not concave and the observed values of the index of aggression were not significantly different to their expected value of 50%. Additionally the nature of interference between the two species in mixture, the competitive ability of each species and their relative dominance were not influenced significantly by any particular combination of light environment and soil fertility level. This result do not support the idea that sugar maple or yellow birch would be a superior competitor for only a optimal resource ratio of light availability, light temporal distribution and soil nutrient availability (Tilman 1982).

Yellow birch appeared more competitive than sugar maple in "full sunlight", under "homogeneous shade", in poor and medium-nutrient conditions, and the competitive interaction was therefore asymmetric, but the intensity of competition was minimal. Intra- and interspecific competition were in balance for both species under "heterogeneous shade"

and in the rich level of soil fertility. The ability of one species to interfere with the other was therefore equivalent and the competitive interaction was symmetric, indicating a competition-mediated coexistence. Symmetric competition occurs when either (i) interspecific interaction is more intense than intraspecific interactions for both species or (ii) interspecific interaction is less intense than intraspecific interactions for both species. The second possibility enables stable two-species equilibrium (Shipley and Keddy 1994). As revealed by the comparison of the standard deviation of the total woody biomass (data not shown), the more uneven biomass distribution would suggest that interspecific interaction was more intense than intraspecific interactions for both species in "heterogeneous shade" and in the rich level of soil fertility (Gurevitch et al. 2002).

Subtle variations in the competitive ability of each species and the relative dominance were uncovered among the three light environments and levels of soil fertility, but sugar maple and yellow birch did not clearly segregate along the gradient of soil fertility, between the two levels and the two temporal patterns of light availability. This result suggests that a strong overlap exist among sugar maple and yellow birch at least for these three dimensions and this two species might belong to the same guild. Under "homogeneous shade", yellow birch was competitively superior and dominated lightly the mixture after two growing seasons. We expected that the competitive ability of yellow birch, the intensity of interspecific competition and the relative dominance of yellow birch would strengthen as light availability increased since Logan (1965) found that the increase of biomass accumulation with light availability was proportionally more important for yellow birch than sugar maple seedlings grown under the range of 13 to 100 % of full sunlight. In fact, an increase in light availability from 20 % to 100 % of full sun decreased to a certain extent the competitive ability of yellow birch but did not affect the competitive ability of sugar maple. As a result yellow birch was still competitively superior to sugar maple, but did not dominate the mixture in "full sunlight". Yellow birch did not seem to respond as much as sugar maple to the increase of light availability from 20% to 100% of full sunlight. Our results indicates that 20% of light availability was limiting the growth of sugar maple in the rich level of soil fertility and that the increase in light availability up to 100% of full sunlight had a positive effect on the growth of sugar maple whatever the nature of competition.

We anticipated that relatively more variable light conditions would decrease the competitive ability of yellow birch and increase that of sugar maple. The intensity of the interspecific competition and the relative dominance of yellow birch would lessen. We observed the expected variations in the competitive ability of sugar maple and yellow birch and found unexpectedly that sugar maple became slightly more dominant in mixture under "heterogeneous shade". Firstly, our study shows that a more variable pattern of light availability reduced the growth of yellow birch but only in interspecific competition, whereas the opposite was observed for sugar maple (i.e. in intraspecific competition). Secondly, more variable light conditions decreased the growth of yellow birch regardless of the level of soil fertility, whereas the growth of sugar maple was negatively affected only in rich-nutrient soil conditions.

Yellow birch was competitively superior to sugar maple except in the rich level of soil fertility. Sugar maple and yellow birch are known to have high requirements of soil nutrients (Anderson et al. 2001), and soil nutrient availability was limiting the growth of sugar maple and yellow birch under certain light environments ("full sunlight" for both species and "heterogeneous shade" for yellow birch). The greater competitive ability of yellow birch observed in limited soil nutrients conditions suggest that yellow birch may be slightly less demanding and/or increase soil nitrogen availability in its rhizosphere due to a greater rhizodeposition (Phillips and Fahey 2005). The competitive ability of yellow birch declined in the rich level of soil fertility and the competitive abilities were equivalent. Nutrient availability could have been sufficient to sustain the growth of both species in the rich level of soil fertility, and thus competition for soil nutrients may not have take place in this high level of soil fertility.

2.5.2 Interspecific differences in ecophysiological traits, phenotypic plasticity and contribution of functional traits to the competitive ability and dominance of sugar maple and yellow birch seedlings

As reported in numerous studies (Bellefleur and Villeneuve 1984, Walters and Reich 1996, Beaudet et al. 2000, Sutherland et al. 2000), yellow birch showed greater size and height growth rate than sugar maple. These two traits have been recognized to confer competitive advantage to tree species in gaps (Gurevitch et al. 2002) and give yellow birch the ability to occupy space and preempt resources more quickly. We also think that interspecific differences in the seasonal pattern of shoot growth may have played a role in the relative performance of these two species and may explain their relative competitive ability. Unlike the determinate and truncated shoot elongation of sugar maple, the indeterminate and continuous shoot growth of yellow birch may confer the possibility to acclimate within a single growing season to changing environmental conditions, and likely take advantage of more favourable conditions along the growing season.

The competitive superiority of yellow birch is consistent with its greater crown volume, live crown ratio, leaf area ratio and specific leaf area, and lower crown profile. Leaf area ratio is an important determinant of growth (Tilman 1988, Walters et al. 1993a). These traits enable yellow birch to maximize light capture. Beside, the superior height basal diameter ratio of yellow birch may give it the possibility to overtop the surrounding competitive understory vegetation. The small competitive suppression of sugar maple is probably related to traits important for tolerance of low resource availability and resource conservation. As already found by Logan (1965), sugar maple allocates relatively more biomass to its root system which may play an important role in the poor and medium growing media not subject to a replenishment of soil nutrients. Differences in specific leaf area and leaf dry matter content reveal substantial functioning differences between the two species: higher SLA and lower LDMC of yellow birch suggest a rapid production of biomass, while lower SLA and higher LDMC confer to sugar maple a more efficient conservation of nutrients (Garnier et al. 2001).

Our study indicated that in general yellow birch showed more phenotypic plasticity, which will confer it the ability to acclimate in the environmental conditions experienced by seedlings (i.e. light availability and variability, and nutrients availability). The broader range of values for chlorophyll a / b and crown profile possibly indicates a better acclimation of sugar maple to a relatively more heterogeneous pattern of light availability, whereas the more important range of values for root volume and root: shoot ratio are likely related with a better tolerance of the scarcity of soil nutrients.

Since the relative performance of functional traits expressed the variations in functional traits among monoculture and mixture, the inspection of the significance and strength of association between the relative performance of functional traits and the relative yield, or the index of aggression allowed us to identify the important determinants of the competitive ability and dominance of sugar maple and yellow birch. Crown and root volumes were positively related with the competitive ability and dominance of yellow birch (except under "heterogeneous shade"), indicating a competition for space but indirectly for light and nutrient availability. By contrast, the positive relationship between root volume and the competitive ability of sugar maple underscored that sugar maple seemed to be more sensitive to the competition for nutrient availability than for light availability. This interspecific difference may be related to the contrasting shade tolerance of these two species. The positive dependence observed for yellow birch between leaf area index and the competitive ability may be related to the role of mutual shading in the attenuation against high irradiance and leaf temperature. Although specific leaf area and the content of chlorophylls are good positive correlates of the photosynthetic capacity of plants, the relative performance of these two indices were negatively correlated with the competitive ability and the dominance of yellow birch, suggesting that the interspecific competition was rather for soil resources than for light. Sugar maple may gain its dominance under "heterogeneous shade" through a more efficient capture of lateral light as indicated by the positive association between its dominance and live crown ratio. The negative relationship of the dominance of yellow birch with a higher allocation of biomass to root may indicate that yellow birch tended to increase its dominance under "heterogeneous shade" by allocating more biomass for above-ground growth, but was constrained for allometric reasons.

2.6 Conclusion

In conclusion, our study showed that the interaction between sugar maple and yellow birch was competitive and that competition was in general very slightly asymmetric. A medium level of soil fertility or a homogeneous shade was particularly favorable for the expression of the competitive ability of yellow birch. Despite a strong gradient of soil fertility and contrasting light environments, we did not observed considerable change in the relative competitive ability and dominance except under "heterogeneous shade", suggesting no niche differentiation along the gradient of soil fertility and light availability. The relative dominance was lightly influenced by the temporal pattern of light availability in shady environment at the advantage of sugar maple. The relative similarity in the competitive ability and the small magnitude of dominance were probably due to the fact that these two co-occuring species belong to the same growth form, were quite similar in their initial size, and have roughly the same ecological requirements. We conclude that the outcome of competition between sugar maple and yellow birch appeared more consistent (*i.e.* shifting competitive hierarchy), based on the absence of a niche differentiation and the consistency of ranking between sugar maple and yellow birch.

Sugar maple and yellow birch display two contrasting growth strategies: sugar maple presents a conservative (or survivalist) strategy whereas yellow birch presents a more exploitative strategy with an opportunistic growth pattern (Bormann and Likens 1979, Beaudet and Messier 1998, Gaucher et al. 2005). A combination of traits (e.g. LAR, SLA) confers yellow birch seedlings its superior ability to preempt resources, allows it to grow rapidly when resources are abundant, and ultimately confers its dominance. Sugar maple possesses functional traits which confer advantages under conditions of low resource availability (e.g. high R: S ratio and LDMC).

Finally, it is questionable if the competition between sugar maple and yellow birch plays an important role in the regeneration of these two species in birch-maple stands. We also think that our study is relevant to forest management since the competitive hierarchy observed in

this study suggests that the regeneration composition can be overall relatively predictable across contrasting understory light environments and levels of soil fertility in birch-maple stands.

CHAPITRE III

DO GROWTH AND SURVIVAL DETERMINE THE SHADE TOLERANCE OF SUGAR MAPLE AND YELLOW BIRCH AT THE JUVENILE STAGE?

3.1 Avant-propos

Ce chapitre sera soumis à la « Revue Canadienne de la Recherche Forestière » avec les co-auteurs suivants : Dodick Gasser, Christian Messier et Yves Mauffette.

3.2 Introduction

Sugar maple (*Acer saccharum* Marsh) and yellow birch (*Betula alleghaniensis* Britton) are two tree species coexisting in the northern hardwood forests of eastern North America. Among several silvical characteristics, the relative degree of shade tolerance is thought to play a major role in explaining their relative competitive ability (Erdmann 1990, Godman et al. 1990) and their regeneration pattern along a gradient of canopy openings (Forcier 1975, Bormann and Likens 1979, Beaudet and Messier 1997, Anderson et al. 2001). Sugar maple and yellow birch differ in their strategy of regeneration and growth. Sugar maple is a shade-tolerant species (Godman et al. 1990), a small-gap specialist (Canham 1988b), and is classified into the "persistent, slow-growing understory tolerant regeneration guild" (Sutherland et al. 2000). Sugar maple is able to sustain multiple episodes of growth suppression and release (Canham 1985, Payette et al. 1990) and can survive for long periods of time under deep shade as advance regeneration (Marks and Gardescu 1998, McClure et al.

2000). In contrast, yellow birch is a intermediate shade-tolerant species, a gap-phase species (Erdmann 1990, Pacala et al. 1996), and one of the "opportunisitic, long lived intermediate regeneration guild" (Sutherland et al. 2000). Yellow birch is thought to be too intolerant to rely on advanced regeneration (Forcier 1975, McClure et al. 2000) and requires canopy openings for growth (Payette et al. 1990, Anderson et al. 2001). Related to the phenology of their shoot growth (Anderson et al. 2001), sugar maple is considered to present a conservative (or survivalist) growth pattern whereas yellow birch displays an opportunistic growth pattern (Bormann and Likens 1979, Beaudet and Messier 1998, Gaucher et al. 2005), but at the expense of its survival (Messier and Nikinmaa 2000).

A better understanding of shade tolerance requires attention to the underlying mechanisms and associated life-history traits. Three possible trade-offs have been proposed to explain variation in shade tolerance among understory tree species: low-light growth versus high-light growth based on ecophysiological differences (Bazzaz 1979, Givnish 1988, Walters and Reich 1999), low-light survival versus high-light growth (Pacala et al. 1993, Pacala et al. 1994a, Kobe et al. 1995, Pacala et al. 1996, Walters and Reich 1999) and height growth versus size (Givnish 1988, Messier et al. 1999, Messier and Nikinmaa 2000). Based on the trade-off between low-light growth and high-light growth, shade-tolerant species may grow faster than shade-intolerant species in low light, and vice versa. According to the trade-off between low-light survival versus high-light growth, shade-intolerant species that grow quickly under high light tend to have low survival under low light. In contrast, shade-tolerant species that grow slowly under high light tend to have high survival under low light. The third trade-off states that an increase in height generates a cost in survival under low light level exhibiting thus a maximum sustainable height. Messier et Nikinmaa (2000) proposed that the slow growth of sugar maple could explain its ability to survive for long periods under deep shade whereas the more explosive height growth strategy of yellow birch would place it in a more vulnerable position.

The response of aboveground growth of juvenile sugar maple and yellow birch to a gradient of light availability has been extensively studied. A relatively faster early growth has been

reported for yellow birch (Logan 1965, Hornbeck and Leak 1992, Sutherland et al. 2000) even under closed canopy (Beaudet and Messier 1998, Ricard et al. 2003, but see Delagrange et al. 2004) whereas the early growth of sugar maple is slow but can be strong after release (Godman et al. 1990). However, the relative responsiveness of these two species in limiting light conditions is not well established. Yellow birch is more (Logan 1965, Walters and Reich 1996, Beaudet and Messier 1998), less (Messier and Nikinmaa 2000) or equally (Delagrange et al. 2004) responsive to increasing light availability. The proportional response to increasing light level is also found to broadly overlap between the two species (Pacala et al. 1993, Pacala et al. 1994a, Pacala et al. 1996). These divergent results might be related to genetic (Young et al. 1993) and phenotypic variability in response to local conditions, and to a lesser extent, to the statistical analysis of growth data. Nevertheless, the design of partial cutting regimes requires a quantitative understanding of the growth response of juvenile sugar maple and yellow birch to variation in light level if one wants to better understand the relative competitive superiority and predict the species composition of the future stand.

Survival has been predominantly related to the ability of understory trees to maintain a positive growth under limited light conditions (Kobe et al. 1995, Pacala et al. 1996, Walters and Reich 1996). Moreover, recent studies indicate that interspecific variation in juvenile tree survival, particularly under low light conditions, plays a far greater role in determining forest community dynamics than does interspecific variation in seedling or sapling growth rates (Pacala et al. 1994a, Kobe et al. 1995, Kobe 1996, Pacala et al. 1996). However, the relative survival of sugar maple and yellow birch is still incompletely defined. Several authors observed a greater mortality rate of yellow birch under both low and high light conditions (Bellefleur and Pétillon 1983, Houle 1991b, 1994, Cogliastro et al. 1997, McClure et al. 2000, Kobe et al. 2002). Nonetheless the juvenile survival functions modelled by Kobe et al. (1995) described a higher but not significant probability of mortality for yellow birch, compared to sugar maple, only below 2 or 3 % of light availability. Above this threshold, probability of mortality was similar between the two species.

The objective of this study was to examine if species-specific differences in growth and survival can explain their relative shade tolerance at the seedling and early sapling stage. More specifically, we wanted to (i) discriminate between dead and alive sugar maple and yellow birch as a function of size, growth rate and light availability; (ii) compare the growth response of sugar maple and yellow birch to a gradient of light availability; (iii) assess if mortality is mainly determined by growth limitation induced by low light level; (iv) determine if small-size seedlings were more vulnerable to mortality. We expected that (i) sugar maple and yellow birch will show the trade-off between low-light survival versus high-light growth rather than a trade-off between low-light growth versus high-light growth; (ii) and the observed trade-off will be related to the different growth strategy of these two species.

3.3 Materials and methods

3.3.1 Study site and experimental design

The study site and experimental design had been set up within the context of an important project which aimed to study the role of selection cutting, liming and competition control on the regeneration of sugar maple and yellow birch, and have been described elsewhere (DeBellis et al. 2002). We used the same study site and experimental design for this research because they provided us with the opportunity of studying the growth response of sugar maple and yellow birch along large gradients of light availability (0.33 ≤sugar maple ≤82.94 % PPFD; 0.27 ≤yellow birch ≤74.77 % PPFD) and size of individuals (3 ≤sugar maple ≤ 160 cm; 5 ≤yellow birch ≤203 cm). In addition, data on growth and survival collected over a 36-months survey enabled us to establish relationships between the probability of mortality on one hand, and either light availability or individuals' growth characteristics on the other hand. This study site is located in the Réserve faunique de Portneuf near Rivière-à-Pierre, Qc, Canada (47°04'N, 72°15'W; 375 m a.s.l). Overstory vegetation is dominated by sugar maple, yellow birch and American beech (*Fagus grandifolia* Ehrh.). The experimental

design is a factorial with three factors: size of canopy gap (3), liming (2) and control of understory competing vegetation (2). The 12 combinations of treatments were replicated 12 times for a total of 144 quadrats, each quadrat with a 49-m^2 area. In practice, three gap sizes were selected after single-tree and group-selection cuttings in autumn 1996: small (approximately 50 m^2), medium (100 to 300 m^2) and large gaps (700 to 1200 m^2). The absence or presence of treatment represented the two levels for liming and competition control.

In autumn 1999, nearly 1500 seedlings of sugar maple and yellow birch were tagged, approximately 10 seedlings of each species per quadrat. All tagged seedlings were from seed origin, and in general, newly established (*i.e.* after logging) for yellow birch. Sugar maple usually presents important advance regeneration. Consequently, we chose sugar maple' seedlings less than 50 cm tall. These seedlings were censused and measured for growth until autumn 2002.

For the study of growth response to variation in light availability led in 2002, we selected at random five seedlings and saplings of sugar maple and yellow birch for each combination of treatments. We limited our sampling to 5 replicates. We sampled therefore 300 individuals of each species (5 x 12 x 5).

3.3.2 Light availability

Instantaneous diffuse non-interceptance (DIFN) through and above the understory vegetation was measured at the centre of each quadrat near the forest floor (< 0.3 m), at 1.0 and 2.5 m above-ground (Q_o) at the end of July 2002 with a LAI-2000 Plant Canopy Analyser (LI-COR, Inc., Lincoln, NE, USA). Photosynthetic photon flux density (PPFD; μmol photon m^{-2} s^{-1}) in the photosynthetically active range (400-700 nm) was measured above the tip of the leader (Q_o) of each sampled individual (i.e. 300/species) at the beginning of August 2002 using a hand-held LI-189 point quantum sensor (LI-COR, Inc., Lincoln, NE, USA). The

instantaneous one-point overcast-sky condition method was used for the two devices. Such measurements obtained under completely overcast sky conditions provide a good estimate of the mean growing season percent photosynthetic photon flux density (PPFD, μmol photon m^{-2} s^{-1}; 400-700 nm) transmitted under the forest canopy (Parent and Messier 1996). Instantaneous measurements (Q_o) were taken with a LI-189 point quantum sensor or a LAI-2000 Plant Canopy Analyser at each measurement point. Above–canopy DIFN and PPFD (Q_i) was estimated by placing a second device on a tripod in a large adjacent clearing. This device was connected to a LI-1000 datalogger which was synchronized and programmed to compute and record for every 1 min period the mean DIFN or PPFD from measurements taken at 5 s interval. The percent transmission of above-canopy DIFN or PPFD was calculated as follows: % DIFN or % PPFD = (Q_o / Q_i) X 100.

3.3.3 Height and basal diameter growth, and survival

Leader length (± 1 cm) and basal diameter (± 1 mm) of each individual was measured near the end of each growing season (mid-August-early November) from 1999 to 2002. The annual (in 2002) leader increment (± 1 cm) was also measured in mid-August 2002. Sugar maple and yellow birch were assumed to have completed the bulk of their growth by this time of the growing season (Anderson et al. 2001). Leader was defined as the shoot that reached the highest point of the crown and its length was measured from the root collar to the tip of the leader. The annual leader increment was measured from the bud scar to the tip of the leader. The annual leader increment and annual basal diameter increment of the growing season 2000, 2001 and 2002 (excepted 2002 for annual leader increment) were obtained by the difference of leader length or basal diameter between two subsequent years. The ratio of leader length to basal diameter in 2002 (unit: cm/mm) was calculated to described the etiolation of the main stem.

All tagged seedlings were censused from autumn 1999 until autumn 2002. The census of dead individuals was carried out twice a year (May-June; mid-August-early November).

3.3.4 Statistical analyses

To suspect a possible trade-off between low-light survival versus high-light growth, the relationship in the absolute frequency of abundance between species' identity and three classes of light availability (very limiting: 0-3.0 % PPFD, limiting: 3.1-20 % PPFD and non-limiting: 20.1-83.0 % PPFD) was examined by contingency table analysis. Measurements of the light availability in 2002 above the tip of the leader of 291 individuals of each species were used to determine the number of individuals of each species in the three classes of light availability.

To examine a possible difference in maximum sustainable height between sugar maple and yellow birch in low-light level (i.e. trade-off between growth rate versus size of individual), variation in leader length between species and classes of light availability was analyzed with a two-way ANOVA. Measurements of the leader length and light availability in 2002 above the tip of the leader of 291 individuals of each species were used.

To test the validity of the trade-offs between low-light survival versus high-light growth, and growth rate versus size of individual for the explanation of the contrasting shade tolerance of sugar maple and yellow birch, canonical discriminant analysis (CDA) was performed. More specifically, we investigated if dead and alive sugar maple and yellow birch formed distinct groups either (i) according to leader length, annual leader increment and light availability, or (ii) according to basal diameter, annual basal diameter increment and light availability. We also examined if the four groups displayed unlike characteristics in terms of light availability, growth rate and size of individuals. CDA was realized on individuals still alive in autumn 2002 (985 sugar maple and 975 yellow birch) and only individuals dead in 2002 (58 sugar maple and 55 yellow birch) since light availability data were not available for previous years. We used measurements of leader length of 2001 and of annual leader increment of 2002 for alive individuals, and measurements of leader length of 2000 and of annual leader increment of 2001 for individuals dead in 2002. The measurements of light availability taken at the centre of each quadrat in 2002 were used to define the understory light environment

experienced by each individual present in the quadrat. We considered that seedlings < 30 cm long received the amount of light measured near the forest floor (< 0.3 m), seedlings with a leader length 30 ≤< 130 cm received the amount of light measured at 1.0 m above-ground, and saplings ≥130 cm long received the amount of light measured at 2.5 m above-ground. This methodological approach was assumed to provide good characterization of light conditions over the two growing seasons (2001 and 2002). Since possible difference in survival among sugar maple and yellow birch have been shown to occur only at very low light levels (Kobe et al. 1995, Walters and Reich 1996, Beaudet et al. 1999, Messier and Nikinmaa 2000), a CDA was also carried out on alive and dead individuals found in very shady environment (0-3.0% DIFN).

To examine the low-light growth versus high-light growth trade-off, variation of the annual leader increment and annual basal diameter increment of the 2002 growing season as a function of light availability was modeled with the non-linear regression formula of Michaelis-Menten: $Y = [(a * LA) / ((a / s) + LA))]$, where LA corresponds to the light availability received by an individual. The parameter a defines the asymptotic growth rate at high light (units: cm or mm) and the parameter s is the growth rate at low light measured as the initial slope at 0 % PPFD (units: cm/% PPFD or mm/% PPFD). Large a values indicate that individuals grow rapidly when light availability is high (and conversely for small values of a). Large s values indicate that when light availability is scarce, a small increase in light availability leads to a large increase in growth (and conversely for small values of s). 95% confidence limits of parameters a and s were used as the basis for comparisons among species of growth rates at high and low light, respectively. Measurements of the annual leader increment, annual basal diameter increment and light availability in 2002 above the tip of the leader of 291 individuals of each species were used.

Prior to growth analysis, we checked for size effect. The annual leader increment and annual basal diameter increment of the 2002 growing season were significantly dependent on leader length and basal diameter of the 2001 growing season, respectively, but the growth response to size variation was biologically very similar between the two study species. Consequently,

we did not take into account size effect in the analysis of growth response to variation in light availability.

For each species, logistic regression was carried out to establish relationships between probability of mortality and characteristics of individuals (leader length, basal diameter, annual leader increment, annual basal diameter increment and ratio of leader length to basal diameter). Mean values for the complete duration of the study (1999-2002) were taken for alive individuals, whereas values of the year before death (either 1999, 2000 or 2001) were used for dead individuals. Logistic regression was performed on the whole set of 2344 individuals present on the study site composed of 985 alive sugar maples, 175 dead sugar maples, 975 alive yellow birches and 209 dead yellow birches. Harvested individuals in 2001, disappeared individuals and certain quadrats were removed from the original database.

The relationship between probability of mortality and light availability was established by logistic regression. For this analysis, the database included individuals still alive (985 sugar maple and 975 yellow birch) and only individuals dead in 2002 (58 sugar maple and 55 yellow birch) since light availability data were not available for previous year. Like the CDA, light level received by each individual was defined by the measurement of light availability taken in 2002 at the centre of each quadrat and at < 0.3, 1.0 or 2.5 m above-ground.

Normality and homoscedasticity assumptions were checked prior to statistical analyses, and data were transformed if necessary. Probability values < 0.05 were considered significant. The contingency table analysis, ANOVA, nonlinear regression and logistic regressions were carried out with JMP software, version 4.0.2 (SAS institute Inc. 2000). CDA was realized with XLSTAT software, version 7.5.2 (Addinsoft 2005). All results presented in the figures are from un-transformed data.

3.4 Results

3.4.1 Absolute frequency of abundance of sugar maple and yellow birch across the light availability gradient

A significant relationship between species and the classes of light availability was noticed ($p = 0.001$). Sugar maple was twice more abundant than yellow birch in very limiting light level (107 *versus* 52) whereas yellow birch tended to be more numerous in limiting light conditions (173 *versus* 151) and twice more abundant in non-limiting light environment (66 *versus* 33) (Table 3.1).

Table 3.1
Absolute frequency of abundance of sugar maple and yellow birch according to three classes of light availability

Class of light availability (% PPFD)	SM	YB
0-3.0	107	52
3.01-20.00	151	173
20.1-83.0	33	66

Abbreviations: SM, sugar maple; YB, yellow birch; %PPFD, percent photosynthetic photon flux density.

3.4.2 Effect of classes of light availability on leader length

The leader length of both species increased with increasing light availability. Yellow birch displayed a longer leader than sugar maple, but only in the two upper classes of light availability ($p < 0.001$) (Table 3.2).

Table 3.2
Mean leader length (± 1 SE) of sugar maple and yellow birch according to three classes of light availability. Letters a, b, c indicate significant differences between classes of light availability for each species. Letters x and y indicate significant differences between species within each class of light availability

Class of light availability (% PPFD)	SM	YB
0-3.0	30.2 (1.9) **ax**	43.3 (4.3) **ax**
3.01-20.00	44.8 (2.6) **bx**	77.7 (3.1) **by**
20.1-83.0	91.1 (8.4) **cx**	155.7 (6.6) **cy**

Leader length: not transformed.
Abbreviations: SM, sugar maple; YB, yellow birch; %PPFD, percent photosynthetic photon flux density.

3.4.3 Discrimination of dead and alive sugar maples and yellow birches

Groups of dead and alive sugar maples and yellow birches found in 0-83% light availability range was significantly discriminated along three canonical axes obtained with the CDA of light availability, leader length and annual leader increment ($p < 0.001$). The first axis explained 96.7% of variance (Eigenvalue = 0.399), the second axis explained 3.3% of variance (Eigenvalue = 0.014) (and the third axis explained 0.001% of variance (Eigenvalue = 0.000)). The first axis discriminated among groups based mainly on differences in leader length (Factor loading = 0.991) and the second axis discriminated among groups based mainly on contrasting annual leader increment (Factor loading = 0.879). The CDA of light availability, basal diameter and annual basal diameter increment showed a significant discrimination among the four groups along three canonical axes ($p < 0.001$). The first axis explained 98.9% of variance (Eigenvalue = 0.147) (the second axis explained 0.8% of variance (Eigenvalue = 0.001) and the third axis explained 0.3% of variance (Eigenvalue = 0.000)). Groups were separated along the first axis mostly by basal diameter (Factor loading = 0.917).

For individuals found in the 0-3% light availability range, the CDA based on light availability, leader length and annual leader increment showed significant discrimination

among the four groups along three canonical axes ($p < 0.001$). The first axis explained 91.5% of variance (Eigenvalue = 0.193), the second axis explained 8.5% of variance (Eigenvalue = 0.018) (and the contribution of the third axis explained 0.007% of variance (Eigenvalue = 0.000)). The first axis mainly discriminated among groups based on differences in leader length (Factor loading = 0.985) and the second axis discriminated among groups based mainly on contrasting annual leader increment (Factor loading = 0.811). Significant discrimination among the four groups was also detected along three canonical axes for the CDA including basal diameter, annual basal diameter increment and light availability ($p < 0.001$). The first axis explained 99.5% of variance (Eigenvalue = 0.083) (the second axis explained 0.476% of variance (Eigenvalue = 0.000), and the third axis explained 0.001% of variance (Eigenvalue = 0.000)). The first axis separated groups based on differences in basal diameter (Factor loading = 0.787).

The groups of dead sugar maples and dead yellow birches were not statistically different, except the result of the CDA based on light availability (0-83%), leader length and annual leader increment, for which dead yellow birches showed a greater leader length and annual leader increment than dead sugar maples ($p < 0.001$). All other pairwise comparisons among groups were statistically different. The groups of alive yellow birches and dead sugar maples were the farthest apart. The groups of dead sugar maples and dead yellow birches were the closest (except the discrimination based on light availability (0-83%), leader length and annual leader increment) (Tables 3.3a, 3.3b, 3.3c and 3.3d).

Table 3.3

Summary of the square of the Mahalanobis distances (and one-tailed p-values associated with Fisher's F statistic) between the mean of two groups obtained by CDA of alive and dead sugar maples and yellow birches according to light availability (0-83% DIFN), leader length and annual leader increment (a); light availability (0-83% DIFN), basal diameter and annual basal diameter increment (b); light availability (0-3% DIFN), leader length and annual leader increment (c); light availability (0-3% DIFN), basal diameter and annual basal diameter increment (d)

a	A SM	A YB	D SM	D YB
A SM	0 (1)	1.440 (< 0.001)	0.579 (< 0.001)	**0.538** (< 0.001)
A YB		0 (1)	**3.815** (< 0.001)	1.857 (< 0.001)
D SM			0 (1)	**0.986 (< 0.001)**
D YB				**0** (1)
b	**A SM**	**A YB**	**D SM**	**D YB**
A SM	0 (1)	0.440 (< 0.001)	0.510 (< 0.001)	0.219 (0.011)
A YB		0 (1)	**1.846** (< 0.001)	1.250 (< 0.001)
D SM			0 (1)	**0.120 (0.354)**
D YB				0 (1)
c	**A SM**	**A YB**	**D SM**	**D YB**
A SM	0 (1)	0.797 (< 0.001)	0.404 (0.002)	0.512 (0.008)
A YB		0 (1)	**2.152** (< 0.001)	1.783 (< 0.001)
D SM			0 (1)	**0.172 (0.464)**
D YB				0 (1)
d	**A SM**	**A YB**	**D SM**	**D YB**
A SM	0 (1)	0.124 (0.002)	0.557 (< 0.001)	0.453 (0.014)
A YB		0 (1)	**1.204** (< 0.001)	1.052 (< 0.001)
D SM			0 (1)	**0.020 (0.959)**
D YB				0 (1)

Leader length, annual leader increment, basal diameter and annual basal diameter increment: Ln- transformed; Light availability: Arc Sine-transformed.

Abbreviations: A SM, alive sugar maples; D SM, dead sugar maples; A YB, alive yellow birches; D YB, dead yellow birches; % DIFN, percent diffuse non-interceptance.

3.4.4 Effect of light availability on height and basal diameter growth

Results of the Michaelis-Menten regressions showed that growth rates of sugar maple and yellow birch vary significantly as a function of light availability. Light availability explained almost 40% of the variation of the annual leader increment of the two study species. Light availability explained moderately the variation of annual basal diameter increment of yellow birch (26%), but little that of sugar maple (15%) (Tables 3.4a and 3.4b). Both species had measurable growth rates even at the lowest light levels sampled in our study. In comparison with sugar maple, yellow birch displayed superior growth rates along the whole gradient of light availability (Fig. 3.1a and 3.1b). The estimate of parameter s for the annual leader increment of yellow birch was significantly greater relatively to sugar maple. Other estimates of parameters a and s tended to be greater for yellow birch than sugar maple, but there was a significant interspecific overlap (Tables 3.4a and 3.4b). Annual leader increment was more sensitive to changes in light level than annual basal diameter increment, showing rapid increases in height growth between 0 and 15% of full sunlight.

Table 3.4

Michaelis-Menten regression parameters and goodness of fit for predicted annual leader increment (a) and predicted annual basal diameter increment (b) of sugar maple and yellow birch using the equation Y = [(a * LA) / ((a / s) + LA))] where LA is the light availability received by an individual

a	S [95% CL] (cm/% PPFD)	A [95% CL] (cm)	n	p	R^2
SM	2.49 [1.94; 3.21]	44.47 [36.19; 55.70]	291	< 0.001	0.375
YB	6.03 [4.83; 7.61]	54.05 [47.97; 60.87]	291	< 0.001	0.380
b	S [95% CL] (mm/% PPFD)	A [95% CL] (mm)	n	p	R^2
SM	0.1 [0.06; 0.17]	4.25 [2.39; 18.32]	286	< 0.001	0.152
YB	0.14 [0.08; 0.21]	9.27 [5.76; 37.12]	288	< 0.001	0.262

Annual leader increment: not transformed; Annual basal diameter increment: not transformed.

Abbreviations: SM, sugar maple; YB, yellow birch; A and S, model parameters; CL, confidence limits; %PPFD, percent photosynthetic photon flux density.

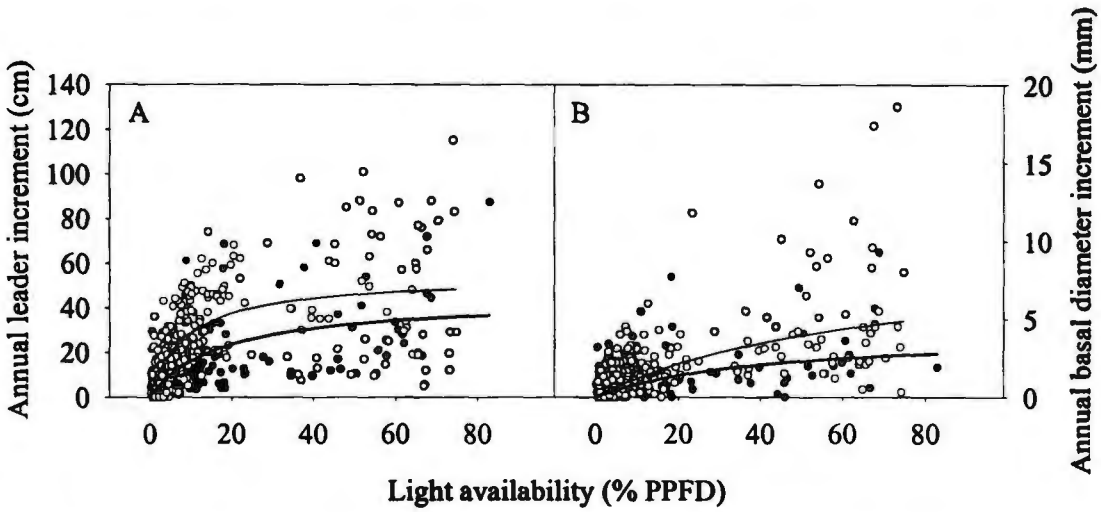

Figure 3.1 Michaelis-Menten regressions for predicted annual leader increment (a) and predicted annual basal diameter increment (b) of sugar maple (•; ___) and yellow birch (o;) using the equation Y = [(a * LA) / ((a / s) + LA))] where LA is the light availability received by an individual.

3.4.5 Relationships of the probability of mortality with growth characteristics and light availability

The probability of mortality of each species was significantly related to individuals' characteristics (leader length, basal diameter, annual leader increment, annual basal diameter increment and leader length to basal diameter ratio) and light availability (Table 3.5). However, leader length, basal diameter and annual leader increment explained a small amount of the probability of mortality of sugar maple and yellow birch, while the contribution of annual basal diameter increment and of leader length to basal diameter ratio was negligible. Despite the very small contribution of light availability, the probability of mortality of yellow birch was relatively more affected by it than sugar maple.

Table 3.5
Logistic regression parameters and goodness of fit for the probability of mortality as a function of leader length, basal diameter, annual leader increment, annual basal diameter increment, leader length to basal diameter ratio and light availability of/ above sugar maple and yellow birch using the equation Y = Probability (mortality) = 1 / (1 + e (- (a + b x))) where x is the status of individuals, dead or alive

Variable x	Species	n	a	b	p	R^2
LL (cm)	SM	1118	4.805	- 2.279	< 0.001	**0.171**
	YB	1140	1.732	- 0.513	< 0.001	**0.184**
BD (mm)	SM	1119	2.142	- 2.472	< 0.001	**0.131**
	YB	1139	1.729	- 1.864	< 0.001	**0.142**
ALI (cm)	SM	1068	- 1.346	- 0.116	< 0.001	**0.081**
	YB	1072	- 1.155	- 0.078	< 0.001	**0.160**
ABDI (mm)	SM	1069	- 1.715	- 0.591	< 0.001	0.029
	YB	1071	- 1.286	- 0.448	< 0.001	0.056
LL/BD (cm/mm)	SM	1115	- 0.046	- 0.961	< 0.010	0.011
	YB	1135	2.983	- 2.065	< 0.001	0.067
LA (% DIFN)	SM	1043	- 2.051	- 3.579	< 0.001	**0.034**
	YB	1030	- 1.157	- 6.672	< 0.001	**0.098**

Leader length, basal diameter and leader length to basal diameter ratio of sugar maple: transformed with Ln (x + 1); Leader length of yellow birch: transformed with $\sqrt{(x + 0.5)}$; Basal diameter and leader length to basal diameter ratio of yellow birch: transformed with Ln (x + 1); Light availability: Arc Sine transformed; Annual leader increment and annual basal diameter increment of both species: not transformed.
Abbreviations: SM, sugar maple; YB, yellow birch; LL, leader length; BD, basal diameter; ALI, annual leader increment; ABDI, annual basal diameter increment; LL/BD, leader length on basal diameter ratio; LA, light availability; % DIFN, percent diffuse non-interceptance; a and b, model parameters.
Note a lack of fit for the logistic regression of the basal diameter of sugar maple.

3.5 Discussion

Our results did not confirm the low-light growth enhancement hypothesis (i.e. the possible trade-off between low-light growth versus high-light growth) (Bazzaz 1979, Walters and

Reich 1999). Sugar maple (the most shade-tolerant species) tended to have weaker responses to an increase in light at low light level (i.e., low *s* values) and also showed relatively low asymptotic growth at high light (i.e., low *a* parameter values). Conversely, yellow birch (the most light demanding species) had the greatest response to an increase in light at low light levels (i.e., high *s* values) and relatively high asymptotic growth at high light (i.e., high *a* parameter values). For example, the annual leader increment of sugar maple and yellow birch sharply increased at very low light levels, but the response was significantly more pronounced for yellow birch. Yellow birch reached 50% of maximum growth at light levels < 10% of full sun and near maximum growth at 40% of full sun comparatively to < 20% of full sun and 60% of full sun, respectively for sugar maple. The lower growth of sugar maple confirmed that shade tolerance difference between sugar maple and yellow birch is not based on the ability of shade-tolerant species to outgrow less tolerant competitors under low light conditions, but instead on adaptations to increase survival (Beaudet and Messier 1998).

As previously mentioned in the introduction, the rank order between sugar maple and yellow birch for the responsiveness of growth to increase in light availability at low level is divergent among studies. This divergence highlights the small interspecific difference and high intraspecific variability despite the relative degree of shade tolerance of sugar maple and yellow birch. Some of the variability of parameters estimates is undoubtedly due to measurement error, but some portion of the variability is certainly due to genetic and phenotypic variability among individuals in response to local conditions. In the present study, the stronger dependency of the height growth of yellow birch on light availability in shade may indicate that mid-tolerant species may lack the ability to temporarily suppress shoot growth under low light levels, and may suggest a light-seeking/shade avoidance strategy for a species adapted to the exploitation of high-resource environments (Beaudet and Messier 1998).

The strength of the trade-off between low-light growth versus high-light growth has been shown to fluctuate across different climatic regions depending on shade tolerance of understory trees: the most shade-tolerant species varied in their response to low light but not

high light, while species with intermediate shade tolerance varied both their amplitude of growth at high light and the slope of the growth response at low light (Wright et al. 1998). Nonetheless, qualitative comparison of our light response curves (established at the northern edge of the distribution range of sugar maple and yellow birch) with those established in more southern parts of their range (Connecticut) (Pacala et al. 1993, Pacala et al. 1994a, Pacala et al. 1996) did not suggest a shift in the functional relationship between light availability and aboveground growth rates across these two geographical locations.

The trade-off between low-light survival versus high-light growth (Pacala et al. 1993, Pacala et al. 1994a, Kobe et al. 1995, Pacala et al. 1996), and the trade-off between annual leader increment and leader length (and by extension, annual basal diameter increment and basal diameter) were not clearly observed in the present study. We expected under growth limiting light conditions that (i) dead sugar maples would be confined to relatively lower light levels compared to dead yellow birches according to the first trade-off; and (ii) dead yellow birches would differentiate from dead sugar maples by greater previous growth rates and sizes according to the first and second trade-off. In the present study, the two trade-offs would be supported by the lower abundance of alive yellow birch (i.e. possible higher mortality) under low light conditions (0-3% full sunlight), the greater leader length and the greater annual leader increment of alive yellow birches and dead yellow birches (0-83% full sunlight), and the significant discrimination of dead sugar maples and dead yellow birches based on leader length, annual leader increment and light availability (0-83% full sunlight). However the present study revealed that dead yellow birches and dead sugar maples were generally the closest groups and can not be distinguished even in very low light conditions (0-3% full sunlight). Dead yellow birches did not exhibit significant differences in size, growth rates and light availability comparatively to dead sugar maples at least in very low light conditions (0-3% full sunlight). This finding cast a doubt on these two trade-offs (low-light survival versus high-light growth, and height growth versus size) at least for these two trees species when young and relatively small.

Although we failed to verify any of the trade-off hypotheses that have been suggested to explain differences in shade tolerance among species, we can not exclude the possibility that yellow birch could be physiologically more stressed than sugar maple but not enough to die under low light levels because of progressive gap closure (Delagrange et al. 2004). Gaucher et al. (2005) found that sugar maple seedlings had higher carbohydrate concentration than yellow birch seedlings under low light conditions (1-18% full sunlight) and suggested that allocation of carbohydrates to storage in roots instead of stem growth may play an important role in seedling survival by providing a buffer against agents of stress and physical damage (but did not find significant differences in the photosynthetic/non-photosynthetic ratio). We propose that mortality was rather caused by other damaging agents, such as extreme weather conditions, herbivory or diseases than related to light availability and growth. Firstly, no difference in survival between sugar maple and yellow birch was found in small gaps in our study site, suggesting therefore that yellow birch (mainly at the seedling stage), a mid-tolerant species, can persist like sugar maple, a shade tolerant species, under low-light level for at least 3 years (Article 1). Secondly, light availability played a negligible role in determining mortality despite the fact that light availability is the overriding factor limiting understory tree growth, at least up to the sapling stage and up to 50% light availability (Ricard et al. 2003). Thirdly, our results reported a significant but surprisingly negligible/small relationship between the probability of mortality and either growth rates or etiolation (i.e. ratio of leader length to basal diameter) for both species. Finally, the survival of small seedlings is relatively insensitive to variation in resource availability, but strongly affected by biotic or abiotic factors that cause defoliation or loss of root or shoot tissues (and the reserves stored in those tissues) (Canham et al. 1999).

Size of individuals affected negatively to some degree the probability of mortality: larger understory trees which were in a more favorable competitive position could capture a higher level of resources and had a better chance to survive (Gurevitch et al. 2002). This is particularly true in more open areas where vertical stratification among understory trees was more pronounced. The poor prediction power of our logistic equations did not allow us to determine if a size threshold below which half of mortality occur differentiate the two study species. Based on our literature review, we think that difference in mortality take place

mainly at very early stage (Houle 1991b, 1994, Anderson et al. 2001). Delagrange et al. (2004) hypothesized that understory trees of both species survived for 4 years under low light levels (0.5-16% of full sunlight) possibly because of higher plasticity when small and the use of stored reserves when taller.

3.6 Conclusion

The difference in shade tolerance among sugar maple and yellow birch is considered to be expressed predominantly at the seedling stage (Sutherland et al. 2000, Delagrange et al. 2004). Sugar maple is a shade-tolerant species and yellow birch is intermediate in its shade tolerance. Shade tolerance has been mainly associated with the growth response and variation in survival of understory tree to the light availability gradient (Kobe et al. 1995, Kobe 1996, Beaudet and Messier 1998, Ricard et al. 2003). In our study, these two sympatric species did not differentiate themselves in terms of both growth and survival responses along a very wide light availability gradient, which seems to disagree with the appellation of sugar maple as a small-gap specialist (Canham 1988b) and yellow birch as a gap-phase species (Erdmann 1990). Overall, yellow birch displayed a greater growth rate than sugar maple under a wide range of light conditions including extremely low light levels. According to Pacala et al. (1996), the rapid growth at all light levels enable yellow birch to catch and surpass advance regeneration of more shade tolerant species. Furthermore, a high and comparable survival rate allows yellow birch to persist in the understory, at least during the first three years (Article 1). Therefore, yellow birch appears to be a better competitor than sugar maple in all light environments during that period. The lower abundance of yellow birch seedlings under dense forest canopy may be caused by a scarcity of suitable seedbed for establishment (Houle 1992a) and the smothering effect of leaf fall on yellow birch germinants (Anderson et al. 2001) rather than a higher mortality rate due to low light conditions. The abundance of sugar maple is probably due to a continuous recruitment of seedlings (Marks and Gardescu 1998) and its ability to germinate well even under a humus layer.

Our results suggest that it is difficult to interpret the contrasting degree in shade tolerance of sugar maple and yellow birch with the growth rate/survival trade-off alone. However, we cannot discard that a higher investment of resources towards growth can possibly lead to a progressive exhaustion of carbohydrates reserves on longer time frame and cause a higher mortality rate to yellow birch later on. A higher biomass and carbohydrate allocation to roots was observed in shade in the more-shade tolerant sugar maple compared with the mid-tolerant yellow birch (Logan 1965, Gaucher et al. 2005). This pattern of resources allocation would tend to enhance the survival of sugar maple (Kobe 1997, Canham et al. 1999) over the longer term. Our results did not show the "wait and sit" or survivalist strategy of sugar maple hypothesised by Messier and Nikinmaa (2000). The trade-off between size of individual and growth rate did not visibly give a straightforward explanation to the relative shade tolerance of sugar maple and yellow birch. But the size of individuals was the most important discriminating variable and undoubtedly mediated indirectly the adaptive response of understory tree to limiting light conditions through its effects on physiological, morphological and allocational plasticity (Delagrange et al. 2004). Finally our study suggests that other factors of mortality than light availability should not be neglected if one wants to better understand the regeneration of sugar maple and yellow birch.

CONCLUSION

1. Contribution de cette thèse à notre compréhension de la coexistence de ces deux espèces

Cette thèse s'appuyait sur deux modèles conceptuels pour examiner la coexistence de l'érable à sucre et du bouleau jaune : la variation de l'habileté compétitive en fonction de la disponibilité des ressources (différentiation fondamentale des niches) et la hiérarchie compétitive. J'ai testé ces deux théories selon les gradients les plus susceptibles de montrer une performance différente de ces deux espèces (taille de la trouée, disponibilité et répartition temporelle de la lumière, la fertilité du sol et la disponibilité en calcium échangeable).

Y-a-t-il un modèle explicatif à privilégier ?

Selon Latham (1992), trois conditions mettent en relief les différences et les similitudes entre les deux modèles :

- La première condition différencie clairement le modèle de la hiérarchie compétitive du modèle de la différenciation fondamentale des niches. La première condition stipule que les niches d'espèces sympatriques sont inclusives, autrement dit, toutes les espèces présentent une meilleure performance à des niveaux élevés de ressources. Selon le modèle de la différenciation fondamentale des niches, la performance maximale des espèces est séparée le long du gradient des ressources et donc ne présente pas le caractère inclusif. Les trois expériences suggèrent que les niches de l'érable à sucre et du bouleau jaune sont inclusives. Le bouleau jaune à une meilleure croissance que l'érable quelque soit la taille de la trouée (chapitre 1; à une exception près où la croissance est comparable entre les deux espèces), la disponibilité de la lumière (chapitres 1 et 3) et la fertilité du sol (apport de calcium et

disponibilité en nitrate) (chapitre 1). L'habileté compétitive du bouleau jaune est légèrement supérieure à celle de l'érable à sucre quelque soit la disponibilité de la lumière et des éléments nutritifs (lorsque la compétition pour les éléments nutritifs est présente) (chapitre 2). L'augmentation de la croissance de l'érable à sucre avec l'augmentation des ressources est généralement plus faible (chapitres 1 et 3). Toutefois, l'augmentation de la croissance de l'érable à sucre est plus forte que celle du bouleau jaune avec l'augmentation de la disponibilité de la lumière et des éléments nutritifs (chapitre 2);

- La deuxième condition, commune aux deux modèles conceptuels, suppose que l'habileté compétitive et la tolérance à des conditions de faible disponibilité en ressources sont principalement inhérentes et spécifiques à l'espèce. L'absence de différence de survie entre les deux espèces (chapitre 1; à l'exception de deux traitements où la survie de l'érable à sucre est supérieure à celle du bouleau jaune) ne permet pas de distinguer de différence de tolérance de ces deux espèces selon la taille de la trouée, la disponibilité en lumière et la fertilité du sol (apport de calcium et disponibilité en nitrate). L'absence de différence de survie entre les deux espèces selon la fertilité du sol (chapitre 2) ne permet pas d'indiquer de différence de tolérance selon la disponibilité en éléments nutritifs. L'absence de différence entre les érables à sucres morts et les bouleaux jaunes morts en terme de taille, de taux de croissance et de disponibilité en lumière (chapitre 3; à une exception près) ne permet pas de distinguer de différence de tolérance de ces deux espèces selon la disponibilité de la lumière. Toutefois, certaines observations suggèrent une tolérance de l'érable à sucre légèrement supérieure à celle du bouleau jaune. Premièrement, la variation de la densité de l'érable à sucre et du bouleau jaune selon le gradient d'ouverture de la canopée (chapitre 1) suggère une plus grande tolérance à l'ombre de l'érable à sucre. Deuxièmement, une légère diminution de l'habileté compétitive du bouleau jaune avec une répartition temporelle de la lumière plus hétérogène suggère une plus faible tolérance du bouleau jaune à ces conditions. Inversement, une légère augmentation de l'habileté compétitive de l'érable à sucre suggère une plus grande tolérance de l'érable à sucre à une répartition temporelle de la lumière plus hétérogène (chapitre 2). Troisièmement, l'érable à sucre présente des traits écophysiologiques qui lui permettent de tolérer des conditions de faible disponibilité en ressources, tandis que le bouleau jaune présente des traits écophysiologiques qui lui confèrent une capacité supérieure à prélever les ressources et à croître rapidement lorsque les ressources sont abondantes

(chapitre 2). Finalement, la plus grande contribution de la disponibilité de la lumière à la croissance et à la survie du bouleau jaune suggère une plus grande dépendance du bouleau jaune à la disponibilité de la lumière (chapitre 3);

- La troisième condition, commune aux deux modèles conceptuels, considère qu'il existe un compromis entre l'habileté compétitive et la tolérance à des faibles niveaux de ressources. Les trois études de cette thèse suggèrent le compromis puisque l'habileté compétitive du bouleau jaune (mesurée en terme de croissance) est supérieure à celle de l'érable à sucre (cf. condition 1) et la tolérance de l'érable à sucre est légèrement supérieure à celle du bouleau jaune (cf. condition 2).

À mon avis, le modèle de la hiérarchie compétitive est certainement un mécanisme qui contribue à expliquer la coexistence de l'érable à sucre et du bouleau jaune puisque le caractère inclusif des niches est observé, malgré des conditions environnementales et des méthodologies expérimentales très différentes. Des études récentes privilégient également le modèle de la hiérarchie compétitive (Whitmore and Brown 1996, Bigelow and Canham 2002, Keddy et al. 2002). L'existence d'un compromis entre la croissance en pleine lumière (habileté compétitive) et la survie en conditions ombragées (tolérance) (Kobe et al. 1995), et d'un compromis entre la croissance sur les sites fertiles (habileté compétitive) et la survie sur les sites pauvres (tolérance) (Schreeg et al. 2005) suggère le modèle de la hiérarchie compétitive. Finalement, le peu de renversements interspécifiques de la croissance le long du gradient de disponibilité de la lumière (autrement dit, l'observation d'un faible compromis entre la croissance en pleine lumière et celle en conditions ombragées) (Kobe et al. 1995, Sack and Grubb 2001) appuie la validité du modèle de la hiérarchie compétitive.

Le modèle de la hiérarchie compétitive est en accord avec la théorie successionnelle des niches puisqu'il tient compte de l'existence d'un compromis entre la croissance et la survie. Il ne contredit pas le mécanisme de l'avantage de la colonisation (compromis entre la capacité de dispersion et l'habileté compétitive) si l'on considère que la compétition se définit par la tolérance d'une espèce à un faible niveau de ressources (définition de Tilman) et non pas par la capacité d'exploitation de ressources abondantes d'une espèce (définition de

Grime) (Grace and Tilman 1990). Enfin, il est en accord avec la stratégie d'exploitation des espèces intolérantes à l'ombre et la stratégie de conservation des espèces tolérantes à l'ombre (Bormann and Likens 1979, Grime 1979, Reich et al. 2003).

2. Contribution de cette thèse à l'amélioration de la gestion et l'aménagement des érablières à bouleau jaune

Puisque le modèle de la hiérarchie compétitive semble être un des mécanismes qui contribuent à expliquer la coexistence de l'érable à sucre et du bouleau jaune (pour les autres mécanismes, cf. introduction), alors il est possible de prédire que le bouleau jaune devrait être relativement plus dominant dans des conditions de disponibilité élevée en ressources (trouées de grande taille) grâce à sa croissance, tandis que l'érable à sucre devrait être relativement plus dominant dans des conditions de faible disponibilité en ressources (trouées de petite taille) grâce à sa tolérance. Les petites trouées contraignent la croissance de l'érable à sucre et du bouleau jaune mais permettent tout de même l'établissement d'une banque de semis et de gaulis d'érable à sucre, tandis que les grandes trouées permettent l'expression de la hiérarchie compétitive. L'érable à sucre et le bouleau jaune nous donnent d'une certaine manière l'illusion de se partager le gradient d'ouverture du couvert forestier car chacune de ses deux espèces domine la régénération à un extrême du gradient, mais par des processus différents. La croissance de l'érable à sucre et du bouleau jaune ne présente pas d'optimum différent le long du gradient de taille des trouées (chapitre 1). L'explication de la coexistence de l'érable à sucre et du bouleau jaune dans les érablières à bouleau jaune nécessite donc la prise en considération simultanée de la croissance et de la survie (Kobe et al. 1995), et pas seulement de la croissance ou de la survie, considérée individuellement. Avec la fermeture du couvert forestier, la disponibilité des ressources va diminuer et la dominance de l'érable à sucre va augmenter. La mise en jeu d'une perturbation sera nécessaire pour libérer un espace à coloniser et augmenter la disponibilité des ressources. Une trouée de grande taille devrait permettre au bouleau jaune de constituer la canopée et d'arriver à maturité (Leak and Filip 1977, Hornbeck and Leak 1992, Anderson et al. 2001), tandis que la formation de petites trouées devrait accélérer la dynamique du peuplement vers le stade de fin de succession

(autrement dit, vers une plus grande composition en érable à sucre) (Jenkins and Parker 1998).

Le modèle de la hiérarchie compétitive fournit un mécanisme pour comprendre l'organisation des communautés forestières et un outil simple, efficace et puissant pour prédire l'assemblage des espèces forestières. Selon le modèle de la hiérarchie compétitive, la coexistence des espèces forestières ne dépend pas de l'interaction de plusieurs facteurs écologiques locaux (existence de niches), mais des caractéristiques inhérentes et spécifiques de l'espèce : l'habileté compétitive dans les conditions élevées de ressources et la tolérance dans les conditions de faible ressources. Cette propriété du modèle permet de prédire que nos observations sont généralisables à d'autres localisations de l'aire de répartition de ces deux espèces tant que le gradient de disponibilité de la ressource (lumière) reste prépondérant. D'ailleurs, n'observons-nous pas une grande similitude dans la réponse de la croissance à la disponibilité de la lumière entre deux régions différentes (article 3) (Pacala et al. 1993, Pacala et al. 1994a, Pacala et al. 1996) ? Le modèle de la hiérarchie compétitive nécessite de caractériser les principaux gradients de disponibilité des ressources et de connaître les traits écophysiologiques des espèces impliquées (adaptation à la tolérance et habileté compétitive).

Finalement, les coupes de jardinage (par pied d'arbre, avec trouée, avec régénération par parquets) permet d'assurer une bonne régénération de l'érable à sucre et du bouleau jaune dans les érablières à bouleau jaune (article 1) (Majcen and Richard 1992, Majcen 1995). Le maintien de la composition des érablières à bouleau jaune démontre la relative stabilité de cet écosystème forestier face aux perturbations anthropiques (Leak and Smith 1996). Toutefois, « l'arbre ne doit pas cacher la forêt ». Si l'on choisit de s'orienter vers une sylviculture qui tente d'émuler le régime des perturbations naturelles, il convient également de considérer les effets des pratiques sylvicoles sur la biodiversité des érablières à bouleau jaune (Gasser et al. 2005).

3. Les atouts et les limites de cette thèse

Les trois études de cette thèse ne cherchaient pas seulement à observer le patron et la stratégie de régénération de l'érable à sucre et du bouleau jaune, mais avaient également pour objectif d'établir des liens de cause à effet. L'approche méthodologique utilisée présente à cette fin de nombreux atouts. Premièrement, les réponses de l'érable à sucre et du bouleau jaune aux conditions environnementales ont été observées à l'échelle de certains traits écophysiologiques (chapitre 2; ex : surface foliaire spécifique), à l'échelle de l'individu (chapitres 1, 2 et 3; croissance et survie) et à l'échelle de la communauté forestière (chapitres 1 et 2; densité et habileté compétitive). De plus, l'observation a été menée sur une base pluriannuelle, ce qui renforce la validité de nos observations. Par ailleurs, les traitements expérimentaux ont été appliqués de façon aléatoire soit en « créant de toute pièce » les conditions expérimentales (chapitre 2), ou bien en « manipulant » une érablière (chapitre 1). Le suivi de la régénération a été effectué autant dans un milieu semi-contrôlé (chapitre 2) qu'en milieu forestier (chapitres 1 et 3), permettant ainsi d'établir des observations plus concluantes. Finalement, l'observation de la régénération de l'érable à sucre et du bouleau jaune était accompagné d'un suivi concomitant des facteurs biotiques (couvert de la végétation) et abiotiques (lumière, pH et fertilité) jugés importants.

Le chapitre 3 a mis à profit l'existence d'un gradient de disponibilité en lumière et de taille des individus, et d'un suivi de la mortalité pour examiner l'existence de trois compromis susceptibles d'expliquer la tolérance à l'ombre de l'érable à sucre et du bouleau jaune.

Une des particularités de cette thèse réside dans la localisation du site d'étude (chapitre 1 et 3). Le site d'étude est situé à l'extrême limite nordique de l'aire de distribution de l'érable à sucre dans la zone de transition entre le domaine bioclimatique de l'érablière à bouleau jaune et celui de la sapinière à bouleau jaune.

Cette thèse est également intéressante puisqu'elle accorde une importance tout particulière à l'effet de la disponibilité des éléments nutritifs (chapitres 1 et 2) et de la répartition

temporelle de la lumière (chapitre 2) sur la performance relative de l'érable à sucre et du bouleau jaune. L'effet de ces facteurs écologiques sur la régénération de ces deux espèces a été très peu étudié. Par ailleurs, cette thèse a mis l'accent sur le suivi de la survie (chapitres 1, 2 et 3). Généralement, les études s'intéressent uniquement à la croissance.

Cette thèse réfute l'hypothèse d'une inhibition allélopathique (Tubbs 1973) et démontre qu'il existe une interaction compétitive entre l'érable à sucre et le bouleau jaune (chapitre 2). Récemment, des observations d'une inhibition allélopathique des extraits de feuilles du hêtre d'Amérique sur la croissance et le développement de l'érable à sucre ravive cette hypothèse pour expliquer la codominance de l'érable à sucre et du hêtre d'Amérique (Hane et al. 2003).

Cette thèse démontre la complexité des réponses de la densité, de la croissance et de la survie de l'érable à sucre et du bouleau jaune à cause de l'interaction de plusieurs facteurs écologiques (chapitres 1 et 2), sans que ces interactions soient fondamentalement importantes pour l'explication de la coexistence de l'érable à sucre et du bouleau jaune (modèle de la hiérarchie compétitive versus différentiation fondamentale des niches).

De plus, cette thèse suggère d'ajouter le rôle de la survie du bouleau jaune dans l'explication de la persistance de cette espèce formulée par Pacala et al. (1996).

Un certain nombre d'éléments méthodologiques, inévitables pour des raisons logistiques, limite la portée des observations. Premièrement, l'utilisation d'un dispositif de séries de remplacement (chapitre 2) est généralement très populaire mais également abondamment critiqué. Néanmoins, ce dispositif expérimental reste valide pour tester notre hypothèse (variation ou uniformité de l'habilité compétitive selon les conditions environnementales). Par ailleurs, certaines précautions ont été prises (ex : limitation du biais initial, durée de l'expérimentation, forte densité des semis, ...).

L'utilisation d'un seul site d'étude dans l'espace et dans le temps (chapitre 1) limite l'extrapolation de nos résultats à l'échelle du domaine bioclimatique de l'érablière à bouleau jaune puisqu'il ne représente à des fins statistiques qu'une seule et même unité expérimentale à l'échelle régionale (pseudoréplication simple). Par conséquent, il serait erroné d'affirmer précipitamment que la coupe de jardinage, le chaulage et le dégagement de la végétation de sous-bois devraient reproduire exactement les mêmes effets dans toute l'aire de répartition des érablières à bouleau jaune. Le modèle de la hiérarchie compétitive devrait demeurer valide, mais la mise en jeu d'autres gradients peut éventuellement modifier quelque peu les tendances (Wright et al. 1998). Par contre, les résultats à l'échelle de l'individu sont certainement valides puisque on peut assumer que les quadrats étaient indépendants les uns des autres à cause de la topographie et de leur dispersion sur une grande aire d'étude.

Une meilleure caractérisation de l'environnement lumineux au niveau de chaque individu aurait été idéal, mais probablement peu réaliste. Il faut donc présumer que la mesure de la disponibilité de la lumière en 2002 au centre de chaque quadrat à la hauteur considérée est satisfaisante pour décrire la quantité de lumière reçue par chaque individu (chapitre 3).

4. Perspectives sur la problématique de coexistence de l'érable à sucre et du bouleau jaune

Cette thèse apporte un certain nombre d'éléments de réponse sur la dynamique de régénération et la coexistence de l'érable à sucre et du bouleau jaune. Néanmoins, je ne pense pas pour autant que l'énigme soit entièrement résolue tant du point de vue des mécanismes que des facteurs écologiques mis en jeu. La quête doit donc se poursuivre ! L'acquisition de connaissances fondamentales sur ces deux espèces permettra d'améliorer nos pratiques sylvicoles et d'atténuer les conséquences des changements globaux sur la régénération de ces deux espèces dans les érablières à bouleau jaune.

Premièrement, il serait pertinent d'examiner la validité du modèle de la hiérarchie compétitive pour plusieurs espèces forestières grâce à la méthode du phytomètre (Keddy et

al. 2002) (c'est-à-dire effectuer un bioessai en mesurant la capacité de chacune des espèces forestières à réduire la croissance d'une espèce cible qui sert de phytomètre) et d'examiner les traits écophysiologiques qui confèrent l'habileté compétitive et la tolérance. Deuxièmement, puisque la tolérance à l'ombre se manifeste ultimement par la capacité de persister en sous-bois, il serait intéressant d'étudier l'importance relative des causes de mortalité des semis en fonction du degré d'ouverture du couvert (lumière, extrêmes climatiques, ravageurs, maladies). Troisièmement, il serait également opportun de comparer la mortalité de ces deux espèces à des stades plus avancés de développement (gaulis et perchis) avec la fermeture concomitante du couvert forestier, et d'étudier les causes écophysiologiques (notamment le patron d'allocation des ressources et des réserves en sucre). D'ailleurs, il n'est pas rare d'observer des chicots de bouleau jaune du stade gaulis - perchis sous couvert fermé. Cette piste de recherche permettrait d'élucider, du moins en partie, si le bouleau jaune est plus susceptible à la mortalité que l'érable à sucre avec l'augmentation de la taille des individus et la diminution de la disponibilité de la lumière, et si le bouleau jaune « s'épuise » dans des conditions ombragées. Dans le même ordre d'idée, nous savons que l'érable à sucre est une espèce « élastique » tandis que le bouleau jaune présente une reprise difficile de la croissance après une période d'oppression (Anderson et al. 2001). Par ailleurs, les coupes de jardinage pourraient être pratiquées tous les 20 ans dans les érablières du Sud du Québec (Bedard and Majcen 2003). La question d'importance sylvicole est actuellement de déterminer quelle est la durée maximale d'oppression du bouleau jaune sans effets dommageables pour sa reprise de croissance et sa survie ? Quatrièmement, la tolérance à la sécheresse semble distinguer l'érable à sucre du bouleau jaune (appendice B). Dans le contexte du réchauffement climatique, il serait opportun d'en apprendre davantage sur les relations hydriques de ces deux espèces et de comparer les effets d'extrêmes microclimatiques observés dans les grandes trouées. À cette fin, une expérience avait été mise en place dans le cadre de ce doctorat, mais ne fut malheureusement pas menée à terme. Cette étude comparait les effets du stress hydrique sur la croissance, la survie et un certain nombre de traits écophysiologiques et proposait l'hypothèse que l'érable à sucre et le bouleau jaune seraient affectés différemment en fonction du moment d'application du stress à cause de leur phénologie de croissance. Cinquièmement, toujours dans le contexte du réchauffement climatique, le long d'un gradient latitudinal, quels sont les facteurs

écologiques (climatiques) qui contribuent à la distribution de l'érable à sucre et du bouleau jaune dans la zone de transition entre les domaines bioclimatiques de l'érablière à bouleau jaune et de la sapinière à bouleau jaune ? Sixièmement, l'étude de la nutrition du bouleau jaune nécessite d'être approfondie si l'on veut mieux comprendre les effets du chaulage sur la densité, la croissance et la survie de cette espèce, surtout dans une situation précaire du statut nutritif des sols forestiers (Huntington 2005). Finalement, relativement peu d'études (Brown 1977, 1979, Brown and Martel 1981, Mladenoff 1987, Wilczynski and Pickett 1993) fournissent une caractérisation des conditions édaphiques dans les trouées racinaires, ce qui limite notre capacité de prédiction de la composition de la régénération le long du gradient de disponibilité des ressources édaphiques.

APPENDICE A

COMPARAISON DES TRAITS D'HISTOIRE DE VIE IMPORTANTS POUR LA REPRODUCTION SEXUÉE DE L'ÉRABLE À SUCRE ET DU BOULEAU JAUNE

	Érable à sucre	Bouleau jaune
Longévité (maximale / moyenne)	400 + / 150 +	300 + / 90 +
Hauteur des arbres matures (m)	27 – 37	20 – 30
Diamètre des arbres matures (cm)	50 – 90	60 +
FLORAISON ET POLLINISATION		
Période de floraison	Fin du printemps	
Susceptibilité des fleurs au gel	Non	Oui
Agent(s) de pollinisation	Insectes + Éventuellement le vent	Vent seulement

PRODUCTION DE SEMENCES			
Âge de production des graines (années, début / début de la production optimale / déclin)	40 – 60 / 40 / 200		40 / 40 / 70
Fréquence des bonnes années semencières (années)	2 – 5		1 – 4
Variabilité temporelle	Moins élevée		Élevée
Période du début de la chute des graines		Début automne	
DISPERSION			
Type de graines	Double samare		Ailée
Masse de la graine (mg)	65 (50 – 140)		1 (0.5 – 2)
Agent de dispersion		Vent	
Distance (mètre)	100 +		400 +
Période de dispersion (mois)	4		12
Mortalité des graines après dispersion (%)	20		99.3
Type de banque de graines	Éphémère (durant l'hiver)		Persistante (1 an et +)
GERMINATION			
Stratification au froid		Nécessaire	
Période de germination	Début du printemps		Fin du printemps
Capacité de germination	95 %		20 – 53 %

LITS DE GERMINATION PRÉFÉRENTIELS POUR ÉTABLISSEMENT		
Nature du substrat	Variable	Sol minéral nu, mousse, bois pourri, crevasses dans les roches, monticules de chablis
Sites d'établissement des semis	Abondant	Rare
Conditions de lumière	Peut germer dans les conditions ombragées de la canopée	Nécessite une ouverture de la canopée
Humidité	Nécessaire	
Température	Fraîche	Chaude
Période d'émergence des semis	Mai	Juin – Septembre
CROISSANCE ET SURVIE		
Tolérance à l'ombre des semis	Très élevée	Intermédiaire
Type de croissance	Déterminée	Indéterminée
Durée (jours)	30 +	90 +
Taux de mortalité des semis	Faible	Élevé
Banque de semis	Abondant	± abondant
Morphologie du système racinaire des semis	Variable	
Réaction à la compétition	Élevée	Moyenne
Tolérance au broutage	Élevée	Faible – Moyenne

Compilé d'après les références suivantes : Tubbs (1977), Erdmann (1990), Godman et al. (1990), Houle et Payette (1991a), Bazzaz et Wayne (1994), Houle (1994), Beaudet et Messier (1997), Iverson et al. (1999), Sutherland et al. (2000), Anderson et al. (2001).

APPENDICE B

COMPARAISON DES CONDITIONS ENVIRONNEMENTALES DE L'HABITAT DE L'ÉRABLE À SUCRE ET DU BOULEAU JAUNE (NICHE ÉCOLOGIQUE)

	Érable à sucre	Bouleau jaune
FACTEURS CLIMATIQUES		
Température annuelle (°C)	10,3 (2,2 < 10,1 < 19,7)	7,1 (2,4 < 7,4 < 16,8)
Température du mois de janvier (°C)	- 3,0 (- 16,6 < -3,5 < 10,4)	- 6,0 (- 17,9 < - 6,3 < 6,3)
Précipitation (mm)	1040 (512 < 1050 < 1780)	1010 (452 < 1000 < 1780)
Évapotranspiration potentielle (mm/mois)	56,7 (12,6 < 56,5 < 100)	44,5 (17,9 < 45,9 < 83,9)
Durée de la saison de croissance (jours)	80 – 260	60 – 150

FACTEURS TOPOGRAPHIQUES		
Altitude maximale (m)	373 (67 < 489 < 2000)	554 (34 < 656 < 2000)
Pente (%)	10,3 (0,0 < 12,7 < 51)	10,1 (0,0 < 13,2 < 51)
FACTEURS ÉDAPHIQUES		
Granulométrie du dépôt de surface	Moyenne	Grosse, moyenne et très fine
Type de sol	Très variable / spécifique selon les régions	Variable
Classe texturale	Sable, sable loameux, loam sableux, loam et loam limoneux	Loam et loam sableux
Argile (% / jusqu'à 152 cm de profondeur ou le socle rocheux)	22 (2,5 < 21 < 51,9)	13,4 (2,5 < 13,5 < 32,0)
Matière organique de l'horizon de surface (%)	2,6 (0,9 < 4,1 < 35,1)	4,7 (1,2 < 6,5 < 35,1)
pH	4,7 (2,5 < 4,8 < 7,9)	4,5 (2,7 < 4,7 < 7,4)
Classe de drainage	Modéré à bon	Imparfait à bon
Taux de perméabilité (cm/h)	1,6 (0,2 < 2,3 < 14,2)	2,9 (0,5 < 3,7 < 13,3)
Capacité de rétention en eau (cm / jusqu'à 152 cm de profondeur ou le socle rocheux)	7,0 (3,1 < 7,4 < 16,1)	6,2 (3,6 < 6,6 < 16,1)
EXIGENCES EN LUMIÈRE		
Taille minimale de la trouée	0,05 ha	0.1 ha
Densité du couvert forestier	60 %	40 %

EXIGENCES EN ÉLÉMENTS NUTRITIFS

Richesse en éléments nutritifs	Très élevée		Variable
Tolérance à la disponibilité en azote		intermédiaire	

EXIGENCES EN EAU

Exigence en eau	Élevée		Modérée à élevée
Tolérance à la sécheresse	-		+
Tolérance à l'inondation		Intolérant	

Médiane (minimum < moyenne < maximum).
La médiane peut être interprétée grossièrement comme l'optimum de l'espèce pour la variable considérée (Iverson et al. 1999).
Compilé d'après les références suivantes : Pastor et Post (1986), Erdmann (1990), Godman et al. (1990), Bazzaz et Wayne (1994), Anonyme (1995), Farrar (1995), Cogliastro et al. (1997), Iverson et al. (1999), Anderson et al. (2001).

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