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Influence de la disponibilité en lumière et de la taille sur les attributs fonctionnels et le bilan de carbone de l'arbre

Sylvain Delagrangé

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Thèse

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par Sylvain DELAGRANGE

Influence de la disponibilité en lumière et de la taille sur les attributs fonctionnels et le bilan de carbone de l'arbre

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"Live and learn"

*Stephanie
Coburn
Head of
Millstream,
NB,
CANADA*

*"Au milieu de la forêt, il y avait
deux chemins. Prendre le moins
emprunté m'a ouvert les yeux"*

*Robert Frost
Poète
Américain*

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RÉSUMÉ

Dans le but de mieux comprendre la régénération des espèces à intérêts économiques importants, il est crucial de s'intéresser à leur capacité à tolérer l'ombrage ainsi qu'aux mécanismes qui la définissent. En effet, en sous couvert, la disponibilité en lumière peut être faible et très variable, ce qui fait de cette ressource l'une des plus importantes dans le développement des jeunes arbres. À l'échelle de l'individu, cette tolérance à l'ombre est définie par la somme de nombreux paramètres physiologiques, morphologiques et d'allocation de biomasse qui déterminent au sein de chaque individu, leur efficacité d'interception et d'utilisation de lumière et donc leur bilan carboné.

Dans cette étude, différentes échelles de processus (physiologie de la feuille, morphologie de la cime, répartition de biomasse dans les différents compartiments de l'arbre) ainsi que le fonctionnement intégré à l'échelle de l'individu ont donc été étudiés chez l'érable à sucre (*Acer saccharum* Marsh., tolérant à l'ombre) et le bouleau jaune (*Betula allghaniensis* Britton, semi tolérant à l'ombre) en relation avec leur disponibilité en lumière et cela durant les premiers stades de développement. Dans un premier temps, la variabilité des différents caractères internes de ces deux espèces a été évaluée au cours de leur régénération le long d'un gradient naturel de lumière et sous ombrage imposé en sous couvert. Par la suite, l'étude plus précise du fonctionnement intégré à l'échelle de l'individu a été rendue possible grâce à l'utilisation, en pépinière, de techniques de mesures novatrices telles que la digitalisation en 3D de l'architecture des semis et la mesure *in situ* et *in vivo* des échanges gazeux des parties souterraines et aériennes par le biais d'encreintes de respiration rhizosphérique ou de bulles incorporant la cime entière.

L'ensemble des résultats obtenus dans les différentes expériences menées en milieu naturel comme en milieu contrôlé, démontre qu'en plus de la disponibilité en lumière, la taille des individus représente un facteur important de variation de la performance des semis. En effet, seule ou en interaction avec la disponibilité en lumière, la taille influence de nombreux paramètres internes aux espèces touchant principalement à leur morphologie de cime et leur répartition de biomasse dans les différents compartiments. En augmentant leur taille, les semis des deux espèces ont démontré une perte de leur efficacité d'interception de lumière et une augmentation de la quantité de tissus non photosynthétiques par rapport aux tissus photosynthétiques. De plus, si certaines différences entre espèces existaient (capacités de photosynthèse, allocation aux branches), ces dernières tendaient à disparaître avec la diminution de lumière, avec l'augmentation de la taille, ou encore à taille égale. De même, malgré les capacités photosynthétiques supérieures du bouleau jaune, il existait peu de différence entre l'assimilation nette de la cime entière des deux espèces, principalement sous faible lumière ou le bouleau soutenait de fortes pertes de CO₂ par respiration.

De ce fait, la performance d'un individu dans un environnement lumineux donné pourrait ne pas être constante tout au long de son développement en taille. Par conséquent, même si peu de différences ont été répertoriées entre l'érable à sucre et le bouleau jaune au niveau de leur fonctionnement intégré à l'échelle de l'individu, des différences apparaissant au niveau de leur patron d'allocation de carbone dans les différents puits (i.e. croissance, maintenance, réserves) pourraient être à la base de leurs degrés distincts de tolérance à l'ombre et de leur mode de régénération.

1. CONTEXTE

Généralisant plus de 60 000 millions de dollars canadien de chiffre d'affaires et près de 250 000 emplois directs, la production forestière correspond à l'un des secteurs économiques les plus importants au Canada. Parallèlement à sa valeur économique, la forêt canadienne possède des intérêts écologiques, récréatifs et touristiques non négligeables qui ne cessent de gagner en importance. Par conséquent, dans le but de conserver l'utilisation multiple et à long terme de cette ressource, une gestion durable et adaptée de son renouvellement doit être appliquée.

Pour cela, il est nécessaire de bien connaître par quels mécanismes les différentes espèces forestières se régénèrent et surtout quels environnements permettent cette régénération. En forêt feuillue tempérée, le remplacement des arbres matures se fait généralement par le biais du régime naturel de perturbations du couvert (i.e. chablis, verglas, feux, etc.). Pour un aménagement réfléchi des forêts, il devient donc primordial de s'intéresser à cette dynamique d'ouverture et de fermeture de la canopée et à son utilisation par les différentes espèces forestières.

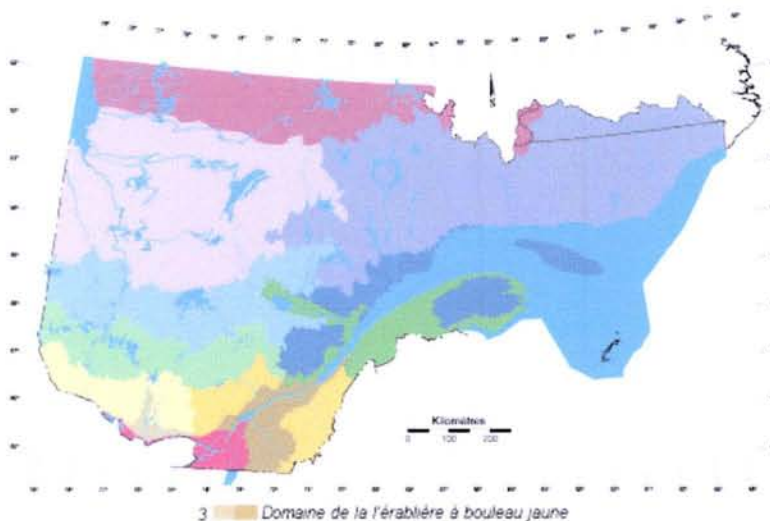


Figure 1.1. Carte représentant les zones de végétation du Québec. Le domaine de l'érablière à bouleau est indiqué en jaune clair (zone Ouest) et en jaune foncé (zone Est). Source : Gouvernement du Québec, Ministère des ressources naturelles.

Dans le sud du Québec, l'érable à sucre (*Acer saccharum*, Marsh.) et le bouleau jaune (*Betula allégamiensis*, Britton) sont deux espèces particulièrement recherchées par les industries forestières. L'étude de leur renouvellement est donc particulièrement importante du fait que ces essences sont régulièrement prélevées lors de pratiques sylvicoles et que leur présence à long terme est souhaitée. Retrouvées en peuplements mélangés, notamment au niveau du domaine bioclimatique de l'érablière à bouleau jaune

(environ 65 000 km², Figure 1.1), ces deux essences ne possèdent pourtant pas le même tempérament écologique. En effet, l'érable à sucre est par exemple reconnu pour être tolérant à l'ombrage alors que le bouleau jaune est lui considéré comme une espèce semi-tolérante à l'ombre. Cette divergence de tempérament est importante dans le contexte de renouvellement de ces espèces car elle suggère des mécanismes de croissance différents lors de leur régénération et donc la nécessité de conditions environnementales distinctes pour leur développement.

Par conséquent, l'aménagement durable de ces deux espèces requiert non seulement une bonne définition de l'environnement associé à leur développement optimal et/ou leur possibilité de survie à long terme mais également la compréhension des mécanismes leur permettant ou non de s'acclimater à la variation de leur environnement (i.e. la compréhension de leur tempérament écologique).

2. INTRODUCTION GÉNÉRALE

2.1. Tempérament écologique des arbres

2.1.1. Interactions avec l'environnement

Tout au long de leur cycle de vie, les arbres sont en constante interaction avec leur environnement, qu'il soit biotique ou abiotique. En effet, toute plante agit sur son environnement en y prélevant des ressources et en y émettant des résidus de même que tout environnement, ou plus précisément toute variation de l'environnement, entraîne une réponse (ou réaction) des plantes (Figure 2.1). Généralement, la variation de l'environnement entourant une plante est associée à la présence d'autres plantes (compétition), à une intervention extérieure (perturbation) ou encore à l'épuisement des ressources par la plante elle-même (Chapin 1980, Fowler 1986, Runkle et Yetter 1987, Bazzaz 1990, Sadamandian-Nambiar et Sands 1993, Casper et Jackson 1997, Valverde et Silvertown 1997). Dans chacun de ces cas, l'accessibilité aux ressources est modifiée et la performance de l'individu est alors reliée à sa capacité de réaction face à cette modification. Cette capacité à réagir se caractérise généralement par deux notions très importantes: **le temps** et **l'espace**.

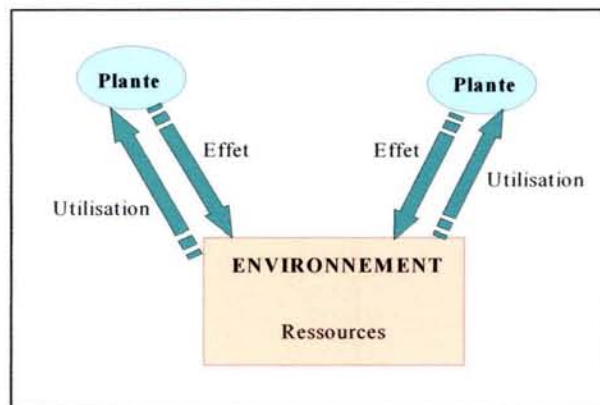


Figure 2.1. Schématisation de l'interaction entre la plante et son environnement. Chaque individu possède un effet sur l'environnement qui en retour influence son développement et celui des autres individus. (Adapté de Casper et Jackson 1997).

Le temps : Dans l'étude du tempérament écologique des arbres, il est plus juste de parler d'acclimatation (réponse à moyen terme) que d'adaptation (réponse à long terme). En écologie, l'adaptation est reliée au principe d'évolution et correspond à l'expression d'un nouveau caractère entraînée par une ou plusieurs modifications du génome qui améliorent la performance d'une espèce dans un environnement donné (Allano et Clamens 2000). Cette réponse nécessite donc plusieurs générations pour être exprimée par un individu et la pression de l'environnement est indirecte. A l'inverse,

l'acclimatation (aussi appelée plasticité par la suite) est liée à une modification phénotypique qui est réalisée par l'individu ou la population qui subit la variation de l'environnement. Cette acclimatation représente la variabilité d'un phénotype ou caractère (e.g. épaisseur des feuilles, angle des branches, allocation aux racines) sous la pression directe de l'environnement. L'apparition d'un phénotype chez un individu est donc fonction à la fois de son patrimoine génétique, de son environnement et de l'interaction entre les deux (cf. Athanasopoulos 2003).

L'espace : La notion d'espace est également très importante dans la réponse d'un arbre à la variation de son environnement car elle définit le lieu de la réponse et l'échelle à laquelle cette réponse se produit. En effet, la réaction d'un arbre peut se situer au niveau d'un ou plusieurs de ses organes (e.g. feuilles, branches, racines) mais également au niveau de sa physiologie, de sa morphologie ou de ses patrons d'allocation de biomasse. De ce fait, réagir à une variation de l'environnement engendre chez l'arbre l'association de plusieurs modifications à petite échelle pour atteindre une réponse à plus grande échelle (Bazzaz 1979, Givnish 1988, Walters et Reich 1999). De plus, du fait de la grande interrelation entre tous les organes et tous les processus de l'arbre (Figure 2.2), certaines modifications peuvent affecter simultanément positivement une fonction de l'arbre et négativement une autre fonction ce qui rend difficile son interprétation au niveau de la performance globale de l'individu (Givnish 1986). Il est donc important de ne pas interpréter la réponse d'un arbre au niveau d'un seul de ses organes ou d'une seule échelle de processus (Vester 2001).

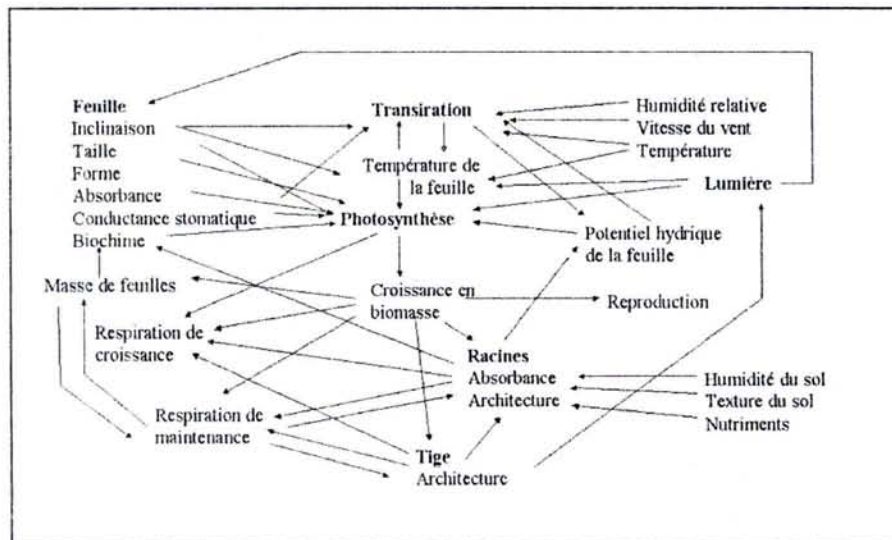


Figure 2.2. Résumé des interactions entre quelques paramètres intervenant dans les processus d'échanges gazeux et de répartition du carbone dans l'arbre et de l'influence des conditions environnementales sur ces paramètres. (Adapté de Givnish 1986)

Le tempérament écologique des arbres peut donc se définir comme étant l'ensemble des acclimations dont ils sont capables pour répondre à moyen terme à des variations de leur environnement dans le but d'améliorer leur performance. A l'échelle de l'individu, ce tempérament est donc déterminé par la somme des caractères qui par leur expression et leur interaction, permettent ses acclimations.

N.B. : Il reste encore très difficile d'utiliser un terme général permettant de décrire la somme des réactions produites par un arbre pour s'acclimater à la variation de son environnement sans être accusé d'anthropomorphisme. C'est pourquoi les termes « comportement » et « stratégie » (bien que souvent retrouvés dans la littérature concernant la physiologie et l'écologie forestière) ne sont pas utilisés ici. En effet, ces termes habituellement utilisés dans la description de réactions animales possèdent une notion de « choix » ou de « réflexion » qui n'a encore jamais pu être démontrée chez les plantes même dites supérieures. C'est pourquoi, le terme de tempérament écologique a été préféré ici car, bien qu'il soit également utilisé dans l'observation des animaux, il réfère (i) aux particularités physiologiques et morphologiques qui différencient les individus entre eux, (ii) à l'activité d'un organisme, (iii) à la structure et la constitution d'un être vivant (Office Québécois de Langue Française, 2004).

Parmi les chapitres qui suivent, le terme de tempérament écologique est traduit en anglais par celui de « functional ecology » qui est largement utilisé dans la littérature scientifique (cf. revue de Messier et al. 1999).

2.1.2. Importance du tempérament écologique chez l'arbre

Contrairement à bien des êtres vivants, les arbres ne peuvent ni « chasser » leurs ressources, ni fuir en cas d'épuisement du milieu. Lors de la modification de leur environnement (e.g. variations de température, de disponibilité en lumière ou en eau) par une action extérieure (perturbation naturelle ou anthropique) ou par leur propre développement (compétition intra ou inter-spécifique), leur capacité à s'acclimater devient alors essentielle à leur survie. Pour ces raisons, l'acclimation des plantes est d'ailleurs reconnue comme étant supérieure à celle des animaux car elle correspondrait à un substitut à la mobilité (Grime et al. 1986, Hallé 1999). Cependant, bien qu'elle puisse être très grande (Figure 2.3), cette capacité d'acclimation est limitée par le patrimoine génétique des espèces et par l'obtention de bénéfices qui doivent rester supérieurs aux coûts engendrés par ces acclimations (Givnish 1986).

Il existe, grâce à la grande diversité génétique, toute une variété de tempéraments écologiques chez les plantes (Ellenberg, 1988). Ces divergences se caractérisent notamment par différents degrés de tolérance à l'ombrage, à la salinité, à la sécheresse, ou encore par différentes capacités à utiliser des trouées ou à envahir des milieux ouverts (cf. Ellenberg 1988). Chez les arbres, ces différences de tempérament écologique (ou d'une de ses composantes) s'avèrent très importantes car elles ont déjà été associées à de nombreux concepts tels que les processus naturels de régénération forestière, la dynamique de répartition spatiale des espèces ou la dynamique de succession (e.g. Bazzaz

1979, Fowler 1986, Ellenberg 1988, McClure et al. 2000, Woods 2000, Arian et Lechowicz 2002).

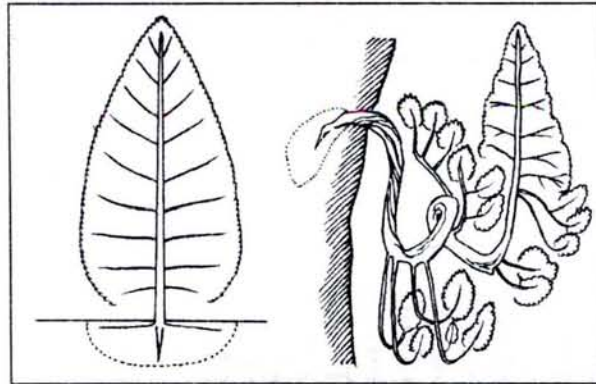


Figure 2.3. Exemple de plasticité d'un arbre poussant en condition normale dans le sol (gauche) et d'un individu se développant dans une crevasse de falaise. (D'après Hallé 1999)

2.2. L'arbre et son environnement

Il existe un grand nombre de ressources utilisées par les arbres pour leur croissance, tant au dessus qu'en dessous du sol (*cf.* Brady 1974). La caractérisation de ces ressources et de leur disponibilité est importante dans l'étude du tempérament des arbres car elles définissent en partie les patrons d'allocation de biomasse dans les différents compartiments de l'arbre responsable de leur prise en charge (Tilman 1988, Gleeson et Tilman 1992).

2.2.1. La lumière

Seule la fraction de la *lumière* comprise entre les longueurs d'onde de 400 et 700nm (Photosynthetic Active Radiation ou PAR) est utilisée par les plantes pour la photosynthèse. Généralement estimée par sa densité de flux (Photosynthetic Photon Flux Density ou PPFD), la disponibilité de cette ressource en forêt est reconnue pour être extrêmement variable en intensité, dans le temps et dans l'espace (Runkle 1982, Canham et al. 1990). Cependant, la lumière est une ressource primordiale tout au long du développement des plantes. Sa quantité, sa qualité et sa rythmicité sont reconnues pour agir au niveau de nombreux processus tels que la germination, la morphogenèse, la floraison, la reproduction (Salisbury et Ross 1978) mais aussi bien entendu la photosynthèse, l'ouverture des stomates (Jarvis 1976, Salisbury et Ross 1978) et l'activité de nombreuses enzymes (Kobza et Seemann 1989, Salvucci 1989).

Après son passage à travers la canopée, il n'est pas rare de retrouver au niveau des sols forestiers moins de 3% du rayonnement externe global (Larcher 1995, Canham et al. 1990, Figure 2.4). De plus, les proportions de rayonnement direct et diffus en sous couvert sont très fluctuantes et peuvent amener à une dynamique complexe de création de taches de lumière et de périodes d'ombre de durée et de taille très variables (Chazdon et Fetcher 1984). En effet, la quantité et la qualité de la lumière disponible en sous bois varient considérablement selon la position du soleil (latitude, saison, heure), la composition et la structure du couvert (espèce, hauteur, densité), la création et la forme de perturbations (pratiques sylvicoles, chute d'arbre(s), feu) et la présence de nuages et de vent (e.g. Runkle 1982, Canham et al. 1990, Denslow et Spies 1990). Enfin, il a déjà été observé que l'absorption sélective des feuilles de la canopée occasionne un appauvrissement marqué de certaines longueurs d'onde au niveau du sol (Holmes et Smith 1977), ce qui peut influencer le développement des semis en régénération (Salisbury et Ross 1978, Turnbull 1991).

Ainsi, la grande variabilité de la disponibilité en lumière en sous couvert en fait souvent l'une des ressources les plus importantes dans le développement et la survie des essences forestières. A l'échelle de l'individu, il est d'ailleurs reconnu que l'investissement pour la capture et l'utilisation de cette ressource représente un facteur primordial dans la performance de l'individu et que des divergences dans cet investissement pourraient être à la base des différentes tolérances à l'ombrage observées entre les espèces (e.g. Boardman 1977, Björkman 1981, Bazzaz, 1979, Givnish 1988, Reich et al. 1998).

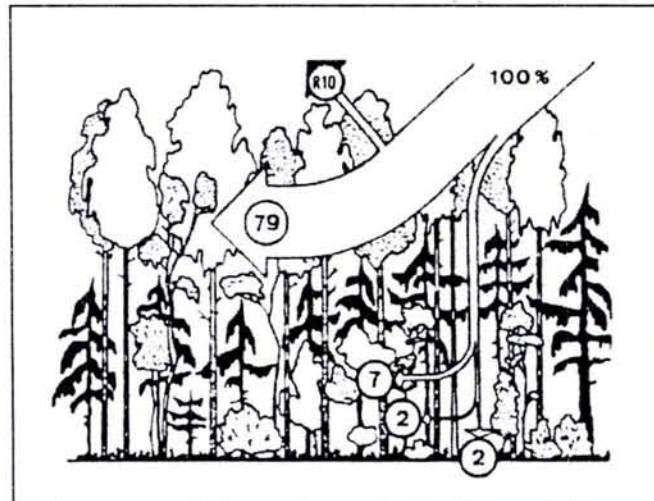


Figure 2.4. Schéma de la répartition de l'interception de la lumière au sein des différentes strates d'une forêt mixte. (D'après Larcher 1995)

2.2.2. Le dioxyde de carbone et l'oxygène

Le *dioxyde de carbone* (CO_2) est une composante primordiale au sein du très complexe cycle du carbone car il matérialise l'un des plus importants liens entre les différents réservoirs de carbone que sont l'atmosphère, la biosphère, les océans et les bassins fossiles. Actuellement, un grand nombre de recherches sont en cours pour déterminer l'importance des plantes et en particulier des écosystèmes forestiers sur les quantités de CO_2 atmosphérique. En effet, le CO_2 est utilisé par les plantes pour la production de matière sèche grâce à la photosynthèse mais il est aussi émis en plus ou moins grande quantité par la respiration des tissus (*cf.* Salisbury et Ross 1978).

Cependant, si tout porte à croire que les concentrations de CO_2 augmentent dans l'atmosphère, la disponibilité de cette ressource dans les écosystèmes forestiers est relativement peu variable à court et moyen terme (Bazzaz et Williams 1991). En effet, actuellement à une concentration de 0.036% de l'air, les variations de la quantité de CO_2 en forêt sont généralement reliées à la vitesse du vent, à la structure verticale du couvert et à la période de la journée mais ne fluctuent jamais au delà de $\pm 10\%$ (Bazzaz et Williams 1991). De plus, si une augmentation de CO_2 est clairement favorable à la croissance de nombreux arbres (*cf.* Larcher 1995, Baldocchi et Amthor 2001), cet effet positif n'est généralement visible qu'à partir d'une augmentation de 200% (e.g. Bazzaz et al. 1990, Harley et al. 1992, Reid et Strain 1994, Andrews et al. 1999, Naumburg et al. 2001).

De la même façon, l'*oxygène* (O_2) est une ressource dont la disponibilité est peu variable à court et moyen terme. Présent dans l'atmosphère à une concentration de 21%, l' O_2 est un gaz utilisé par les plantes pour la respiration des tissus afin de fournir l'énergie nécessaire à la création de nouveaux tissus et à la maintenance et l'entretien des tissus formés (*cf.* Larcher 1995, Amthor 1986, Amthor et Baldocchi 2001). Cependant, l' O_2 peut devenir un facteur limitant la croissance des plantes comme par exemple dans le cas d'inondations catastrophiques ou d'arrosage des sols. En effet, dans ces conditions,

l'aération des sols est entravée ce qui empêche l'oxygénation des racines et peut altérer leur fonctionnement (McKee 1996).

2.2.3. L'eau et les nutriments

L'eau est essentielle à toute forme de vie et bien qu'elle soit absorbable par l'entière surface des plantes, ces dernières la puisent principalement dans le sol grâce à leurs racines. L'absorption de l'eau par la plante est un processus passif au sens où peu d'énergie est investie pour sa prise en charge par les racines. L'absorption de l'eau (E_{abs}) est fonction de la surface d'échange (S_{Ra} ; surface de racines absorbantes), de la résistance des racines au passage de l'eau (R_{Ra}) et de la différence de potentiel hydrique entre le sol (Ψ_{Sol}) et les racines absorbantes (Ψ_{Ra}) :

$$E_{\text{abs}} = S_{\text{Ra}} \cdot \frac{1}{R_{\text{Ra}}} \cdot (\Psi_{\text{Sol}} - \Psi_{\text{Ra}}) \quad 1$$

L'eau est utilisée par les feuilles pour la photosynthèse et la régulation de la température (via la transpiration) mais sa conduction du sol jusqu'aux feuilles (dirigée par un gradient de potentiels hydriques, cf. Larcher 1995) sert également aux transports des éléments minéraux pris en charge par les racines. Les plantes perdent en très grande partie leur eau sous forme de vapeur d'eau transpirée par les feuilles au niveau des stomates (i.e. évapotranspiration). Cette perte d'eau est donc particulièrement élevée durant les périodes de photosynthèse, où les radiations sont plus élevées (température foliaire augmente) et où les stomates sont ouverts. Cependant, si le passage de l'eau à travers l'arbre jusqu'à l'atmosphère se fait par un processus physique dépendant principalement des conditions environnementales (e.g. humidité et température de l'air), les arbres ont la capacité de moduler cette transpiration par la régulation de l'ouverture et de la fermeture de leurs stomates. Ces mécanismes physiologiques, permettent en cas de déstabilisation de l'équilibre hydrique d'un individu, lors par exemple d'une sécheresse du sol, d'éviter une déshydratation dommageable de ses tissus.

La disponibilité en eau d'un sol peut donc jouer un rôle important dans l'établissement du bilan carboné d'un individu car elle influence la dynamique d'ouverture et de fermeture des stomates et donc l'entrée du CO_2 dans la plante pour la photosynthèse. Caractérisée par la rapidité d'induction et la conductance maximale ($G_{\text{s,max}}$), cette régulation stomatique est très variable entre espèces (Larcher 1995) et pourrait jouer un rôle important dans l'établissement et la croissance des espèces sur des sols susceptibles à des périodes de sécheresse.

Les *nutriments* sont majoritairement pris en charge par les plantes au niveau du sol, et si certains sont nécessaires en relativement grande quantité (macro-éléments), d'autres sont absorbés en très faible quantité (oligo-éléments). L'absorption des nutriments se fait généralement en même temps que celle de l'eau, cependant plusieurs éléments requièrent une absorption active (i.e. coûteuse en énergie) par les racines. Les éléments minéraux proviennent de l'érosion de la roche mère, mais sont, en milieux forestiers, principalement fournis par la dégradation de la matière organique tombant sur le sol (Nye 1961, Vitousek et Sanford 1986). Cette dégradation, réalisée par les microorganismes du sol (insectes, champignons, bactéries), détermine la richesse du sol et conditionne donc la possibilité de

production de biomasse des plantes. Cette dégradation de la matière organique des sols est également dépendante des conditions environnementales (e.g. température et humidité du sol), de la quantité de litière déposée et de la composition de cette litière (e.g. % de lignine). Elle varie donc grandement avec la latitude et la composition du couvert (Brady 1974).

Parmi les nutriments du sol, l'azote (N) est reconnu comme le principal élément pouvant limiter le développement des arbres avant le phosphore (P) et le calcium (Ca) (Brady 1976). En effet, l'azote est présent tant au niveau de la structure (lignine, protéines structurelles, etc.) que du fonctionnement (enzymes, pigments, acides nucléiques, etc.) des plantes supérieures (Skiredj 2004). Des limitations de la croissance peuvent donc être observées lorsque les nutriments ne sont pas recyclés assez rapidement (i.e. minéralisation lente), ou encore lorsqu'ils ne sont pas bien équilibrés entre eux (i.e. excès de calcium réduisant la disponibilité en fer ou en zinc). Les patrons de répartition, de retranslocation et de stockage de ces éléments minéraux (tels que l'N) dans l'arbre sont donc primordiaux dans leur fonctionnement et leur croissance (Evans 1989, Chapin et al. 1990, Larcher 1995, Niinemets 1997, Kull et al. 1998, Frak et al. 2001). Cependant, au niveau de nombreux biomes forestiers, cette limitation reste inférieure à celle impliquée par la disponibilité en lumière de l'environnement (Coomes et Grubb 2000, Annexe C).

2.2.4. La température

La *température* n'est pas à proprement parler une ressource utilisée par les arbres, mais elle exerce cependant une influence prépondérante sur leur fonctionnement et donc le déroulement de leur développement. La température intervient au niveau des processus de germination, de floraison, de production de graines (Salisbury et Ross 1978, Larcher 1995) et bien entendu au niveau du fonctionnement des organes tels que les feuilles (Ryan et al. 1996, Dreyer et al. 2001) ou les racines (Ryan et al. 1996, Zogg et al. 1996, Atkin et al. 2000). La responsabilité de la température dans ces mécanismes est liée à la dépendance thermique de l'activité des enzymes impliquées dans les réactions métaboliques. La température influence le taux (i.e. la vitesse) de la réaction et agit donc sur la création des produits de la réaction.

Durant l'augmentation de température, le taux de réaction atteint un maximum (température optimale) avant de diminuer si la température continue de s'accroître. Ceci est relié à l'épuisement des substrats de la réaction et à la modification d'autres processus associés à la réaction tels que la solubilité des substrats ou la perméabilité des membranes (Baldocchi et Amthor 2001). Enfin, sous des températures extrêmes, la détérioration de l'enzyme et de la structure des cellules peuvent amener à l'arrêt complet de la réaction (Larcher 1995).

L'augmentation du taux de la réaction avec l'augmentation de température peut être décrite assez simplement en utilisant un coefficient de dépendance thermique (Q_{10}) (Stanford et al. 1973) ou plus précisément avec des relations de thermodynamique décrivant les énergies d'activation des réactions (Dreyer et al. 2001, Leuning 2002, Medlyn et al. 2002a, 2002b). Le Q_{10} est reconnu comme un bon moyen d'isoler la dépendance thermique d'un processus biologique (Thornley et Cannell 2000). Cependant, il existe une grande variabilité de ce paramètre notamment vis-à-vis du processus de respiration qui dans la littérature, varie entre espèces mais également entre les différents tissus de l'arbre (Larcher 1995, Sprugel et al. 1995, Atkin et al. 2000, Ryan et al. 2000).

Au niveau du bilan carboné, l'influence de la température peut devenir importante puisqu'elle agit à la fois sur la quantité de CO₂ incorporée par les feuilles et sur celle émise par la respiration des tissus (*cf.* Sprugel 1989, Atkin et al. 2000, Thornley et Cannell 2000, Amthor et Baldocchi 2001). Cependant, la photosynthèse, la respiration et la photorespiration ne répondent pas de manière identique à l'augmentation de la température. Des études ayant évalué la dépendance thermique de processus tels que la photosynthèse et la respiration, ont permis de déterminer l'intervalle de température pour lequel l'assimilation de carbone est maximum. Cet intervalle est très variable selon les espèces et se situe entre 20 et 25°C pour les feuillus de zones tempérées (Larcher 1995).

Dans des différents biomes forestiers, la température varie grandement en fonction de la latitude et bien entendu de la saison. Pour ces raisons, la productivité des forêts est très variable selon leur localisation sur la planète et la période de l'année (Amthor et Baldocchi 2001).

2.2.5. L'espace

Il a déjà été supposé que l'espace en tant que volume puisse être considéré comme une ressource par les plantes, puisque l'occupation d'un plus grand espace permet d'acquérir plus de ressources (e.g. lumière, eau, nutriments). Les quelques études réalisées au niveau de l'occupation du sol (McConnaughay et Bazzaz 1991, 1992), ont montré qu'il pouvait exister une modification de la croissance due à la restriction racinaire, quelle soit reliée au volume de sol disponible, à la présence d'autres racines ou à la présence d'objets dans le sol. Ceci peut s'expliquer par l'obstruction physique qui empêche la formation des embranchements programmés des racines et le déploiement des racines absorbantes (McConnaughay et Bazzaz 1992). On notera que cette obstruction physique est potentiellement similaire au dessus du sol pour le déploiement de la tige, des branches et des feuilles en vue de la capture de lumière.

Il semblerait également qu'une reconnaissance des racines entre individus de même espèces et d'espèces différentes peut exister et qu'elle pourrait amener à la sécrétion de composés organiques secondaires toxiques ou inhibiteurs de la croissance des racines (Larcher 1995, Falik et al. 2003). Il est donc très complexe de quantifier le réel impact de cette obstruction physique de l'espace sur la croissance des plantes. Il est d'ailleurs raisonnable de croire que cet effet pourrait être confondu aux mécanismes de compétition ayant cours au dessus comme en dessous du sol (Grubb et al 2000, Annexe C). En effet, il reste difficile de séparer la notion d'espace disponible avec celles de compétition pour les ressources ou de richesse du milieu. L'occupation du sol par d'autres racines correspond à un appauvrissement du milieu au même titre que la présence d'objets dans le sol tend à réduire la quantité de ressources disponibles dans un volume donné et oblige donc la prospection d'un plus grand espace (Chapin 1980, Bazzaz 1990, Casper et Jackson 1997).

2.2.6. La taille

Si la taille ne peut être vue comme une ressource nécessaire au développement de l'arbre, celle-ci correspond à un facteur primordial souvent ignoré. En effet, durant son développement, l'arbre investit une grande proportion de sa biomasse au niveau de ses tissus non photosynthétiques (TNP) dont les principales fonctions sont (i) le support et le

déploiement des tissus fonctionnellement très actifs (e.g. feuilles et racines fines), (ii) le transport de l'eau et des nutriments vers les feuilles et celui des assimilats vers les organes et (iii) le stockage de réserves (cf. Givnish 1995, Larcher 1995, Gougeon 2000). Un investissement en biomasse pour la croissance en hauteur et la production de tissus non photosynthétiques est donc reconnu pour améliorer la compétitivité d'une espèce vis-à-vis de la capture de ressources telles que la lumière ou l'eau présente dans le sol. Certaines études sous-entendent également l'implication positive de cette augmentation du volume de tissus non photosynthétiques pour augmenter la surface de transport de l'eau dans l'arbre et ainsi compenser la perte de conductivité observée pendant son développement en hauteur (Ryan et al. 2000, McDowell et al. 2002).

Cependant, il a déjà été montré que cette augmentation de tissus non photosynthétiques (en surface ou en volume) est grandement supérieure à celle des tissus photosynthétiques (Givnish 1988, Perttunen et al. 1996, 1998). Cette augmentation différentielle pourrait donc impliquer d'importants coûts de construction et de maintenance qui déséquilibreraient le bilan carboné d'un individu et le fragiliseraient face à une situation de stress (Waring 1987, Givnish 1988). Givnish (1986, 1988) émet même l'hypothèse que cette augmentation du rapport des tissus non photosynthétiques par rapport aux tissus photosynthétiques seraient à la base de la taille limite des arbres.

De plus, l'augmentation de biomasse à la verticale suppose également une augmentation des contraintes physiques et mécaniques appliquées par la gravité terrestre ou le vent (Givnish 1986, Niklas 1992, 1994, Hallé 1999, West et al. 1999). Ces lois externes appliquées par l'environnement physique des arbres (Figure 2.5) ont une influence directe sur leur ancrage et la densité de leur bois (King 1986), le transport de l'eau contre la gravité (Ryan et Yoder 1997, Mencuccini 2001) ou encore les patrons d'architecture de la cime (Niklas 1992, Givnish 1995). Un nombre grandissant d'études montrent également l'importance directe ou indirecte de la taille dans la modification de nombreux caractères morphologiques et de répartition de biomasse des plantes (Sterck 1997, Gardiner et Hodges 1998, McConnaughay et Coleman 1999, Messier et Nikinmaa 2000, Sterck et Bongers 2001, Claveau et al. 2002).

D'ailleurs, l'implication de la gravité a déjà été reconnue au niveau du transport et de la distribution de l'auxine dans les plantules (Kamada et al. 2003). Or cette substance est reconnue pour tenir un rôle important dans les patrons d'embranchement, le développement des bourgeons axillaires et la dominance apicale (Booker et al. 2003).

L'ensemble de ces résultats suggère donc une importance de la taille dans l'évolution de l'acclimatation des différents caractères de l'arbre et donc la possibilité d'une modification de leur tempérament écologique (e.g. leur tolérance à l'ombrage) durant leur développement (Messier et Nikinmaa 2000, Naumburg et al. 2001).

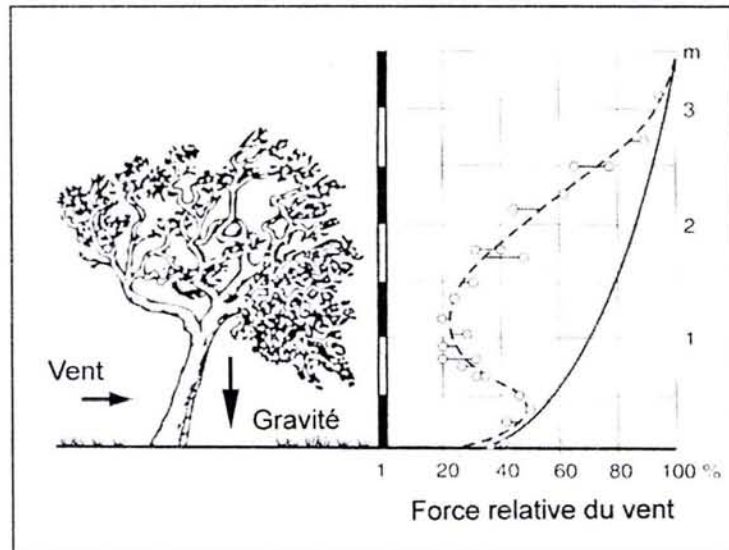


Figure 2.5. Exemple des forces physiques imposées par l'environnement pendant le développement en taille et en biomasse de l'arbre. (Adapté de Larcher 1995).

2.3. Le bilan de carbone à l'échelle de l'individu

2.3.1. Introduction sur le bilan carboné

Sous l'hypothèse réaliste qu'un individu réalisant un bilan de carbone positif peut continuer sa croissance alors qu'un individu ayant un bilan négatif consomme ses réserves et se fragilise devant une situation de stress (Waring 1987), la mesure ou l'estimation de ce bilan, et/ou des mécanismes dont il résulte, représente une nécessité dans l'étude de la performance d'un individu dans un environnement donné et donc de ses potentialités de survie. On notera qu'il est ici question du bilan de carbone découlant de la sommation des échanges gazeux à l'échelle de l'individu. C'est-à-dire qu'il n'est pas question du carbone perdu (i) à l'automne pendant la chute des feuilles, (ii) durant la dispersion des semences ou (iii) lors de la dynamique de remplacement des racines fines. Par conséquent, le bilan carboné d'un individu lorsque l'on considère uniquement les échanges gazeux, est défini par la compilation du CO_2 incorporé par la photosynthèse auquel sont soustraites les pertes de CO_2 liées à la respiration des feuilles, branches, tiges et racines (Figure 2.6).

A l'échelle de l'individu, les gains en carbone sont une fonction de l'interception de la lumière disponible et de l'utilisation (ou conversion) de la lumière interceptée (Boardman 1977, Björkman 1981, Stenberg et al. 1995) alors que la libération de carbone par respiration est fonction du taux de croissance et de la biomasse mis en place par l'individu (e.g. McCree 1970, Thornley 1970, Penning de Vries 1979, Amthor 1986, 2000, Thornley et Cannell 2000).

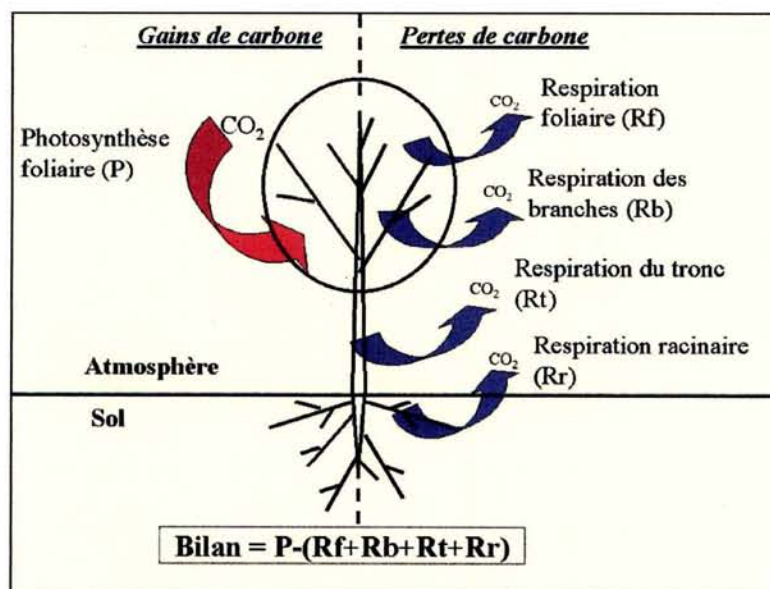


Figure 2.6. Schéma résumant l'ensemble des gains et des pertes de CO_2 à l'échelle de l'individu qui définissent le bilan des échanges gazeux.

2.3.2. L'interception de la lumière

2.3.2.1. Généralités

Il existe un grand nombre de facteurs influençant l'interception de lumière réalisée par un individu. Bien entendu, la quantité de lumière interceptée par un individu est grandement reliée à la quantité et la qualité de la lumière disponible dans son environnement. Cependant, il a également été rapporté que cette interception pouvait être associée à l'architecture (patron d'embranchement et phyllotaxie), la morphologie de la cime (hauteur et diamètre) ou au nombre de couches de feuilles développées dans le volume de cime (Leaf Area Index; LAI) d'un individu (e.g. Horn 1971, Waring 1987, Ellsworth et Reich 1993, Sipe et Bazzaz 1994, Beaudet et Messier 1998, Millet et al. 1998, Sterck 1999, Claveau et al. 2002). De plus, à plus petite échelle, de nombreux autres paramètres propres aux différentes espèces, tels que la longueur des pétioles et leur rotation, l'arrangement spatial des feuilles à l'intérieur de la cime, la taille des feuilles, leur forme, leur durée de vie, mais aussi leur propriété optique, ont été associés avec la quantité de lumière finalement utilisable pour la fixation du CO₂ (e.g. Stenberg et al. 1995, Ackerly et Bazzaz 1995b, Planchais et Sinoquet 1998, Beaudet et Messier 1998, Farque et al. 2001, Galvez et Pearcy 2003).

L'importance de l'ensemble de ces facteurs réside principalement dans le fait qu'ils permettent plus ou moins efficacement de réduire l'effet négatif de l'auto-ombrage causé par le déploiement des feuilles qui à l'intérieur de la cime se superposent. En effet, il est maintenant reconnu qu'il existe une diminution importante de la quantité de lumière disponible à l'intérieur de la cime d'un individu due à l'auto-ombrage (Sinoquet et al. 1998, Beaudet et al. 2000). De plus, cet auto-ombrage augmente avec l'augmentation de la surface foliaire de l'individu (Farque et al. 2001). Or, si dans un environnement où la disponibilité en lumière est grande, l'auto-ombrage induit peu d'impacts sur la croissance de l'individu, cette perte de rendement en situation d'ombrage peut être très importante dans la survie des branches les plus basses et même dans celle de l'individu (Waring 1987, Sprugel et al. 1991, King et al. 1997).

2.3.2.2. Notion d'efficacité d'interception de lumière

Chez les feuillus, la feuille correspond généralement à l'élément de base largement reconnu dans l'interception de lumière. Cependant, la comparaison de la surface interceptant la lumière entre individus se fait par unité de surface (m²) et l'étude de leur efficacité d'interception se fait grâce au calcul d'une efficacité d'interception de lumière (LIE). L'efficacité d'interception est généralement considérée comme le rapport entre la surface interceptant la lumière dans une direction donnée (surface foliaire projetée; S_{fp}) et la surface foliaire produite (surface foliaire totale; S_{ft}) :

$$LIE = \frac{S_{fp}}{S_{ft}} \quad 2$$

Ce rapport, aussi appelé le STAR (Silhouette to Total Area Ratio) a l'avantage de prendre en compte l'ensemble des caractères régissant l'organisation des feuilles dans la cime. Ce ratio est d'ailleurs de plus en plus utilisé pour l'étude comparative de l'interception de lumière de différentes espèces sous des conditions de croissances variables (e.g. Farque et al. 2001, Coll submitted). L'efficacité d'interception de lumière est aussi parfois estimée par le calcul d'un coefficient de capture qui correspond à la

quantité de lumière interceptée par 1 m² de feuillage (organisé dans la cime) par rapport à une surface horizontale de 1 m² (Valladares et Pearcy 1998, Valladares et al. 2002, Galvez et Pearcy 2003).

La variation de ces rapports, calculés pour une direction, une branche ou une plante entière, est fréquemment reliée à la disponibilité en lumière. Sous ombrage, l'efficience d'interception est reconnue pour être plus importante afin de maximiser la capture de cette ressource, alors que sous des régimes lumineux moins limitants, la diminution de l'interception est plutôt perçue comme un mécanisme permettant la pénétration de lumière plus profondément dans la cime et la réduction de l'interception des radiations directes pouvant endommager le fonctionnement des feuilles (Planchais et Sinoquet 1998, King et al. 1997, Valladares et Pearcy 1998, Farque et al. 2001, Valladares et al. 2002, Fleck et al. 2003, Galvez et Pearcy 2003).

On notera qu'il est important de pouvoir intégrer l'estimation d'une telle efficience au niveau de l'individu (i.e. intégration dans l'espace) et jusqu'à un certain point sur une période de temps longue (i.e. intégration dans le temps). En effet, la disponibilité en lumière étant elle-même très variable dans le temps et dans l'espace, il est nécessaire de considérer l'efficacité de capture de cette ressource à plus long terme (intégration temporelle) et dans plus qu'une seule direction (intégration spatiale). Ceci est maintenant possible grâce à l'avancée des modèles permettant l'étude de l'interception de lumière en 3 dimensions (cf. Pearcy et Yang 1996, Sinoquet et al. 1998).

2.3.3. L'utilisation de la lumière interceptée

2.3.3.1. Généralités

L'utilisation de la lumière interceptée par les feuilles correspond à l'ensemble des processus permettant aux plantes chlorophylliennes de fixer le CO₂ atmosphérique pour le transformer en composés carbonés à partir de l'énergie lumineuse (i.e. autotrophie). Ces composés carbonés ou photosynthétats sont alors utilisables par les plantes pour la création de nouveaux tissus (i.e. croissance), la réparation et la protection des tissus existants (i.e. maintenance) et la production d'énergie nécessaire à toutes les réactions impliquées dans la croissance et la maintenance des tissus. L'utilisation de la lumière, aussi appelée la conversion de la lumière, regroupe trois grands mécanismes qui ensemble sont à la base de la fixation du CO₂ atmosphérique : la photochimie, la biochimie de la photosynthèse et la diffusion du CO₂. On notera que les deux premiers sont souvent regroupés sous le terme générique de photosynthèse.

La photochimie se divise en deux étapes qui sont (i) l'absorption de l'énergie lumineuse et (ii) la conversion de cette énergie lumineuse en énergie métabolique. La première étape est gouvernée par la quantité de pigments (principalement la chlorophylle) qui, organisés en antennes collectrices, vont diriger l'énergie lumineuse vers des centres réactionnels (les photosystèmes I et II). La seconde étape correspond à la création d'énergie métabolique (l'ATP et le NADPH) à partir de ces centres réactionnels. Cette énergie, nécessaire à la quasi totalité des réactions enzymatiques des plantes, est produite grâce à un flux d'électrons généré par une chaîne de réactions d'oxydoréduction. Le flux maximal de transfert des électrons (J_{\max}), estimable à partir de mesures d'assimilation nette des feuilles (Farquhar et al. 1980, Niinemets et Tenhunen 1997, Von Caemmerer 2000), symbolise donc un paramètre important dans la description des capacités d'utilisation de la lumière.

La biochimie de la photosynthèse correspond à l'ensemble des réactions enzymatiques permettant l'incorporation du CO₂ atmosphérique en molécules plus élaborées (i.e. composés à plusieurs atomes de carbone) telles que la saccharose et l'amidon. Ces réactions sont consommatrices d'énergie métabolique telle que l'ATP et le NADPH. Au centre de ces réactions se trouve la rubisco (ribulose 1,5 bis phosphate carboxylase oxygénase), l'enzyme responsable de la fixation du CO₂. La vitesse maximale de carboxylation de cette enzyme (V_{cmax}) représente comme J_{max} , un paramètre essentiel de l'utilisation de lumière par les plantes qui est estimable à partir de mesures d'échanges gazeux (Farquhar et al. 1980, Niinemets et Tenhunen 1997, Von Caemmerer 2001). On notera que l'autre fonction de la rubisco, la fonction oxygénase, entre en compétition directe avec la carboxylation et produit à l'inverse de cette dernière, du CO₂ à partir de molécules d'O₂. Cette photorespiration, indétectable lors de la mesure d'échanges gazeux est bien entendu prise en compte lors de l'élaboration de modèles de photosynthèse (Farquhar et al. 1980, Von Caemmerer 2000) car elle correspond à une réutilisation pouvant aller de 20 à 50% du carbone préalablement fixé (Sharkey 1988).

La diffusion du CO₂ est un processus très important de l'utilisation de lumière par les plantes du fait qu'il permet l'apport du CO₂ atmosphérique jusqu'au sein des chloroplastes où il sera incorporé par la rubisco. Au cours de cette diffusion, le CO₂ atmosphérique rencontre un certain nombre de résistances (aérodynamique, stomatique et mésophyllienne) qui s'opposent à son entrée dans la plante. Bien que la résistance mésophyllienne ait déjà été estimée (Epron et al. 1995), cette résistance est souvent négligée dans l'élaboration des modèles de photosynthèse ou de conductance stomatique (Farquhar et al. 1980, Farquhar et Wong 1984, Von Caemmerer 2001) faute de ne pouvoir la mesurer avec précision. En revanche, par le biais de la loi de diffusion de Fick (équation 3), il est possible de calculer à partir de la concentration de CO₂ atmosphérique (C_a), du flux entrant de CO₂ (A) et de la conductance stomatique des feuilles (g_s), la concentration en CO₂ intracellulaire (C_i) :

$$A = g_s (C_i - C_a) \quad 3$$

Actuellement, les mécanismes physiologiques entourant la dynamique d'ouverture et de fermeture des stomates sont encore mal connus. Par conséquent, seule la voie empirique se basant sur la réponse des stomates aux conditions environnementales est utilisée pour modéliser g_s (Jarvis 1976, Le Roux et al. 1999a).

2.3.3.2. Notion d'efficacité de conversion de la lumière

Il existe de nombreux facteurs influençant chez un individu le fonctionnement instantané de la photochimie, de la biochimie de la photosynthèse et de la diffusion de CO₂ à l'intérieur des feuilles. En effet, la photosynthèse (i.e. photochimie et biochimie de la photosynthèse) est directement affectée par la quantité instantanée de lumière disponible (PPFD), la température et la concentration en CO₂ de l'atmosphère (e.g. Björkman 1981, Larcher 1995, Dreyer et al. 2001). La dynamique d'ouverture des stomates est également très sensible aux conditions environnementales citées ci-dessus, auxquelles on peut ajouter le déficit de saturation de l'air ou encore l'humidité du sol (Jarvis 1976, Leuning 1995, Le Roux 1999a). C'est pourquoi, dans le but de comparer la capacité d'utilisation de la lumière entre individus, il sera préférable d'évaluer leur efficacité de conversion de lumière plutôt que leur assimilation instantanée. Ceci est

réalisable en estimant le rapport entre l'assimilation de CO₂ réalisée par la cime de l'individu (A_{tot}) et la quantité totale de lumière captée par cette même cime (L_{tot}) :

$$LCE = \frac{A_{tot}}{L_{tot}} \quad 4$$

Il est également possible d'évaluer cette efficacité de conversion de lumière par l'estimation de paramètres reliés aux trois principaux processus retrouvés dans l'incorporation de CO₂ dans la plante. Ces paramètres sont J_{max} pour la photochimie, V_{cmax} pour la biochimie de la photosynthèse, $g_{s\ max}$ pour la diffusion de CO₂ ou encore A_{max} pour l'assimilation dans son ensemble. La concentration d'azote contenue dans les feuilles par unité de masse (N_m) ou de surface (N_a) représente également un paramètre permettant la description de l'efficacité de conversion de la lumière par un individu si l'on considère la grande dépendance de J_{max} , V_{cmax} et A_{max} pour ce paramètre (Walcroft et al 1997, Niinemets et Tenhunen 1997, Le Roux et al 1999a, Lusk et Reich 2000).

Cependant, certaines précautions dans la mesure et l'interprétation de la variation de ces paramètres à l'échelle de la cime doivent être prises du fait par exemple que la concentration d'azote foliaire est extrêmement variable à l'intérieur même de la cime d'un individu (Ellsworth et Reich 1993, Le Roux et al. 1999b) et que la dépendance thermique de paramètres tels que J_{max} , V_{cmax} est maintenant bien reconnue (Dreyer et al. 2001, Medlyn et al. 2002a, Leuning 2002).

2.3.4. Le carbone libéré par la respiration

2.3.4.1. Généralités

Une grande fraction du carbone assimilé via la photosynthèse est réutilisée par les plantes par la respiration des tissus vivants (Amthor et Baldocchi 2001). Cette respiration est une composante importante du bilan en carbone des plantes et des écosystèmes car elle influence la quantité de carbone disponible pour la croissance; plus la respiration est importante, plus la quantité de carbone utilisable pour la croissance est faible. Pour les écosystèmes forestiers, l'estimation des pertes de CO₂ dues à la respiration a déjà été évaluée entre 40 et 90% des gains réalisés par la photosynthèse (Larcher 1995, Amthor et Baldocchi 2001). Cependant, la respiration ne correspond pas simplement à une perte de carbone abaissant le bilan carboné d'un individu. Au même titre que la photorespiration, la respiration fournit, par la consommation de molécules carbonées, de l'énergie sous forme métabolique (e.g. ATP, NADPH, NADH) et de petits squelettes carbonés qui serviront de substrats de base pour les biosynthèses de molécules structurales et fonctionnelles (*cf.* Amthor 1986). Ces composés issus de la respiration sont donc essentiels aux mécanismes de croissance, de transport et de maintenance qui tiennent place dans les plantes (Amthor et Baldocchi 2001).

En effet, il est maintenant reconnu que la respiration (R) est la somme de deux composantes; la respiration de maintenance (R_m) et la respiration de croissance (R_c) (*cf.* McCree 1970, Thornley 1970, Penning de Vries et al. 1979):

$$R = R_m + R_c \quad 5$$

Ces composantes ne sont pas biochimiquement séparables, mais leur clivage a permis de mieux concevoir et surtout de pouvoir modéliser ce processus de respiration (*cf.* revues par Amthor 1986, 2000, Thornley et Cannell 2000). La respiration de maintenance est fonction de la biomasse du plant (B) et correspond principalement à la synthèse des protéines de remplacement, au transport actif des composés entre cellules, à la réparation des tissus et à la capture active des nutriments au niveau des racines. La respiration de croissance, de son côté, est fonction du taux de croissance (donc de la photosynthèse ; P), et se caractérise par les biosynthèses mises en jeu lors de la production de nouveaux tissus. Dans l'équation 6, g et m sont respectivement les constantes de maintenance et de croissance.

$$R = (m \cdot B) + (g \cdot P)$$

6

De grandes variations de respiration entre plantes mais également entre compartiments d'un même individu ont déjà été mesurées notamment par le fait que les constantes m et g sont très variables entre espèces et entre tissus (Penning de Vries 1975, Amthor 1984, Ryan 1990, Ryan et al. 1996, Amthor et Baldocchi 2001). De plus, ces composantes R_m et R_c de la respiration sont reconnues pour être très fluctuantes dans le temps à cause de modifications des conditions environnementales (e.g. température) et de variations d'activité tissulaire (rythme circadien et phénologie) (Amthor 1986, Larcher 1995, Thornley et Cannell 2000).

2.3.4.2. Respiration des différents compartiments de l'arbre

Tous les tissus vivants des plantes respirent. Pour sa part, la respiration des feuilles est étudiée depuis de nombreuses années et est maintenant relativement bien connue (e.g. Boardman 1977, Björkman 1981, Givnish 1988, Reich et al. 1998, Lusk et Reich 2000, Turnbull et al. 2001). De son côté, celles des tissus de soutien (Wullschleger et al. 1995, Edwards et Hanson 1996, Ibrahim et al. 1997, Ceschia 2001, Bosc et al. 2003) et des racines (Walters et al. 1993a, 1993b, Zogg et al. 1996, Bouma et al. 1997, Reich et al. 1998, Huc 2000, Burton et Pregitzer 2002, Burton et al. 2002, Fu et al. 2002), bien que de plus en plus étudiées restent encore difficiles à estimer précisément. Il est cependant clair que la variation de ces respirations est très liée aux conditions environnementales tels que la température, l'humidité du sol, le CO₂, ainsi qu'à des paramètres internes aux espèces tels que la concentration en azote des tissus et la phénologie des compartiments (*cf.* revues par Amthor 1986, 2000 et Thornley et Cannell 2000). De plus, il semble que les tissus les plus actifs tels que les feuilles et les racines fines possèdent des taux de respiration plus importants que les autres tissus de l'arbre (Ryan et al. 2000) ce qui suggère l'importance de leur prise en compte dans l'établissement d'un bilan carboné. D'après Amthor (1986), il pourrait également exister des différences dans le taux de respiration des tissus entre les périodes de jour et de nuit (rythme circadien). Ceci s'expliquerait par le fait que dans la journée, une partie des besoins en énergie des feuilles pourrait être couverte par la photochimie ce qui diminuerait leur respiration de maintenance. De même, la respiration des racines absorbantes pourrait être diminuée pendant la nuit du fait de la baisse des besoins en minéraux liée avec l'arrêt de la photosynthèse durant cette période. Cependant, il n'existe encore aucune évidence

expérimentale allant dans l'observation de ces mécanismes. De plus, il est important de noter que la quantification de ces respirations sur un pas de temps long est encore très complexe et peu précis tant au niveau de la mesure qu'à celui de l'estimation (Waring et al 1998, Amthor 2000).

2.4. La régénération en milieux forestiers

2.4.1. La dynamique de perturbation

La régénération des semis en sous couvert forestier est directement liée à la présence et à la variation des ressources nécessaires à leur développement ainsi qu'à leur capacité d'acquies ces ressources. Dans la majeure partie des biomes forestiers, la régénération des semis se fait par l'intermédiaire de l'utilisation du régime de création de perturbations naturelles des couverts forestiers (Figure 2.7) (Lorimer 1989, Denslow et Spies 1990, Runkle 1990, Coates et Burton 1997).

Ce régime dynamique est relié à la formation d'un gradient de trouées dans la canopée qui peut se définir par leur taille, leur forme et leur fréquence (e.g. Runkle 1982, Runkle et Yetter 1987, Lorimer 1989, Lawton 1990). Allant de la chute de branches aux feux de forêt, en passant par des chablis d'un ou plusieurs arbres ou la création d'une multitude de petites ouvertures lors de pluies verglassantes, l'importance de ces perturbations réside dans le fait qu'elles augmentent la disponibilité en ressources au dessus du sol (Canham et al. 1990, Denslow et al. 1998, Annexes C) comme en sous sol (Mladenoff 1987, Denslow et al. 1998, Ostertag 1998, Annexes C). En effet, l'ouverture du couvert augmente la quantité de lumière qui atteint le sol mais également, la disponibilité en eau et la température du sol et donc le recyclage des éléments minéraux.

Cependant, si la dynamique d'ouverture des couverts est cruciale dans le processus de régénération des semis, la dynamique de fermeture de ces trouées l'est tout autant car elle modifie là encore de façon cruciale l'environnement des semis en régénération (Van der Meer et Bongers 1996, Valverde et Silvertown 1997, McClure et al. 2000).

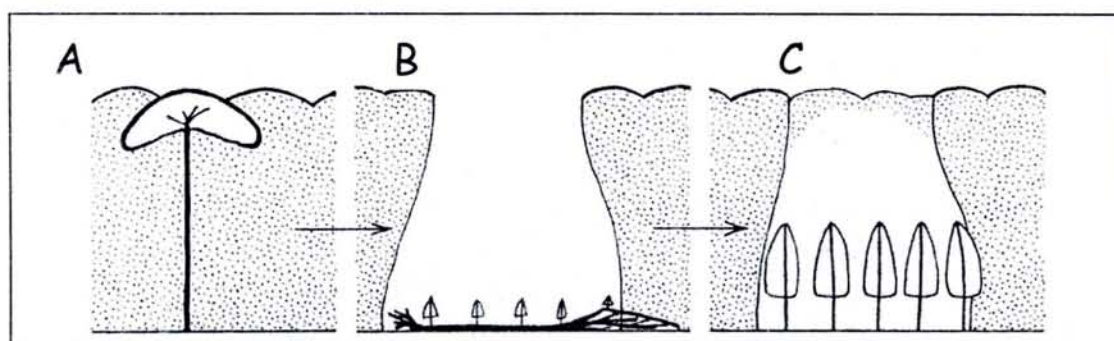


Figure 2.7. Schéma symbolisant le processus de régénération naturelle des couverts forestiers par l'utilisation de la dynamique de perturbation de la canopée. (D'après Hallé 1999)

2.4.2. Facteurs limitants dans le domaine de l'érablière à bouleau jaune

Dans la zone de forêts feuillues tempérées de l'est de l'Amérique du nord (dont le secteur climatique de l'érablière à bouleau jaune fait partie), la disponibilité en lumière représente, parmi les ressources nécessaires au développement des arbres, l'une des plus incontournables lors de l'étude de la croissance des semis en régénération. En effet, il a récemment été mis en évidence que la taille des trouées et donc la disponibilité en lumière était déterminante dans la régénération et la présence à long terme de ces deux espèces, particulièrement pour le bouleau jaune qui nécessiterait des trouées plus grandes du fait de sa tolérance à l'ombre plus faible (McClure et al. 2000, Woods 2000, Messier et al. 2002, Morin et al. 2003).

De plus, la limitation de la croissance des semis et des gaulis en régénération de ces deux essences a également été exclusivement associée à la disponibilité en lumière (cf. Annexes C et D). Cela s'explique par le fait qu'au niveau de ces forêts, les sols mésiques présents sont considérés comme relativement riches durant la saison de croissance, tant au niveau des éléments minéraux que pour leur disponibilité en eau (Ricard 1999). Bien entendu, ceci n'enlève en rien l'importance des ressources du sol pour la croissance des arbres de ces régions, mais indique plutôt que le facteur limitant le plus la croissance dans ces peuplements est la variation de la disponibilité en lumière. On notera également que ces deux espèces possèdent en milieu naturel des associations avec des mycorhizes (cf. Annexes A et B) ce qui améliore leur prise en charge des éléments du sols (Dexheimer 1997, Le Tacon et Selosse 1997, Moussain et al. 1997).

3. PROBLÉMATIQUE

Au même titre que les perturbations naturelles, les pratiques sylvicoles (e.g. coupes de jardinage, coupes par parquets, coupes par bandes) entraînent l'ouverture du couvert et donc l'augmentation de la disponibilité en ressources telles que la lumière (Coates et Burton 1997, Beaudet et al. 2002). Ces perturbations appliquées par l'homme et nécessaires dans un contexte économique peuvent donc permettre le renouvellement des couverts forestiers. Cependant, afin de favoriser la régénération plus spécifique d'espèces à intérêts économiques importants (espèces souvent originellement présentes avant la coupe forestière) plutôt qu'une régénération aléatoire, ces pratiques pourraient être adaptées (par leur taille et leur fréquence) dans le but de fournir les conditions environnementales appropriées au développement de ces essences cibles.

Dans cette approche d'aménagement écosystémique (cf. Attiwil 1994, Bergeron et al. 1999), il est donc primordial de bien connaître les mécanismes régissant la régénération naturelle des espèces mais également les environnements pour lesquelles les espèces possèdent le meilleur bilan en carbone et donc les meilleures possibilités de croissance et/ou de survie à long terme.

Au niveau de la zone climatique de l'érablière à bouleau jaune, la régénération de l'érable à sucre (*Acer saccharum* Marsh.) et le bouleau jaune (*Betula alleghaniensis* Britton) est principalement limitée par la disponibilité en lumière. Il est donc primordial d'étudier le bilan de carbone (i.e. les gains et les pertes de CO₂), ainsi que les différents caractères qui à l'échelle de l'individu le définissent (paramètres physiologiques, morphologiques et d'allocation, efficacité d'interception et d'utilisation de lumière), vis-à-vis de la variation de cette ressource. En d'autres termes, il est nécessaire de s'intéresser tout particulièrement à leur tempérament écologique associé à la modification de la disponibilité en lumière soit à leur capacité de tolérer l'ombrage ou non.

Toutefois, en plus de la disponibilité en lumière, il est important de tenir compte de la taille des individus en régénération du fait de son implication dans la variation de nombreux caractères définissant le bilan carboné. En effet, ces changements liés à l'accroissement en taille des semis, laissent supposer l'existence d'une possible modification de la capacité de tolérance à l'ombre des espèces pendant leur développement, ce qui aurait une grande importance dans leur processus de régénération.

Finalement, en plus d'aider à mieux comprendre les mécanismes de régénération de ces espèces d'arbres dans un contexte de régénération naturelle ou dans celui d'un aménagement écosystémique, l'utilisation de la somme d'informations acquises aux différentes échelles de processus pourrait également servir à la création (i.e. paramétrisation et validation) de modèles de croissance à l'échelle de l'individu. En effet, ces modèles sont à l'heure actuelle de plus en plus utilisés car ils représentent un potentiel toujours grandissant de possibilités de recherches qui sur le terrain sont excessivement coûteuses en temps et en argent.

4. OBJECTIFS ET SITES DE MESURES

4.1. Les objectifs du projet

L'objectif principal de ce travail réside donc dans l'obtention de connaissances liées aux caractères physiologiques, morphologiques et d'allocation qui, à l'échelle de l'individu définissent le bilan carboné et donc les possibilités de croissance de l'érable à sucre (*Acer saccharum* Marsh.) et du bouleau jaune (*Betula alleghaniensis* Britton). De plus, la plus grande tolérance à l'ombre observée pour l'érable par rapport au bouleau jaune (Baker 1949, Forcier 1975, Annexes A et B) ajoute à cet objectif général, celui de possiblement mieux comprendre quels sont les mécanismes qui pourraient être impliqués dans ces divergences de tolérance à l'ombre. Bien entendu, devant l'importance de la disponibilité en lumière dans la régénération naturelle de ces deux espèces et l'implication soupçonnée de la taille d'un individu dans la variation de certains de ces caractères, ces deux facteurs seront pris en compte dans la réalisation de ces objectifs.

Afin d'atteindre ces objectifs, deux sites de mesure sont utilisés dont l'un est situé en milieu naturel (station forestière, Duchesnay, Qc, Canada) et l'autre en milieu plus contrôlé (pépinière, Nancy, France). L'utilisation de ces deux sites est importante car elle permet de combiner à la fois (i) la récolte de données en conditions naturelles et donc de conserver un lien avec la réalité et (ii) l'obtention de mesures et d'estimations très précises nécessitant un appareillage plus lourd qui à l'heure actuelle n'est pas utilisable en milieux naturels.

Ainsi, les objectifs plus détaillés de cette étude ont pu être répartis en quatre études distinctes et complémentaires qui définissent les quatre chapitres de ce travail :

En milieu naturel :

(Chapitre 1.)

Cette partie vise à étudier sur des semis des deux espèces en régénération naturelle :

- (i) la plasticité physiologique, morphologique et d'allocation en biomasse en fonction de la taille des individus et sous un gradient de conditions lumineuses créée par différentes tailles de trouées. L'hypothèse principale soutenue ici est que la lumière serait plus responsable de la variation de la morphologie et la physiologie des espèces alors que la taille serait elle plus responsable de modifications dans les patrons d'allocation de biomasse.
- (ii) la réponse à un ombrage artificiel simulant la fermeture du couvert forestier et la réduction drastique de la disponibilité en lumière. Dans ce cas, on suppose une meilleure acclimatation de l'érable à sucre par rapport au bouleau jaune, spécialement au niveau de sa morphologie.

En milieu semi contrôlé :

(Chapitre 2.)

Ce chapitre a pour but d'étudier chez des semis des deux espèces :

- (i) la morphologie de la cime et l'organisation des feuilles dans la cime grâce à l'utilisation du procédé de digitalisation en trois dimensions en fonction de la disponibilité en lumière et de l'âge des semis.
- (ii) l'efficacité d'interception de lumière de ces semis et sa variation en fonction de la disponibilité en lumière et de l'âge des semis. Ici, on s'attend à une diminution significative de l'efficacité d'interception des semis avec le développement en âge des semis, l'augmentation de la disponibilité en lumière, ainsi qu'une meilleure interception de l'érable à sucre par rapport au bouleau jaune.

(Chapitre 3.)

Cette étude concerne des semis de un an des deux espèces :

- (i) l'estimation de la respiration rhizosphérique (i.e. des échanges gazeux réalisés par les parties souterraines de la plante) à l'aide d'un système de mesure novateur permettant une mesure *in vivo* et *in situ*.
- (ii) l'étude de la variation de cette respiration rhizosphérique en fonction de la disponibilité en lumière et de la quantité de racines fines contenues dans l'enceinte de mesure. En relation avec les taux de croissance relatifs aux espèces et aux différents régimes lumineux, on s'attend à ce que la respiration rhizosphérique du bouleau jaune soit supérieure à celle de l'érable et la respiration rhizosphérique soit supérieure sous les lumières les plus élevées.

(Chapitre IV-4.)

Finalement, ce dernier chapitre a pour but chez des semis de deux ans des deux espèces :

- (i) d'estimer les capacités de photosynthèse telles que décrites par le modèle de photosynthèse de Farquhar et al. (1980) en fonction de la disponibilité en lumière et de la saison chez les deux espèces. On s'attend à ce que le bouleau jaune possède des capacités de photosynthèse supérieures à l'érable à sucre mais qu'un renversement des différences entre espèces soit observé sous les lumières les plus faibles.
- (ii) de mesurer le bilan des échanges gazeux des parties aériennes de ces semis et de le lier aux patrons de répartition de biomasse observés sous différents environnements lumineux. Ici, on teste l'hypothèse que le bouleau jaune posséderait un bilan instantané de carbone des parties aériennes plus faible que l'érable à faible lumière et que ceci serait relié au fait que cette espèce alloue moins de carbone à ses feuilles comparativement à ses tissus non photosynthétiques par rapport à l'érable à sucre.

Tous ces objectifs sont rappelés dans l'introduction de chacun des chapitres et les détails concernant les analyses statistiques utilisées se trouvent dans la partie de description du matériel et méthodes.

4.2. Sites de mesure

4.2.1. Milieu naturel

Le site de Duchesnay

La station forestière de Duchesnay (46°55' N, 71°40' O) se trouve dans le domaine climatique de l'érablière à bouleau jaune (cf. Figure 1.1) proche de la ville de Québec (QC, Canada). Le site repose sur un till glaciaire moyennement bien drainé dont la pente ne dépasse pas 20%. Le sol de la station est relativement profond (généralement > à 1 m) et se compose d'une litière moyennement épaisse (5 cm) et d'horizons Ah, AB et B (Figure 4.1). Les précipitations moyennes par année s'élèvent environ à 1220 mm et les températures moyennes minimales et maximales sont de -12°C en janvier et 28°C en juillet (Ricard 1999, Environnement Canada 2000).

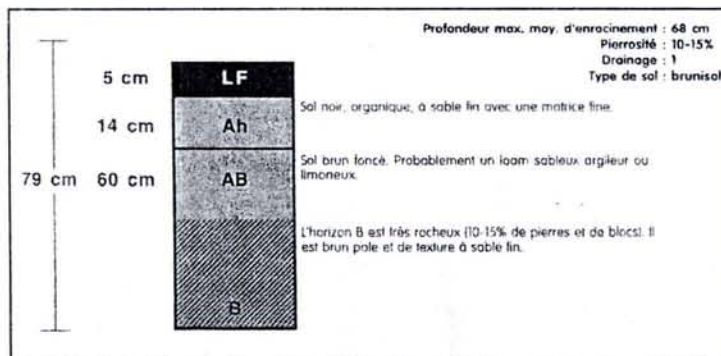


Figure 4.1. Exemple de la composition du sol de la station forestière de Duchesnay (Qc, Canada). Pédon réalisé sur le site de la coupe de jardinage de 1989.

La canopée est dominée par la présence d'érable à sucre (*Acer saccharum* Marsh.), de bouleau jaune (*Betula alleghaniensis* Britton) et de hêtre à grande feuilles (*Fagus grandifolia* Ehrh.). L'if du Canada (*Taxus canadensis* Marsh.) l'érable de Pennsylvanie (*Acer pennsylvanicum* Lam.) et la viorne à feuilles d'aulne (*Viburnum alnifolium* Marsh.) composent majoritairement le sous couvert (Ricard 1999). Les arbres dominants avoisinent les 90 ans pour une taille moyenne de 22 m (Ressources naturelles du Canada, 2003). La surface terrière totale sur le site de Duchesnay est d'environ 27 m² par hectare (596 tiges à l'hectare).

En 1989 et en 1994, deux coupes de jardinage ont permis la création d'une multitude de petites (30 m²), moyennes (70 m²) et grandes trouées (>100 m²) dans la canopée ce qui apporta un gradient de disponibilité en lumière en sous couvert. Dans une partie de ces trouées, des ombrières réduisant de 50% la disponibilité en lumière (Ricard 1999) ont été placées à environ 1 m au dessus des semis en régénération afin d'appliquer une réduction drastique de lumière simulant la fermeture du couvert par la croissance latérale de la canopée (Figure 4.2). L'ombrage a été maintenu durant quatre saisons de croissance (1997, 1998, 1999 et 2000) en prenant soin de ne pas interférer avec la croissance des

semis en développement (i.e. les ombrières étaient élevées chaque année pour suivre la croissance des semis sans la perturber).

On notera que les deux âges de coupes ont permis l'obtention d'un gradient de taille allant jusqu'à 6 mètres pour les plus vieux et jusqu'à 2 mètres pour les plus jeunes.



Figure 4.2. Exemple d'ombrière installée en sous couvert à la station forestière de Duchesnay afin de réduire de 50% la disponibilité en lumière. Des semis étaient suivis à côté et sous les ombrières (étiquette rouge).

4.2.2. Milieu semi contrôlé

Pépinière de l'INRA de Nancy.

Pour les études réalisées en milieu contrôlé, des graines des deux espèces fournies par le Ministère des Ressources Naturelles du Québec et provenant de la station forestière de Duchesnay ont été mises à germer après l'application de traitements de pré-germination. Ces traitements consistaient à la disposition des graines d'érable à sucre dans un terreau légèrement humide en chambre froide (4°C) et par l'ajout de fertilisant minéral liquide pour les graines de bouleau jaune disposées à la surface d'un terreau laissé à température ambiante. Les graines germées ont alors été transplantées en pots de 10 L contenant un mélange de sable et de tourbe (3 volumes de sable pour 1 volume de tourbe). Les pots ont ensuite été placés en pépinière (48°44' N, 6°14' E) sous quatre traitements lumineux différents : 2, 7, 16, et 40% du rayonnement externe global.

Les quatre régimes lumineux ont été obtenus par la disposition d'une ou plusieurs couches de toile d'ombrage aluminisées (Figure 4.3). Les ombrières avaient la propriété de diminuer la quantité de lumière sans toutefois modifier la composition de son spectre.



Figure 4.3. Photos des ombrières de la pépinière de l'INRA de Nancy (France). A gauche, vue extérieure, à droite vue intérieure du traitement 17% de lumière.

La fertilisation des pots s'est faite à deux reprises chaque année (début mai et début août) par l'apport de billes d'engrais à libération lente (Nutricote N/P/K, 13/13/13 100+ avec oligo-éléments). Le fertilisant permettait un apport de minéraux sur une base de 100 jours à 20°C pour un terreau humide. L'arrosage était fourni par un système de goutte à goutte (Irrigoutte) contrôlé par une horloge automatique (Figure 4.4). La distribution se faisait donc deux fois par jour (matin et soir) à la capacité au champ. La quantité d'eau apportée était donc plus faible sous les régimes lumineux plus ombragés du fait de l'évapotranspiration plus faible du sol sous ces conditions lumineuses.



Figure 4.4. Semis d'érable à sucre dans un pot de tourbe-sable (une couche supérieure de sable est ajoutée pour empêcher le développement d'algues) et système tubulaire d'irrigation contrôlé par une horloge.

Pour le cas particulier des mesures de respiration rhizosphérique, les semis ont été transplantés en pots ne contenant que du sable grossier d'aquarium (Figure 4.5). De plus, pour cette étude, les pots n'ont été placés que sous les régimes lumineux de 7, 16 et 40% (cf. matériel et méthodes du **Chapitre 3**).



Figure 4.5. Pots utilisés pour mesurer la respiration rhizosphérique. Le substrat est non respirant (i.e. sable grossier + couche de billes d'argile expansé).

5. RÉSULTATS

*"Trees are green,
and can be very tall."*

*Paul Puettmann
9 years old
Corvallis Oregon, USA*

"Because sometime size matters."

Unknown woman

5.1. Chapitre 1: Physiological, morphological and allocational plasticity in understory deciduous trees: importance of individual size and light availability

5.1.1. Abstract

The integrated study of physiological, morphological and allocational plasticity in trees as they develop in the forest understory can provide insight into the underlying mechanisms of shade tolerance and survival. In this experiment, we investigated how juveniles of a shade tolerant species (Sugar maple; *Acer saccharum* Marsh.) and an intermediate shade tolerant species (Yellow birch; *Betula alleghaniensis* Britt.) modify their leaf physiological, crown morphological and whole tree allocational traits as they grow under a wide range of understory light conditions (0.5 to 35%), for individuals ranging in size from 25 to 600 cm. Concurrently, light availability above half of these understory trees was reduced by 50% using shading nets during four years to examine their response to a variation in light regime that simulated gap closure.

Most of the leaf physiological parameters under study were mainly influenced by the light gradient, whereas most of the crown morphological and whole tree allocational parameters were mainly influenced by tree size. Results did not point to any single physiological, morphological or allocational trait that could explain species differences in shade tolerance. Yellow birch showed higher growth rates, higher biomass allocation to branches, higher leaf physiological plasticity, and lower crown morphological plasticity in natural conditions than sugar maple. Sugar maple did not express any significant physiological plasticity, but it showed a high crown morphological and whole tree allocational plasticity mainly associated with tree size. Sugar maple allocated a higher proportion of its whole tree biomass to roots when small, possibly as a mechanism to increase its storage capabilities to survive in low light. However, physiological differences between the two species decreased with decreasing light and most morphological and allocational differences tended to attenuate or disappear with increasing tree size. This suggests that many species differences in shade tolerance mechanism may be mainly expressed during the seedling stage. Finally, all measured sugar maple and yellow birch seedlings and saplings were able to survive the sudden 50% light reduction created by shading nets, possibly owing to their plasticity when small and to their added storage capabilities when larger.

Key words: *Acer saccharum*, *Betula alleghaniensis*, Biomass partitioning, Carbon assimilation, Carbon balance, Crown morphology, Shading, Sugar maple, Tree height, Yellow birch.

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5.1.2. Introduction

During their development, trees are subjected to diverse environmental constraints that are believed to influence their growth and survival. Global patterns of carbon allocation and tree structural modifications during ontogeny are directly linked to the availability of above- and below-ground resources (Tilman 1988, Gleeson and Tilman 1992) and to constraints imposed by some basic mechanical laws (Niklas 1992). Due to these external pressures, juvenile trees are required to constantly modify their physiology and morphology to optimise the capture of resources (e.g. water, nutrients and light) they need to grow and survive.

Light, which is often very low in the understory of temperate deciduous forests in eastern North America (Beaudet and Messier, 1998; Beaudet et al., 2000), is considered to be the most limiting resource for the growth of understory seedlings and saplings (Bellefleur and LaRocque, 1983*b*; Ricard et al., 2003). Recent studies have shown the importance of gap size in the regeneration of trees with different successional status (McClure et al., 2000; Woods, 2000). The importance of light for understory regeneration comes in part from its great spatio-temporal variability due to the random occurrence of canopy gaps of different shapes, sizes and frequencies (e.g. Runkle, 1982; Canham et al., 1990).

In forests, understory tree growth and survival are thus directly linked to their capacity to acclimate to the highly variable light environment. Understory trees must be able to respond quickly to any sudden increase in light, and tolerate low light levels for more or less long periods until the occurrence of the next gap (i.e. they must show plasticity). Although trees constantly balance and modify their leaf physiology, crown morphology and whole tree allocation to respond to the spatio-temporal variations of light (Walters and Reich, 1999; Beaudet and Messier, 1998; Gardiner and Hodges, 1998; Canham et al., 1999), many traits also vary with tree size (King, 1986; Sterck and Bongers, 2001; Naumburg et al., 2001; Claveau et al., 2002). Furthermore, several recent studies indicate that individual size matters in tree survival, especially in terms of shade tolerance (Givnish, 1988; Messier et al. 1999; Messier and Nikinmaa, 2000).

Consequently, when studying the functional ecology of trees in relation to their shade adaptation, it is necessary to consider both light and size, which represent respectively the resource constraint and the physical and mechanical constraint that trees face as they develop. Such investigations are difficult to carry out because of the number of scales and processes involved (leaf, crown, tree, physiology, morphology and biomass partitioning). In addition, some important traits investigated at the scale of the seedling crown may become inconsequential at taller stages (Sterck 1999). The wide variety of shade tolerance levels observed in trees (Baker 1949, Forcier 1975, Bazzaz 1979 and many others) is thus the consequence of differences in the combination and interaction of numerous and multi-scale traits (Givnish 1988). These diverse combinations define various efficiencies for resources capture and utilisation that finally play a key role in tree functional ecology. But how do these combinations of traits change with increasing tree size? As suggested by Meinzer (2003), to understand such whole-tree level mechanism, it is important to investigate at more than a single scale and from different points of view.

In this study we investigated how leaf physiology, crown morphology and whole tree biomass partitioning vary along both light and size gradients in two temperate deciduous tree species; yellow birch (*Betula alleghaniensis*, Britt.) and sugar maple (*Acer saccharum*, Marsh.). In eastern North-America, sugar maple and yellow birch are two co-occurring species despite their contrasting functional ecology and successional status. Sugar maple is a late successional and very shade tolerant species (Baker 1949, Godman

et al. 1990) with a relatively good growth rate in more open conditions (Canham 1988). Yellow birch is considered an intermediate shade tolerant and mid successional species (Baker 1949, Erdmann 1990), which shows a rapid growth in open conditions (Bellefleur and LaRocque 1983a, Beaudet and Messier 1998). Here, regenerating juveniles of both species were investigated under natural conditions and under artificial shading provided by nets set in the forest understory. The main objectives of this study were thus (i) to assess how various sugar maple and yellow birch traits are affected by an increase in tree size, light availability and their interaction, (ii) to investigate how inter-specific differences in functional and structural traits change as juveniles increase in size, and (iii) to evaluate how these two species are able to adjust effectively to a sudden artificial decrease in light availability that mimics the closing of a canopy gap.

5.1.3. Materials and Methods

5.1.3.1. Study site

This study was carried out in the Duchesnay experimental forest (46°55' N, 71°40' W) located near Quebec city, Canada. At this location, elevation ranges from 200 to 300 m, annual rainfall is around 1220 mm/year and mean daily temperature ranges from 28°C in July to -12°C in January. The soil is a ferro-humic podzol with a thin humus layer over a more or less well-drained glacial till. The forest canopy is mainly dominated by sugar maple (*Acer saccharum* Marsh.), yellow birch (*Betula alleghaniensis* Britt.) and American beech (*Fagus grandifolia* Ehrh.). American yew (*Taxus canadensis* Marsh.), striped maple (*Acer pensylvanicum* Lam.) and moosewood (*Viburnum alnifolium* Marsh.) predominate in the understory. Dominant trees of the experimental forest were around 90 years old and 22 meters tall. Stand total basal area was 27 m² per hectare (596 stems per hectare). Mean tree diameter at breast height (dbh) was 26 cm but 61% of living stems were under 20 cm of dbh.

5.1.3.2. Shading treatment and light measurements

We sampled two stands in close proximity that had been selectively cut at two different times: one in 1989 and the other in 1994. This allowed us to find natural regenerating seedlings and saplings of different sizes along a wide gradient of light conditions (Table 5.1). To simulate the rapid closing of a canopy gap, 32 shading nets were installed in gaps of each stands during the spring of 1997. Nets were removed during winter time and reinstalled each spring at least 1 meter above the growing regeneration. One meter net curtains walls were sewed to the main horizontal net to further reduce lateral irradiance.

Seedlings and saplings light availability was quantified on four overcast days during the month of July 2000 (Messier and Puttonen (1995); three instantaneous light measurements were taken 5 cm above the top of the seedling using a LI-189 light radiometer (LI-COR, Lincoln, Nebraska, USA). At the same time, a quantum sensor linked to a LI-1000 datalogger (LI-COR, Lincoln, Nebraska, USA) measured light every 5 seconds and recorded the average every minute, in an adjacent open area. To calculate the percentage of total overstory light available, the values recorded above the trees were divided by the reference value taken at the same time in the open area. Such instantaneous light measurements taken under overcast conditions, have been shown to be highly correlated to the mean seasonal daily light percentage (Gendron et al. 1998).

Available light measured at the top of un-shaded trees in year 2000 varied from 0.5 to 35% of full sunlight whereas light ranged from 0.5% to 16% of full sunlight above the artificially shaded trees.

	Old cut (1989)		Young cut (1994)	
	M	B	M	B
Number of harvested trees	23	20	23	24
Tree size (cm) mean ($\pm SE$)	175.50 (± 18.73)	269.22 (± 27.39)	54.02 (± 5.73)	102.62 (± 10.15)
Tree age (years) mean ($\pm SE$)	13.87 (± 0.77)	10.55 (± 0.52)	9.09 (± 0.53)	5.17 (± 0.17)

Table 5.1. Description of harvested seedlings and saplings sampled in summer 2000 in two selection cuts in close proximity at the Duchesnay experimental forest station in Quebec, Canada (46°55' N, 71°40' W). (B = yellow birch; M = sugar maple; *SE* = Standard Error).

5.1.3.3. Tree measurements and harvesting

During summer 2000, 46 sugar maple and 44 yellow birch were studied and then harvested. Leaf maximal CO₂ assimilation (A_{\max} ; $\mu\text{molCO}_2\cdot\text{m}^{-2}\cdot\text{s}^{-1}$), leaf maximal stomatal conductance ($G_{s_{\max}}$; $\mu\text{molCO}_2\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) and leaf dark respiration (R_d ; $\mu\text{molCO}_2\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) were measured between July 10-27 using a LI-6400 gas-exchange analyser (LI-COR, Lincoln, Nebraska, USA). For A_{\max} , R_d and $G_{s_{\max}}$ measurements, 1 leaf by individual was chosen in the upper crown layer. During the measurements, light was maintained at 1500 $\mu\text{mol photon}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ and 0 $\mu\text{mol photon}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ of PPFD, for A_{\max} and R_d measurements respectively, leaf temperature was set at 25°C, air CO₂ concentration at 375 $\mu\text{molCO}_2\cdot\text{mol}^{-1}$ and relative humidity was maintained between 60% and 75%. A_{\max} measurements were recorded after an activation period of at least 10 minutes; R_d measurements were taken after 5 minutes of darkness when gas-exchanges reached a steady state. Measured leaves were then harvested and dried at 65°C for 48 hours to estimate leaf nitrogen content on a area basis (N_a ; $\text{g}\cdot\text{m}^{-2}$) using an elemental NCS 2500 analyser (ThermoQuest, Milan, Italia).

At the end of August 2000, both above- and below-ground parts of all the experimental individuals were carefully harvested and several biomass partitioning and morphological traits were measured. We tried to collect as much fine root biomass for each tree as possible by digging out each root by hand; it took 200 persons-hours to excavate the root system of one large 5 m tall sapling. Individual tree size was determined by measuring main stem length and stem diameter was recorded at the soil-air interface. Using crown base determination (i.e. first living branch) and the mean of two perpendicular crown diameters, (i) crown height over crown diameter ratio (CrownH/D), (ii) percent of live crown in total tree size (%Crown) and (iii) number of first order living branches by crown dm were calculated. Roots (fine: <2mm, coarse: >2mm), stem, branches and leaves were then separated, dried at 65°C for 48h, and weighed to calculate the fine root mass ratio (FRMR; g of fine roots in 100 g of total tree dry mass), leaf,

branches, stem, and total root percentage in total tree dry mass (i.e. %PT, %Branches, %Stem %Root) and the non-photosynthetic to photosynthetic tissues ratio (NPT/PT). Two to six leaf disks (depending on crown size) of 7cm² each were randomly taken within the crown and dried to obtain the Leaf Mass Area (LMA: g.m²). Total leaf area for each tree was calculated using the total foliar dry mass without petiole and LMA and from these data we calculated the leaf area ratio (LAR: m².g⁻¹ plant). Finally, annual height growth for the last 2 years using bud scars and radial growth using growth ring analysis of the bisector of the smaller and larger radius of a sanded stem section were calculated. Radial increment measurements were made using a Quick Chek measuring unit (QC1000, Metronics inc., Bedford, NH, USA) coupled with a computer program (MeasureJ2X, V3.1, VoorTech Consulting, Holderness NH, USA). Relative height and radial growth (RHG and RRG) were calculated from the height and radial growth measurements using equations 1 and 2:

$$\text{RHG of year } n = [(\text{Height}_{\text{year } n} - \text{Height}_{\text{year } n-1}) / \text{Height}_{\text{year } n}] \quad (1)$$

$$\text{RRG of year } n = [(\text{Radial}_{\text{year } n} - \text{Radial}_{\text{year } n-1}) / \text{Radial}_{\text{year } n}] \quad (2)$$

5.1.3.4. Data analysis

All statistical analyses were performed using SAS version 8.02 (SAS institute, Cary, North Carolina, USA). Two distinct analyses were used to address the three main questions of this study;

First, to investigate how various traits of both species are affected by an increase in tree size along a large understory light gradient and to follow the modification of inter-specific differences over the size gradient, we used only those seedlings and saplings found in natural light conditions (i.e. we did not include artificially shaded trees). Analyses of each tree trait against gradients of light percentage and tree size were thus made with un-shaded individuals of both species ($n = 44$), using an analysis of covariance (ANCOVA) where species was a factor and light percentage and tree size were co-variables. Data transformations were made when necessary on co-variables (i.e. size and light) to reach residue normality and variance homogeneity needed for these analyses.

To evaluate how the two species responded to a sudden 50% decrease in light availability, we compared individuals of two size groups (small and tall) found under the nets with those found outside the nets. Here we tried to define traits that separated small and tall sugar maple and yellow birch grown under natural and shaded conditions. To do so, we did a Canonical Discriminant Analysis (CANDISC procedure in SAS program V 8.02, Cary, North Carolina, USA) with the distance ANOVA option that uses the Mahalanobis distance parameter to determine statistical differences between the mean vector of each group. The 87 individuals in the analysis were separated into 8 groups (Table 5.2). Coding for each group was defined by treatment (Sh: shaded and USh: un-shaded), size of our populations (S: small and T: tall cf. Table 5.1) and species (M: sugar maple and B: yellow birch). Traits included in the analysis were chosen to represent all possible aspects of physiological, allocational and morphological adjustments to light regime (i.e. A_{max} , %PT, %Branch, %Root, Crown H/D and Number of branches per dm of crown; refer to the "*Tree measurements and harvesting*" section for details about acronyms). Traits were chosen to be statistically independent from each other and the total number of traits used in the analysis was kept small to avoid artefacts that can arise when numerous parameters are incorporated in a single canonical analysis.

Selection cuts (cf. Table 1)	Treatment	Sp.	n	Code	Individual growth history after cutting
Old cut (taller trees)	Sh	M	11	ShTM	At least 6 years USh then 4 years Sh
		B	11	ShTB	At least 6 years USh then 4 years Sh
	USh	M	11	UShTM	At least 10 years USh
		B	10	UShTB	At least 10 years USh
Young cut (smaller trees)	Sh	M	12	ShSM	At least 1 years USh then 4 years Sh
		B	12	ShSB	At least 1 years USh then 4 years Sh
	USh	M	11	UShSM	At least 5 years USh
		B	9	UShSB	At least 5 years USh

Table 5.2. Summary of the experimental design that leads to the 8 groups used in the canonical discriminant analysis (CDA) to evaluate the effect of a sudden imposed shading (Sh) compared to un-shading situation (USh) in two contrasting populations (tall: T and small: S) of yellow birch (B) and sugar maple (M).

5.1.4. Results

5.1.4.1. Effects of light and size gradients

Tree growth

For both species, relative height growth (RHG) was significantly and almost significantly influenced by light availability and species, respectively, whereas relative radial growth (RRG) was associated with tree size and tree species (see *growth* in Table 5.3). Yellow birch showed greater height and radial growth than sugar maple along the entire light and size gradients but differences were not significant (data not shown).

Leaf physiology

Light was a significant factor affecting $G_{s \max}$, whereas size and species alone were not significant (see *physiology* in Table 5.3). The significant interaction between light and species is clearly seen in Figure 1a, where $G_{s \max}$ increased more rapidly with increasing light for yellow birch compared to sugar maple. A similar pattern was observed for A_{\max} (Figure 5.1b), while light was the only significant factor for R_d . For both species, A_{\max} was clearly correlated with $G_{s \max}$ ($A_{\max} = 0.0374 G_{s \max} + 5.6026$ [$r^2 = 0,54$] for yellow birch and $A_{\max} = 0.0574 G_{s \max} + 4.389$ [$r^2 = 0,50$] for sugar maple, data not shown). For N_a , the three single factors were significant or almost significant (see *physiology* Table 5.3, Figure 5.1d).

Yellow birch had increasingly higher $G_{s \max}$ and A_{\max} than sugar maple (Figure 5.1a and b) as light availability increased, whereas it was the case at all light levels for N_a . None of the measured leaf physiological parameters varied with tree size, although size-dependence was almost significant for N_a (see *physiology* in Table 5.3).

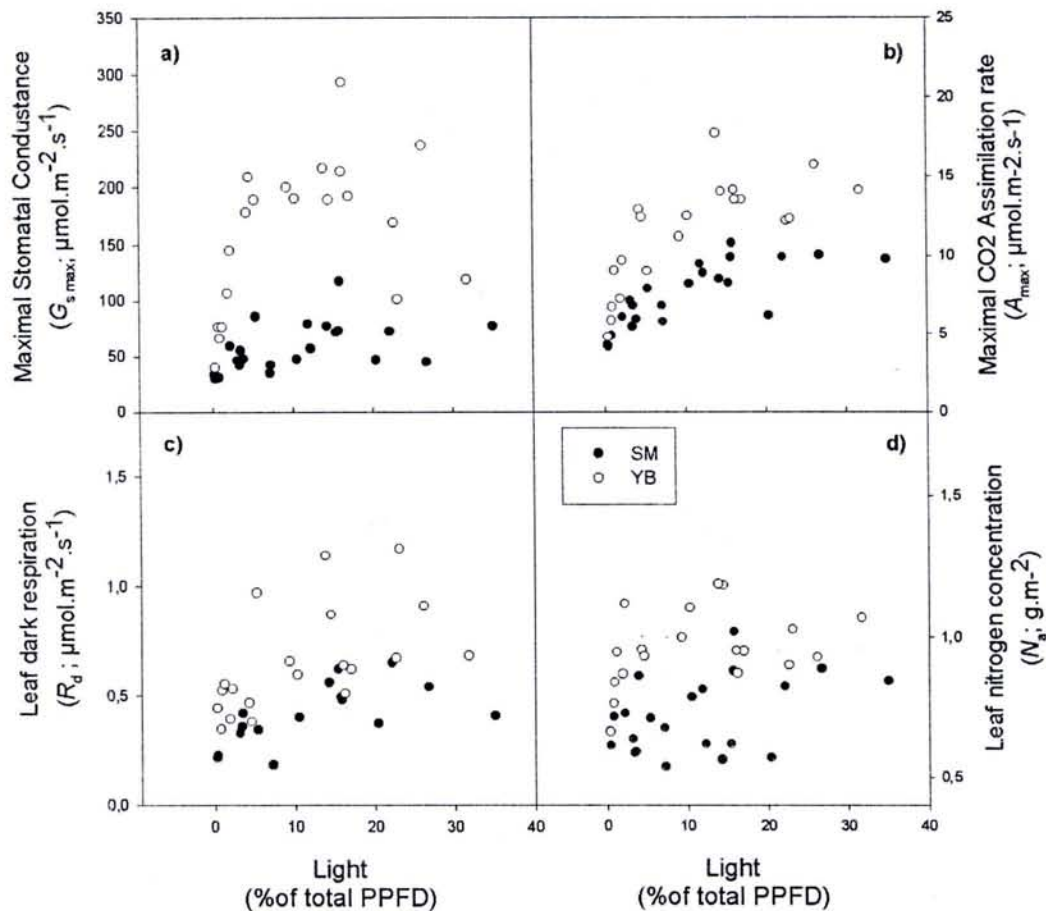


Figure 5.1. Leaf physiological parameters variation in sugar maple (SM; filled symbols) and yellow birch (YB; open symbols) seedlings and saplings measured in Duchesnay forest station (Quebec, CANADA). Results were plotted versus the natural light gradient for a): maximal stomatal conductance ($G_{s,max}$: $\mu\text{mol.m}^{-2}.\text{s}^{-1}$), b): maximal CO₂ assimilation rate (A_{max} : $\mu\text{mol.m}^{-2}.\text{s}^{-1}$), c): leaf dark respiration (R_d : $\mu\text{mol.m}^{-2}.\text{s}^{-1}$) and d): leaf nitrogen content (N_a : g.m^{-2}) since light was the most significant factor affecting these parameters (cf. Table 5.3).

Biomass partitioning

Tree size was clearly the main factor associated with biomass partitioning variations, whereas light was almost completely non-significant except for an interaction between species and light for %Branches (see *allocation* in Table 5.3). %PT significantly decreased with increasing tree size (Figure 5.2) and there were no significant differences between species or in relation to light (see *allocation* in Table 5.3). %Branches significantly increased with size, but there was a significant interaction between size and species, and light and species. These interactions indicate that yellow birch tends to have more biomass allocated to branches than sugar maple, and that this difference tends to disappear as the trees get larger or as light availability increases (data not shown). The %Stem significantly increased with tree size and there was no effect of species or light and no significant interaction whereas %Roots tended to decrease with tree size (see

allocation in Table 5.3); the significant interaction between species and size suggests that this decline is stronger for sugar maple than yellow birch (data not shown).

LAR, as for %PT or %NPT, differed significantly only with tree size and not with species (see allocation in Table 5.3). LAR decreased rapidly with increasing tree size and a very similar pattern was observed for FRMR (Figures 5.3a and 5.3b). Indeed, variations in FRMR were clearly related to tree size and not to any other factor (see allocation in Table 5.3).

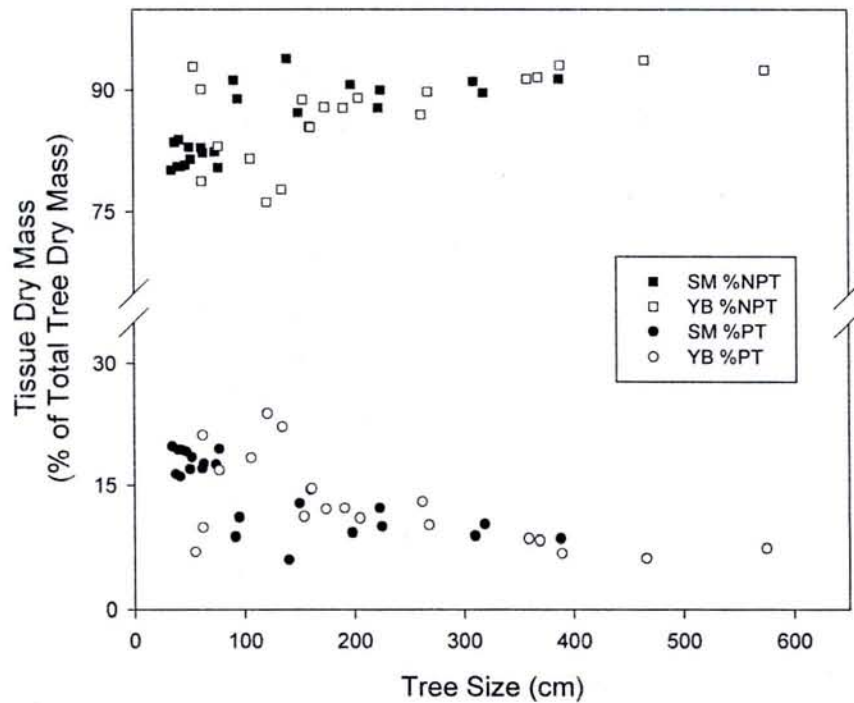


Figure 5.2. Proportion of Non Photosynthetic Tissues (NPT; square) and Photosynthetic Tissues (PT; circles) in total tree dry mass in sugar maple (SM; filled symbols) and yellow birch (YB; open symbols) seedlings and saplings measured in the Duchesnay forest station (Quebec, CANADA). Results were plotted versus the size gradient since individual size was the most significant factor affecting these parameters (cf. Table 3).

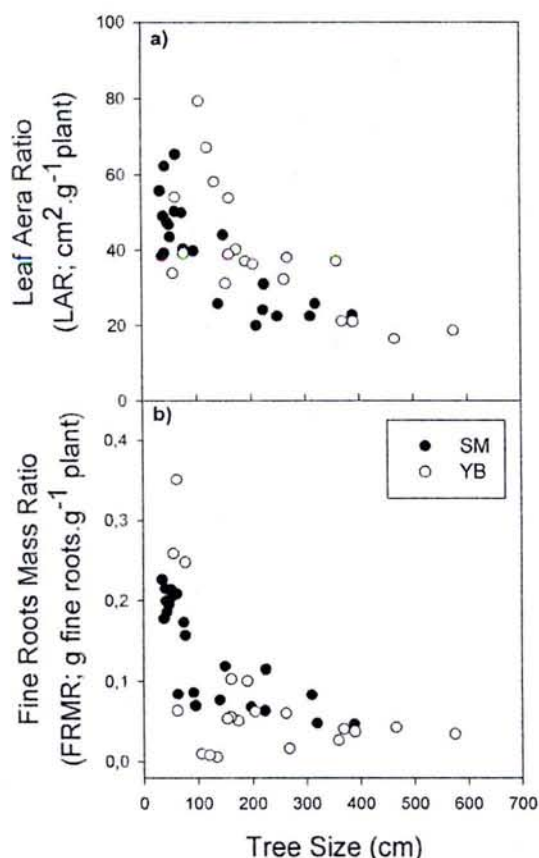


Figure 5.3. Whole tree allocational parameters variation in sugar maple (SM; filled symbols) and yellow birch (YB; open symbols) seedlings and saplings measured in Duchesnay forest station (Quebec, CANADA). Results were plotted versus the size gradient for a): leaf area ratio (LAR; cm².g⁻¹) and b): fine root mass ratio (FRMR; g.g⁻¹) since individual size was the most significant factor affecting these parameters (cf. Table 5.3).

Crown morphology

Crown% varied significantly for all three variables investigated, but it also showed strong significant interactions between light and size and species and size (see *morphology* in Table 5.3). Crown% was mainly influenced by light when individuals were small and differences between species decreased with increasing tree size. Yellow birch showed overall a greater Crown% (data not shown), a greater CrownH/D (Figure 4a) and a higher number of branches per unit of crown's length than sugar maple (Figure 5.4b). However the significant interaction between size and species for these three parameters indicated a decrease in species differences with increasing tree size. Yellow birch CrownH/D variation was less associated with tree size than sugar maple (Figure 5.4a). As for the number of branches per dm of crown, a contrasting pattern was observed for yellow birch compared to sugar maple (Figure 5.4b). Yellow birch showed a high number but declining ratio with increasing tree size whereas sugar maple showed a highly variable ratio when small stabilising with increasing tree size. Most sugar maple seedlings had fewer branches than yellow birch, but above 1m tall, sugar maple individuals reached the same number of branches per dm of crown as for yellow birch.

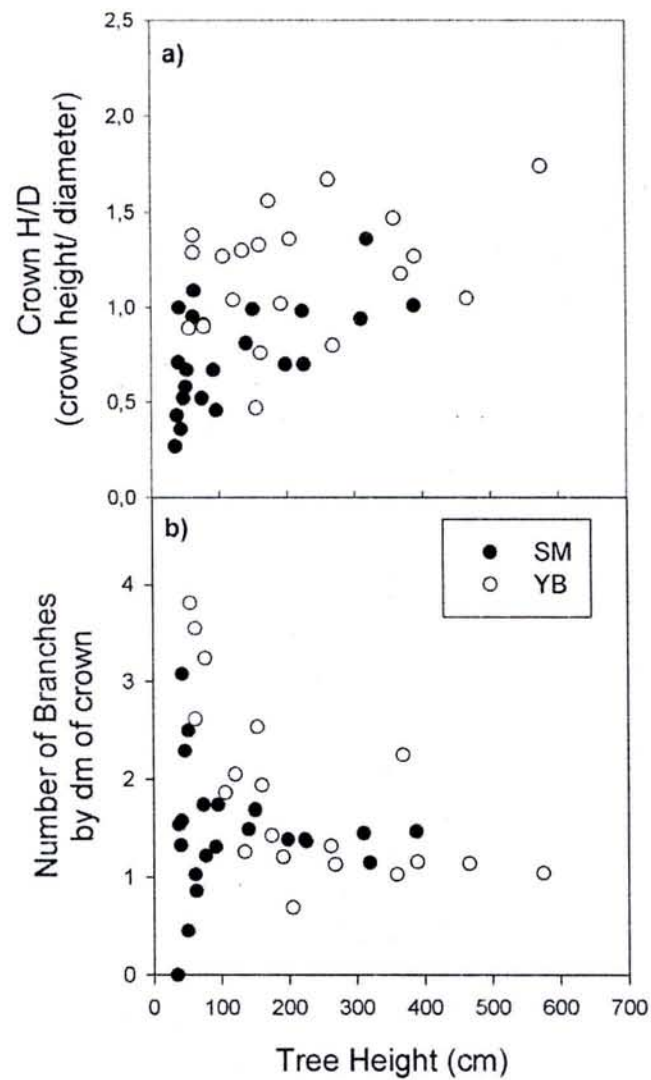


Figure 5.4. Crown morphological parameters variation in sugar maple (SM; filled symbols) and yellow birch (YB; open symbols) seedlings and saplings measured in Duchesnay forest station (Quebec, CANADA). Results were plotted versus a size gradient for a): crown shape (Crown height over crown diameter ratio), and b): number of branches per dm of crown since individual size was the most significant factor affecting these parameters (cf. Table 3).

	SP	S	L	SP x S	SP x L	S x L	SP x S x L
<i>Growth</i>							
RHG	0.0577	0.2198	0.0082	0.4810	0.4906	0.1987	0.4619
RRG	0.0106	0.0049	0.1523	0.6415	0.2207	0.1387	0.2104
<i>Physiology</i>							
$G_{s\ max}$	0.5108	0.5285	<0.0001	0.3427	0.0003	0.2691	0.0970
A_{MAX}	0.8671	0.3853	<0.0001	0.0884	0.0066	0.8876	0.0843
R_d	0.5401	0.2926	0.0497	0.7437	0.4940	0.6001	0.8211
N_a	0.0137	0.0679	0.0141	0.5677	0.4727	0.2348	0.7664
<i>Allocation</i>							
%PT or %NPT	0.1703	0.0096	0.2769	0.1760	0.0663	0.3358	0.0825
%Branches	0.0001	<0.0001	0.1359	0.0041	0.0181	0.5364	0.0870
%Stem	0.8972	0.0094	0.4335	0.3713	0.7067	0.7449	0.9335
%Roots	0.0380	0.0006	0.4465	0.0132	0.2032	0.2482	0.0659
LAR	0.5481	0.0047	0.7357	0.4407	0.1838	0.9069	0.1940
FRMR	0.1000	<0.0001	0.3240	0.1118	0.0881	0.3431	0.0944
<i>Morphology</i>							
Crown %	0.0108	0.0089	0.0143	0.0295	0.3741	0.0061	0.0695
Crown H/D	0.0100	0.0683	0.1322	0.0483	0.8848	0.3230	0.1792
Branches per dm of Crown	0.0041	0.0336	0.2424	0.0163	0.1018	0.3551	0.1499

Table 5.3. ANCOVA results for growth, physiological, morphological and allocational parameters. Summary of p value for relations between species (SP), tree size (S), light (L) and interactions and *Growth traits* [relative height growth (RHG) and relative radial growth (RRG)], *Physiological traits* [maximal stomatal conductance ($G_{s\ max}$; $\mu\text{mol photon}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$), maximal CO_2 assimilation rate (A_{max} ; $\mu\text{mol CO}_2\cdot\text{m}^{-2}\cdot\text{s}^{-1}$), leaf dark respiration (R_d ; $\mu\text{mol CO}_2\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) and leaf nitrogen amount (N_a ; $\text{g}\cdot\text{m}^{-2}$)], *allocational traits* [percentage of photosynthetic tissues (%PT), non photosynthetic tissue (%NPT) and percentage of branches, stem and roots dry mass in total tree dry mass, leaf area ratio (LAR; $\text{cm}^2\cdot\text{g}^{-1}\text{plant}$) and fine root mass ratio (FRMR; $\text{g fine roots}\cdot\text{g}^{-1}\text{plant}$)] and *morphological traits* [percentage of live crown in total tree height (Crown %), crown height on diameter (Crown H/D), number of lateral meristems by dm of crown (Branches per dm of crown)]. Values in bold are significant at $\alpha=5\%$.

5.1.4.2. Effect of artificial shading.

CDA showed significant discrimination among the 8 groups along 3 canonical axes. However, the first axis (CAN1) explained 76% of the variation (Eigenvalue = 4.2275; $F = 5.43$; $p < 0.001$) and the second 14% (Eigenvalue = 0.7783; $F = 2.50$; $p < 0.0001$), while the third explained only 8% and was at the limit of significance (Eigenvalue = 0.4756; $F = 1.58$; $p = 0.0413$). Consequently, the results presented in Figure 5.6 only show the discrimination on the two first axes. CAN1 mainly discriminated groups based on differences in the allocational traits (see parameter vectors in Figure 5.5) such as %Root and %PT versus %Branch. CAN1 also separated groups based on their size over diameter ratio (i.e. TreeH/D) and A_{\max} . In Figure 5.5, CAN2 discriminated groups mainly based on contrasting A_{\max} , %Root, N_a and Crown H/D, and CAN3 separated groups via differences in A_{\max} and %PT (vectors not shown).

Groups	ShTB	UShTB	ShTM	UShTM	ShSB	UShSB	ShSM	UShSM
ShTB	1	0.0050	0.0141	0.0005	<0.0001	0.0019	<0.0001	<0.0001
UShTB	-	1	0.0002	<0.0001	<0.0001	0.0013	<0.0001	<0.0001
ShTM	-	-	1	0.8376	<0.0001	0.0004	<0.0001	<0.0001
UShTM	-	-	-	1	<0.0001	0.0029	<0.0001	<0.0001
ShSB	-	-	-	-	1	0.0086	0.0017	<0.0001
UShSB	-	-	-	-	-	1	<0.0001	<0.0001
ShSM	-	-	-	-	-	-	1	0.0439
UShSM	-	-	-	-	-	-	-	1

Table 5.4: Summary of the p value for significantly different distance between the mean of two groups in the canonical discriminant analysis (CDA) using the Mahalanobis parameter. Refer to Table 2 or material and methods for details on groups and acronyms. Values in bold are significant at $\alpha=5\%$.

Yellow birch had consistently higher N_a and A_{\max} than sugar maple, higher %Branch, higher TreeH/D, but lower %Root (Table 5.4, Figures 5.6a-5.6c vs. 5.6b-5.6d). Also, a clear separation exists between smaller and taller groups. In both species, smaller saplings showed higher A_{\max} and higher %Root and %PT whereas taller saplings had higher N_a , %Branch and higher Crown H/D (Table 5.4, Figure 5.6a-5.6b vs. 5.6c-5.6d).

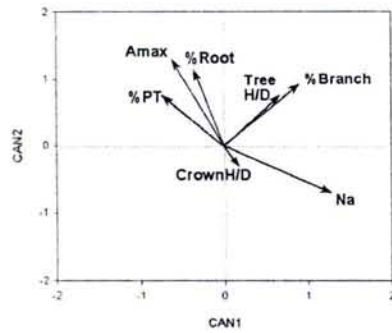


Figure 5.5. Graphic representation of the 7 parameters vectors driving individuals discrimination in the canonical discriminant analysis (CDA). Here, vectors are represented among the two main axes that cumulatively assumed 90% of the variation. For more details on the discriminant analysis, refer to the *data analysis* in Material and methods.

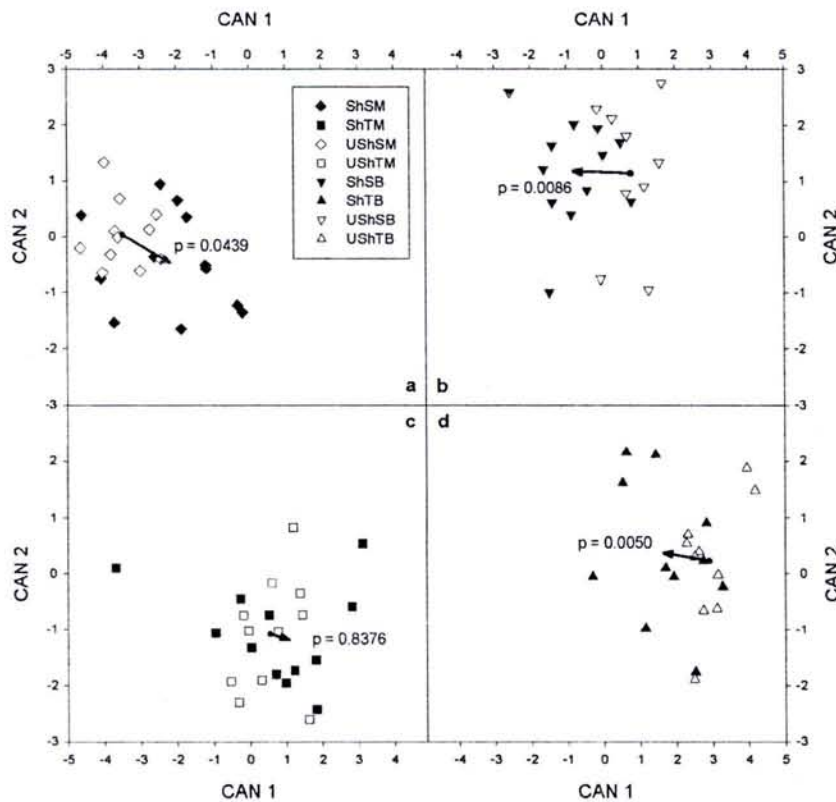


Figure 5.6. Graphic representation of the canonical discriminant analysis (CDA) results for the shaded (filled symbols) and un-shaded (open symbols) sugar maple and yellow birch divided in two size groups. Only the two main axes that cumulatively assumed 90% of the total variation are represented for shaded and un-shaded a) small sugar maple groups (diamonds), b) small yellow birch groups (down-triangle), c) tall sugar maple groups (squares) and d) tall yellow birch groups (up-triangle). Vectors from the mean of un-shaded groups to the mean of shaded groups as well as probability for the two mean to be significantly different at $\alpha = 5\%$ are indicated. Refer to Table 2 and *material and methods* for details on groups and shading treatment.

Although the shading treatment didn't have any strong impact on individual mortality, it significantly affected leaf physiology, crown morphology and whole tree biomass partitioning in both species and size groups (except for taller sugar maples where the difference was not significant $p = 0.8376$; Table 5.4, Figure 5.6c). Differences between shaded and un-shaded groups were higher for yellow birch than for sugar maple (Table 5.4). In Figures 5.6b and 5.6d, N_a , %Branch and Crown H/D were clearly lower in shaded vs. un-shaded yellow birch. In contrast, shading did not have any significant impact on taller sugar maples, while the effect on smaller seedlings was a reduction in A_{max} , %PT and %Root (Figure 5.6). In addition, both species were slightly affected in a similar way by shading through a reduction in A_{max} and a reduction in %PT along CAN3 (data not shown). However, this slight effect of shading on both species is only clear when looking at the NPT/PT ratio versus the individual tree size (Figure 5.7). Shading dramatically increased NPT/PT ratio for several small individuals that owned to the ShSM or ShSB groups. These seedlings were obviously in stressful conditions since they all showed clear signs of slowly dying off (i.e. few leaves, yellow leaves and dead branches).

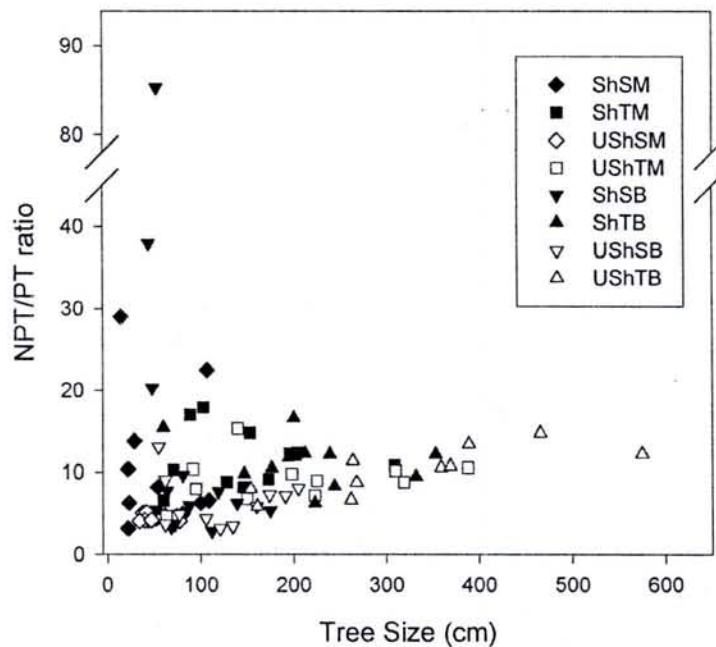


Figure 5.7. Effect of simulated shading on Non Photosynthetic Tissues over Photosynthetic Tissues ratio (NPT/PT) along an individual tree size gradient in sugar maple (M; squares) and yellow birch (B; triangles) individuals measured in Duchesnay forest station (Quebec, CANADA). Straight squares and up-triangles correspond to taller groups whereas diamonds and down-triangle are related to smaller groups for sugar maple and yellow birch respectively. Shaded individuals are represented by filled symbols and un-shaded ones by open symbols.

5.1.5. Discussion

5.1.5.1. Traits plasticity along light and size gradients

Variation in light availability was mainly responsible for variations in leaf physiological traits, especially for the more shade intolerant yellow birch (Figure 1). The strong and direct effect of light on photosynthetic capacities (A_{\max}) was mainly related to light-induced variations in the pool of proteins, pigments and enzymes (i.e. N_a) that supports light capture and CO₂ fixation by leaves (Niinemets et al. 1998, Le Roux et al. 1999). Increasing A_{\max} with increasing light was also associated with greater stomatal conductance. Higher $G_{s \max}$ enhances CO₂ diffusion into leaves which in turn increases photosynthetic rates. However, even if increased light availability has been shown to be associated with greater stomatal conductance (Jarvis 1976, Le Roux et al. 1999), stomatal regulation mechanisms remain poorly understood and the variations in $G_{s \max}$ observed here (Figure 1a, Table 2) might be more dependent on stomatal density and size than on any other factor.

Variation in light availability also induced variations in CO₂ losses due to leaf respiration (R_d in Figure 1c, Table 3). Higher light levels probably increased R_d because of higher maintenance costs caused by higher photosynthetic rates (Amthor 1986, Niinemets et al. 1998), higher proteins turnover and higher needs in the production of secondary compounds such as radiation protective components (i.e. flavonoids or carotenoids). The higher R_d observed for yellow birch is also likely related to its continuous growth that leads to constant and higher growth respiration costs (cf. Amthor 1986) compared to sugar maple. However, since carbon lost by respiration is at least 10 times less than carbon gained by photosynthesis even in higher light (see Figure 1 and Beaudet and Messier, 1998), enhancing leaf mass and physiological functioning when light increase and water is not limiting seems appropriate to increase leaf carbon balance. In fact, Gansert (1994) already suggested that at the leaf level, carbon released through respiration is of little importance for tree growth compared to carbon uptake.

In contrast, we found that traits associated with the partitioning of tree biomass were mainly dependent on individual tree size as has also been reported for diverse annual plant species by McConnaughay and Coleman (1999). In agreement with Givnish's hypothesis (1988) and results for evergreen conifers (Claveau et al. 2002), we found that the ratio of non-photosynthetic to photosynthetic tissues (NPT/PT) increased with tree size. Here NPT also included below-ground parts, which have rarely been quantified for such large saplings growing in natural conditions. This increase of NPT in total tree dry mass (Table 3) is the direct consequence of the annual addition of new branches, roots and trunk rings that support tree foliage (Givnish 1995). Indeed, based on the pipe model theory (cf. Perttunen et al. 1998) every increase in leaf area exponentially increases the surface needed for water transport and will increase the volume of NPT. Concurrently, this increasing investment in woody tissues is surely imposed by the need to maintain mechanical strength to face the increasing stress due to wind and gravity pressure as tree size increases (King 1986, Niklas 1992).

According to Givnish's hypothesis (1988), such increase in NPT/PT ratio with increasing tree size will affect negatively the carbon balance, which may particularly be the case for smaller seedling as long as all their NPT are active and respiratory tissues. However, it is difficult to consider the increase in NPT/PT ratio as having a negative impact on taller tree carbon balance. Indeed, taller trees annually reduce active NPT tissue dry mass by producing inactive heartwood (Ceschia 2001) that reduce respiratory cost without reducing physical support. Taller trees may also benefit from an increase in

NPT/PT ratio by improving their hydraulic conductance (Ryan et al. 2000, McDowell et al. 2002) and increasing tissues for carbohydrate storage. Nevertheless, to firmly test the overall effects of increasing tree size on tree's functioning, accurate estimations of daily or seasonal individual carbon balance under contrasting light environment and particularly at different developmental stages (using individual tree growth models) are needed.

At the level of the crown morphology, tree size, species and light were associated with most of the variation in crown form and proportion. Our results agree with other studies that found that crown morphology is not only influenced by light availability but also is associated with size and intrinsic species differences (Poorter and Werger 1999, Naumburg et al. 2001, Sterck and Bongers 2001, Claveau et al. 2002). Interestingly, at the whole tree level, the decreasing LAR with increasing tree size follows exactly the same pattern as the FRMR, further suggesting that above- and below-ground active tissues are diluted in total tree dry mass as they increase in height. LAR and FRMR declined rapidly until trees were around 1 m tall, a trend already reported for LAR in other species by Claveau et al. (2002). Being small (i.e. less than 1 m) in a resources limited environment may thus be advantageous in survival, since higher LAR and FRMR are related to a higher light and nutrient capture efficiency per unit of total tissue produced.

All of these results that emphasize the effects of size alone (or in interaction) on various traits require some rethinking of the interpretation of many field and greenhouse studies that have investigated these traits in contrasting light environments. In many cases, the observed morphological and allocational differences found in many traits (e.g. variations in LAR), were probably the direct consequences of contrasting sizes rather than contrasting light environments.

5.1.5.2. Variations in tree species plasticity

Although we compared only two species with a relatively narrow range of shade tolerance, it is interesting to see how variations in many traits (i.e. their plasticity) varied in relation to both light and size gradients since this may help to explain their autecology.

In our study, yellow birch overall had higher physiological plasticity than sugar maple, primarily in response to light environment (Figure 1). Similar light-dependent physiological plasticity has already been reported for most shade intolerant (or pioneer) species (Bazzaz and Carlson 1982, Canham 1988, Valladares et al. 2002). As proposed by Valladares et al. (2002), a rapid acclimation of photosynthetic processes is critical for a rapid use of higher irradiance that increases carbon gain and thus allows greater growth rates and competitive abilities in open areas. On the contrary, the wide and deep crown of yellow birch showed no significant plasticity during its development whereas sugar maple crown did (Figure 4a). Thus, in lower light, the rather mono-layer, umbrella-shaped crown (Waring 1987) that sugar maple exhibits when small is likely to be more efficient than the multi-layer crown of yellow birch. In addition, sugar maple tends to allocate less of its total biomass to branches and more to roots when small compared to yellow birch. Kobe (1997) linked this ability to a better survival in low light, because of a greater allocation to storage, which provides a buffer against stresses by allowing survival of existing tissues or production of new tissues. Furthermore, it has been shown that small understory sugar maple seedlings allocate more reserves to roots per unit of biomass than yellow birch (Gaucher et al. submitted). For our two species, these specific combinations of traits fit well with the observed greater competition ability of yellow birch in gaps and the better overall shade tolerance of sugar maple (Beaudet and Messier 1998, Ricard et al. 2003).

However, all of these physiological, morphological and allocational differences found between the two species did not hold constant along both light and size gradients investigated in this study. Physiological differences between species were usually found to decrease with decreasing available light (see $G_{s\ max}$, A_{max} , N_a , Table 3), whereas morphological and allocational differences decreased with increasing tree size (see Crown%, Crown H/D, Branches per dm of crown and %Root, %Branch in Table 3). As Meinzer (2003) suggested, there might be a limited number of physiological solutions to adapt to a stressful environment. This may explain the convergence of leaf physiological traits between the two species under lower light regimes. Likewise, a decrease in morphological and allocational differences between species with increasing individual size is possibly related to the mechanical and physical constraints imposed on larger trees (King 1986, Niklas 1992). Setting up a horizontal crown at 6 meters involves totally different constraints and thus carbon costs compared to setting up a horizontal crown for a 0.5 meter tall seedling that is much less affected by wind and its own mass. This increasing exposure to external forces as trees increase in size and total biomass may slowly constrain a species' ability to express some of the specific differences observed at the seedling stage. Since tree species may only be able to express some of their phenotypic particularities when they are of small size, we need to be careful when interpreting forest dynamics based only on physiological and morphological studies made at seedling stage.

5.1.5.3. Effect of a simulated sudden reduction in light

Using canonical discriminant analysis (CDA), we found a clear separation between the two species and size groups. This highlights important differences between species in terms of leaf physiological, crown morphological and tree allocational traits during their early development (Figure 6).

The sudden artificial shading affected the crown morphology of yellow birch more drastically than that of sugar maple. Indeed, yellow birch lower branches appear to have died under the light reduction, probably because they were not able to maintain a positive carbon balance (Sprugel et al. 1991). On the contrary, sugar maple crown organisation was much less affected by artificial shading (i.e. no reduction of crown size, and even an enhancement towards longer crown for smaller seedlings, Figures 6a and 6c). However, for both species (except taller sugar maple), the shading treatment decreased A_{max} and %PT which in turn affected individuals carbon gain through a decrease in photosynthetic potential. Thus, in such environment where carbon gains are limited, patterns of biomass partitioning became of critical importance. We suggest that sugar maple was less affected by a sudden shading than yellow birch (Table 4, Figure 6), because of its slow growth rate, flat crown shape when small and higher allocation to roots (and thus reserves) (Gaucher et al. submitted) which may allow sugar maple to avoid self-shading and cope better with prolonged low light conditions.

Finally, smaller individuals of both species were more affected (i.e. few leaves, yellow leaves and dead branches) by shading than taller ones (Figure 6), which was somewhat unexpected. Since tree morphological plasticity and LAR decrease with increasing tree size (Messier and Nikinmaa 2000, this study), we expected taller trees to be more affected by a sudden simulated shading than smaller ones. However, when shaded, smaller seedlings unbalanced their NPT/PT ratio to very high values compared to un-shaded seedling of the same size (Figure 7). So even if small seedlings have higher LAR and a better ability to modify their crown morphology, they may not have the necessary reserves to absorb such drastic reduction of light. Larger trees, on the other

hand, may be able to use their accumulated reserves to survive this sudden reduction of light, at least for the four years of the study. Thus, the greater morphological plasticity and higher LAR found in smaller seedlings may allow them to survive to lower light environments, but the larger reserve pool of taller trees may allow them to survive better a sudden and drastic reduction in light availability. Nevertheless, in order to validate those ideas further research is needed in storage allocation and consumption in small as well as taller trees under contrasting environmental conditions.

5.1.6. Conclusions

The ability of tree species to modify their crown morphology and whole tree biomass partitioning is definitively not modified by light environment alone. Indeed, for many morphological and allocational traits, individual size seems to act concurrently or even more than light availability. Our findings agree with recent similar conclusions reported in the literature on annual, coniferous and deciduous species (McCaunnaughay and Coleman 1999, Bond 2000, Messier and Nikinmaa 2000, Naumburg et al. 2001, Claveau et al. 2002). It is clear that our understanding of the complex combination of traits that explain differences in species functional ecology at the seedling stage cannot be extrapolated to later growth stages. Indeed, increasing tree size seems to decrease several inter-specific differences in crown morphology and biomass partitioning, probably because of the increasing pressure imposed by physical and mechanical constraints associated with vertical growth. Thus, only small seedlings seem to be able to express fully those specific morphological and allocational traits that confer their level of shade tolerance or gap use efficiency. Our study also highlights the importance of staying small in a deeply shaded environment, which is something that most shade tolerant tree species can do due to their ability to persist at very growth rates (Messier et al. 1999). However, the greater morphological plasticity observed in small seedlings may not allow them to survive very long after a sudden and drastic reduction of light, something taller juvenile trees may be able to do owing to their greater reserve storage in perennial tissues.

5.1.7. References

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*"Celui qui brise une chose pour savoir ce qu'elle est,
a quitté le chemin de la raison."*

*J.R.R. Tolkien
Le seigneur des anneaux*

"La lutte est sévère entre l'arbre et la lumière."

*Martine Le Coz
Celeste, 2001*

5.2. Chapitre 2: Variation in crown structure and efficiency of light interception in *Acer saccharum* and *Betula alleghaniensis* seedlings.

5.2.1. Abstract

Growth of tree seedlings is largely governed by their capacity to intercept incoming light from their surrounding environment. Species differences in Light Interception Efficiency (LIE) are thus believed to be closely associated with their ability to survive during forest regeneration processes in the understorey where light is highly variable in time and in space. We analysed the changes in crown morphology, leaf organisation and LIE induced by growth under contrasting light regimes (40, 17, 6 and 2% of full sunlight) in a nursery (INRA de Nancy France). 1- and 2-year-old seedlings of the shade tolerant *Acer saccharum* Marsh. (sugar maple) and the intermediate shade tolerant *Betula alleghaniensis* Britton (yellow birch) tree species were used and their crown geometry was measured directly or by using explicit 3D plant reconstructions and interception modelling. Results pointed to a larger interception efficiency (especially in vertical directions) of 1-year-old and shaded seedlings owing to more horizontal leaves and lower leaf overlapping. However, 2-year-old and less shaded seedlings displayed larger leaf re-orientations and thus an improved multidirectional light interception. Despite several inter-specific differences in fine-scale crown traits, resulting LIE were very similar between *A. saccharum* and *B. alleghaniensis*, especially when comparisons were made at equivalent seedling size. However, a significant reduction in light capture was observed as both species increased in size suggesting an ontogenic variation in LIE during development. These results are discussed with respect to the observed functional ecology (i.e. shade tolerance) of both species.

Key words: age, functional ecology, leaf angle, light capture, shade tolerance, simulations, size, sugar maple, yellow birch.

5.2.2. Introduction

To acquire the energy required in the numerous processes involved in the conversion of atmospheric CO₂ into biomass, plants need to capture solar radiation from their surrounding environment. In the forest understory, where light is often highly variable in time and in space (Runkle 1982, Canham et al. 1990), growth and survival of regenerating seedlings are thus closely linked to their capacity to efficiently intercept light under contrasting light environments.

At the individual tree scale, light interception efficiency (LIE) is governed by the combination of the total leaf surface developed for interception (i.e. the total leaf area) and the arrangement of this surface within the crown volume. Crown geometry and particularly branching pattern (Sipe and Bazzaz 1994), leaf number, dynamic, size and shape (Niklas 1989, Ackerly and Bazzaz 1995b, Farnsworth and Niklas 1995), leaf density and dispersion (Planchais and Sinoquet 1998) and leaf orientation (Planchais and Sinoquet 1998, Farque et al. 2001, Galvez and Pearcy 2003) contribute to a large extent to the display of an efficient intercepting leaf surface.

Significant differences in LIE among species are expected since fine-scale studies of crown morphology and architecture usually reveal numerous inter-specific differences (e.g. Hallé et al. 1978, Sterck 1997, Beaudet and Messier 1998, King and Maindonald 1999, Poorter and Werger 1999, Kawamura and Takeda 2002). Indeed, potential differences in the sum of numerous fine-scale crown traits are likely to imply contrasting light interception efficiencies among species which may be critical for survival in forest understorey. Such differences might, in turn, contribute to the distinct functional ecology (e.g. degree of shade tolerance) observed among forest tree species (cf. Baker 1949, Forcier 1975).

Until now, variations in LIE for single branches or whole crowns were widely associated with variations in light availability during development (Valladares and Pearcy 1998, Planchais and Sinoquet 1998, Farque et al. 2001, Fleck et al. 2003, Gálvez and Pearcy 2003): under low light regimes, LIE is frequently improved by low leaf inclination angles (i.e. horizontal leaves), few leaf layers and petiole twisting mechanisms that all limit the detrimental effect of leaf self shading. On the other hand, LIE is decreased under higher light regimes because of denser crown and larger leaf area that increase leaf overlapping and self shading. However, this decrease in LIE with higher light availabilities is often linked to a deeper light penetration within the crown and a reduction in the interception of damaging high and direct sunlight radiations.

On the other hand, little information is available about the variability in LIE of woody species with respect to their ontogeny or development in size (Farque et al., 2001). However, an increasing number of studies have emphasized the importance of increasing tree size by itself or in interaction with light availability on crown morphology and biomass allocation (Messier and Nikinmaa 2000, Naumburg *et al.* 2001, Sterck and Bongers. 2001, Claveau *et al.* 2002, Delagrangé *et al.* 2004). Recently, Kawamura and Takeda (2002) reported in two *Vaccinium* species the critical importance of individual height and ontogeny in determining crown dimensions and branching pattern, respectively, whereas light availability mostly affected phyllotaxic traits. Consequently, in addition to acclimation to variation in light conditions, intra- and inter-specific in LIE are likely to happen during the early development of regenerating trees.

Here, we examined the variation of crown morphology, leaf organisation and crown light interception of the shade tolerant *Acer saccharum* Marsh. (sugar maple) and the intermediate shade tolerant *Betula alleghaniensis* Britton (yellow birch) using direct measurements and spatially explicit 3D model simulations. To do this, we analyzed the

crown morphology of 1- and 2-year-old seedlings grown in a nursery under four contrasting light regimes (40, 17, 6 and 2% of full sunlight) provided by neutral shading nets. Furthermore, a sub-sample of 31 individuals was digitised in 3 dimensions to assess the precise organisation (i.e. orientation and display) of leaves within the crown volume. Then, using reconstructed 3D images of digitised seedlings in the plant functional and structural model *vegeSTAR* (Adam B., Sinoquet H. and Donés N. 2002), the integrated crown Silhouette to Total leaf Area Ratio (*STAR*) and daily Light Capture Coefficient (LCC) under contrasting light conditions were estimated.

We had three main objectives in this study:

(i) to determine the variation in crown morphology, leaf organisation and resulting crown light interception efficiency in relation to contrasting light regimes, seedling age, species and interactions, (ii) to assess the importance of individual size in the variation of light interception efficiency, and (iii) to discuss the contribution of light interception efficiency variations to the shade tolerance and functional ecology of *A. saccharum* and *B. alleghaniensis*.

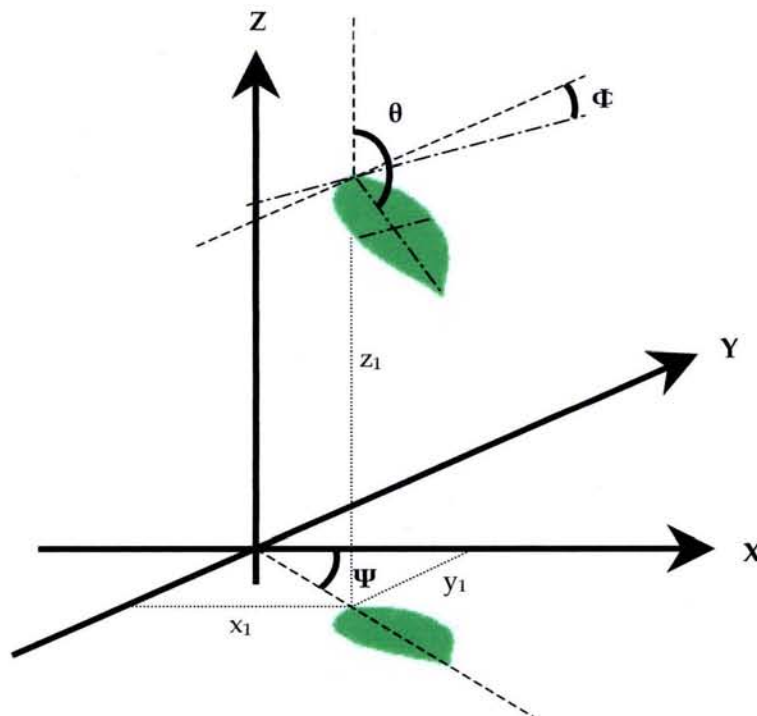
5.2.3. Material and methods

5.2.3.1. Plant material and experimental design

Seeds of the shade tolerant species *Acer saccharum*, Marsh. (sugar maple) and of the intermediate shade tolerant species *Betula alleghaniensis*, Britton (yellow birch) were provided by the Natural Resources Ministry of Quebec from the Duchesnay forest station (46°55' N, 71°40' W). In May 2001, seeds were germinated in a green house at Champenoux (48°44' N, 6°14' E) near Nancy, France, using a cold storage pre-treatment for *A. saccharum* and adding a liquid fertilizer for *B. alleghaniensis*. Then, a total of 200 germinated seedlings were transplanted into 10L pots filled with a mixture of peat and sand (1/3 v/v) and placed in a nursery under 4 aluminized shading nets which provided 4 contrasting light regimes (40, 18, 8 and 3.5% of full sunlight). Seedlings were fertilised twice during the growing season (when potted in May and at the beginning of August) with 40 g (4 g·l⁻¹ of soil mixture) of a slow-release fertiliser (Nutricote 100+, 13/13/13 N/P/K containing oligo-elements). Water was provided every day to field capacity using a drip irrigation controlled by a time switch. In 2002, using the same protocol of germination pre-treatment and potting, a total of 40 new seedlings per species (i.e. germinated in May 2002) was added under the 4 light regimes. During the 2002 growing season, watering and fertilisation were provided for all seedlings at the same frequency as in 2001.

5.2.3.2. Seedlings digitising

At the end of July 2002, 32 individuals were selected for digitising in order to obtain 2 repetitions of each age (1- and 2-year-old) under the four light regimes (40, 18, 8 and 3% of full sun light) for both species. Leaf organisation in crown volume was recorded using a Fastrak electromagnetic 3-D equipment (Polhemus Inc., Colchester, VT, USA)



Figures 5.8. Representation of a leaf (L), its vertical projection (Lp) and the three Euler angles (i.e. leaf inclination angle (θ), leaf rolling angle (Φ) and leaf azimuth angle (Ψ)) in a 3-D space. In Figure 1, x_1 , y_1 and z_1 are the three co-ordinates of the petiole-lamina junction of the leaf L on X, Y and Z axes respectively.

as described by Sinoquet *et al.* (1998). This apparatus associated with the 3A computer software (Adam B., Sinoquet H., Godin C. and Donés N. 1999) allowed a precise description of each leaf. Size, position (co-ordinates: x, y and z) and orientation as given by the three Euler angles (i.e. leaf inclination angle [θ], leaf rolling angle [Φ] and leaf azimuth angle [Ψ], *c.f.* Figure 5.8) were obtained for each individual leaf. This method, first tested by Sinoquet and Rivet (1997), was recently applied to describe the canopy structure of several plant species (Sinoquet *et al.* 1998, Rakocevic *et al.* 2000, Casella and Sinoquet 2003). To prevent canopy movements due to wind and interferences in the electromagnetic field of measurement (Sinoquet and Rivet 1997), digitising was performed inside a small woody cabin that contained no structural metallic elements. One measurement at the lamina-petiole junction described the leaf spatial co-ordinates and Euler angles since the pointer was held parallel to the leaf blade and along the main leaf vein axis. Another recording at the lamina extremity was used to record leaf length; in controlled conditions the digitiser error in spatial measurements is less than 1 mm (*cf.* Sinoquet *et al.* 1998). Time necessary for measurement ranged from 10 min to digitise a 20-cm tall *A. saccharum* to 2 days for a 190-cm tall *B. alleghaniensis*.

5.2.3.3. Canopy reconstruction of digitised individuals and light interception simulations

From the x, y and z co-ordinates and the 3 Euler angles acquired after seedling digitising, the precise position, length and orientation of each leaf were then used to reconstruct the crown of each individual in the 3D explicit model *vegeSTAR* 3.02 (Adam B., Sinoquet H. and Donés N. 2002). For each species, the specific relationship between leaf area (L_{area}) and leaf length (L_{length}) was computed ($L_{area} = 0.75 L_{length}^2$ [$r^2 = 0.97$] and $L_{area} = 0.34 L_{length}^2$ [$r^2 = 0.95$] for *A. saccharum* and *B. alleghaniensis*, respectively). This relationship was used to calculate seedling total leaf area. For both species, leaf surfaces were visualized in the model by polygonal leaf prototypes that mimicked real leaf shape.

To validate the 3D reconstructions, we compared total leaf area estimated by the model to total leaf area measured directly from harvested seedlings (Figure 5.9).

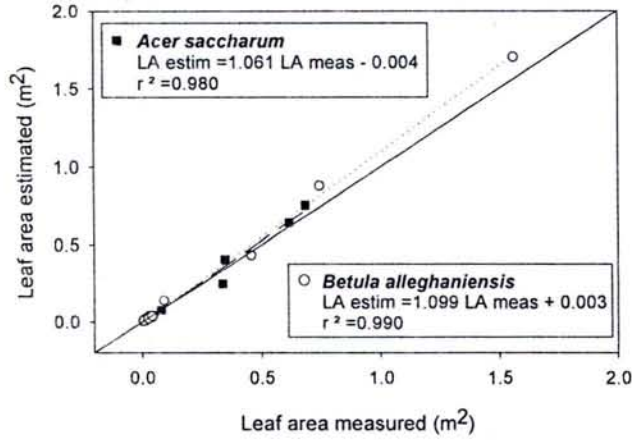


Figure 5.9. Relationship between total measured leaf area and the total calculated leaf area using leaf reconstruction with the *vegeSTAR* model for digitized *A. saccharum* and *B. alleghaniensis* seedlings. For both species, linear regression (long dash and dotted line for *A. saccharum* and *B. alleghaniensis* respectively), equation and r^2 are presented as well as the 1:1 relation line.

To calculate Silhouette to Total leaf Area Ratio (*STAR*), *vegeSTAR* 3.02 software counted the projected number of pixels of leaves in a given line of sight as viewed by an orthographic camera (i.e. a camera with parallel beams). Here we chose 46 lines of sights (i.e. 46 beams passing through the centre of the sectors of a 46-sector-turtle-sky representation of the sky). For each line of sight Ω defined by an elevation (Ω_{El}) and an azimuth (Ω_{Az}) angle, the *STAR* was calculated as the ratio of total projected leaf area (A_p) over total leaf area (A_t). *STAR* values were written as a product of leaf orientation and leaf overlap effect since leaf dispersion effect has very little impact in *STAR* determination (cf. Farque *et al.* 2001):

$$STAR_{\Omega(El,Az)} = \frac{\sum L_{p\Omega}}{A_t} \cdot \frac{A_p}{\sum L_{p\Omega}} \quad (1)$$

where $L_{p\Omega}$ is the projected surface of a leaf with area L for the line of sight Ω and $A_t = \sum L$. For both leaf orientation and leaf overlap effects, values close to 1 have little impact on *STAR* whereas those close to 0 critically reduce it.

For every leaf, L_p was calculated from L as:

$$L_p = \cos(\alpha) \cdot L \quad (2)$$

α is the angle between the leaf normal and the line of sight Ω calculated as:

$$\alpha = \arccos \left\{ \begin{aligned} & [(\cos(\Phi) \cdot \sin(\theta) \cdot \cos(\Psi) + \sin(\Phi) \cdot \sin(\Psi)) \cdot \cos(\Omega_{El}) \cdot \cos(\Omega_{Az})] \\ & + [(\cos(\Phi) \cdot \sin(\theta) \cdot \sin(\Psi) - \sin(\theta) \cdot \cos(\Psi)) \cdot \cos(\Omega_{El}) \cdot \sin(\Omega_{Az})] \\ & + [\cos(\Phi) \cdot \cos(\theta) \cdot \sin(\Omega_{El})] \end{aligned} \right\} \quad (3)$$

where Φ , θ and Ψ are the leaf rolling, inclination and azimuth angles, respectively. To obtain a whole crown integrated value of STAR ($STAR_{int}$), the 46 STAR values were weighted for each individual using their corresponding SOC (standard overcast sky distribution model) coefficient (i.e. directions close to the zenith were more important than horizontal ones since their irradiance is greater).

Simulations of individual-level light interception were performed using light sequences that recreated accurate light quantity and proportion of direct and diffuse light experienced under each of the four shading net treatments for a sunny or an overcast day. This was obtained by (i) reducing external global light and (ii) defining the proportion of direct present in remaining light according to each net characteristics previously determined using light quantity and quality measurements taken outside and under each net (data not shown). In practice, for both scenarios, global light corresponded to 40, 17, 6 and 2% of the total external radiations. However, proportions of diffuse light remaining in net-transmitted light were fixed at 54, 46, 16 and 1% (for the 40, 17, 6 and 2% light treatment respectively) for sunny conditions and 100% for all light regimes for the overcast conditions. It is noteworthy to mention that (i) total external radiations were set to be equivalent for both scenarios, meaning that only the proportion of direct and diffuse light differed for seedlings of the same light regimes and (ii) simulated global light as well as the proportion of direct and diffuse light were very consistent to the real conditions experienced by seedlings during their growth.

During the simulations, the model computed each individual leaf's interception of direct (if any) and diffuse light for 10 minute periods. Direct light was set to come from lines of sights corresponding to the sun course of the 27th of July 2002 at the nursery latitude, whereas diffuse light was set to come from the 46-sector-turtle-sky representation previously chosen for *STAR* calculations. For each time period, a Light Capture Coefficient (*LCC*) was calculated by dividing the photon flux intercepted per m² of individual leaf surface by the equivalent photon flux intercepted by a horizontal plane of 1 m². This coefficient includes both leaf orientation and overlap effect. Finally, to determine a whole crown daily integrated *LCC* in sunny (*LCC_s*) and totally overcast (*LCC_o*) conditions, each *LCC* value was weighted by the quantity of incoming light during the corresponding 10 minute periods (i.e. values of the middle of the day were more important than values of sun rise or sun set) and summed together.

5.2.3.4. Seedling harvest and crown morphology measurement

A total of 123 seedlings classified into 2 ages, 4 light regimes and 2 species (i.e. between 5 and 8 repetitions per class) were harvested at the beginning of September 2002. The individual size (i.e. length of the main stem, cm), crown height (from the first live branch), crown diameter (mean of 2 perpendicular directions), and total leaf area (Planimeter, Delta T, Hoddesdon, UK) were recorded. Tree biomass was divided into leaf, branches, stem and roots and dried at 60°C for 48 hours and then weighted. Using those measurements, Crown H/D (crown height over crown diameter ratio), Crown% (proportion of stem length with live crown) and Leaf Area Ratio (LAR; cm².g⁻¹ of total plant) were calculated.

5.2.3.5. Statistical analyses

All statistical analyses were performed using StatView version 5 (SAS institute Inc., Cary, North Carolina, USA). The statistical significance of stem size, CrownH/D, Crown% and LAR as well as mean leaf inclination, $STAR_{int}$, LCC_s and LCC_o variation between light regimes, ages and species classes were tested using an analysis of variance (ANOVA). Similar analyses were performed to assess (i) the variability of STAR as a function of light regimes, ages, species and line sight elevation classes and (ii) the variation of leaf orientation and leaf overlap effects on STAR determination between classes of line of sight. On the other hand, to test the importance of stem size for LAR and $STAR_{int}$ variation, we used an analysis of co-variance (ANCOVA) where species was set as a factor and stem size as a co-variable (i.e. pooling all ages and light regimes together). The model used to reach normality of the residue and homogeneity of the variance was in both cases: $y = a \log(x) + b$. In all analyses, differences were considered statistically significant at $p < 0.05$.

Table 5.5. ANOVA results for individual tree size and crown morphology (i.e. crown height over crown diameter ratio (Crown H/D), live crown proportion (Crown%) and Leaf Area Ratio (LAR)). F ratios and p values are presented for relations between species (Sp: *A. saccharum* and *B. alleghaniensis*), Light Regimes (LR: 40, 17, 6 and 2% of full sun light), Age (1- and 2-year-old seedlings) and their interactions. Values in bold are significant at $\alpha = 5\%$.

Source of variation	Tree Size		Crown H/D		Crown%		LAR	
	F	p	F	p	F	p	F	p
Sp	1.374	0.2438	11.515	0.0010	100.167	<0.0001	0.077	0.7821
LR	79.636	<0.0001	21.157	<0.0001	31.055	<0.0001	26.338	<0.0001
Age	201.446	<0.0001	59.297	<0.0001	24.085	<0.0001	54.302	<0.0001
Sp · LR	3.233	0.0253	10.904	<0.0001	1.075	0.3631	1.128	0.3413
SP · Age	0.231	0.6316	9.297	0.0029	16.411	<0.0001	20.137	<0.0001
LR · Age	52.193	<0.0001	10.673	<0.0001	3.239	0.0251	1.908	0.1328
Sp · LR · Age	5.010	0.0027	6.530	0.0004	1.955	0.1252	2.311	0.0804

5.2.4. Results

5.2.4.1. Tree size and crown morphology

For both species, individual size increased with increasing light availability but the differences among light regimes were larger for the 2-year-old seedlings (Table 5.5, Figure 5.10A). Differences in final individual size between species were small in the 1-year-old seedlings. *Betula alleghaniensis* was generally taller than *A. saccharum* but differences were not significant. On the other hand, differences between species were greater for the 2-year-old seedlings since *B. alleghaniensis* reached significantly taller sizes under all light regimes (excepted under the 40%). Indeed *A. saccharum* showed almost no growth under the 2 and 6% light regimes, whereas *B. alleghaniensis* had

relatively good growth under all light regimes. (Table 5.5, Figure 5.10A). The CrownH/D ratio for *B. alleghaniensis* was similar among the four light regimes and was slightly higher in the 2- compared to the 1-year-old seedlings (Table 5.5, Figure 5.10B). In contrast, *A. saccharum* showed a completely different pattern of CrownH/D variation that significantly increased with increasing light regimes especially for 2-year-old seedlings (Table 5.5, Figure 5.10B). For both species, seedlings grown under higher light regimes showed greater Crown% especially for the 2-year-old seedlings (Table 5.5, Figure 5.10C). Crown% was generally higher for *B. alleghaniensis* compared to *A. saccharum* but differences between species decreased under higher light regimes and were less pronounced in 2- compared to 1-year-old seedlings (Table 5.5 and Figure 5.10C). Finally, *LAR* was significantly lower in 2- compared to 1-year-old seedlings especially for *B. alleghaniensis*. For both species, *LAR* decreased under higher light regimes (Table 5.5, Figure 5.10D). Variations in *LAR* were found to vary strongly with individual size with no significant species differences (Figure 5.11).

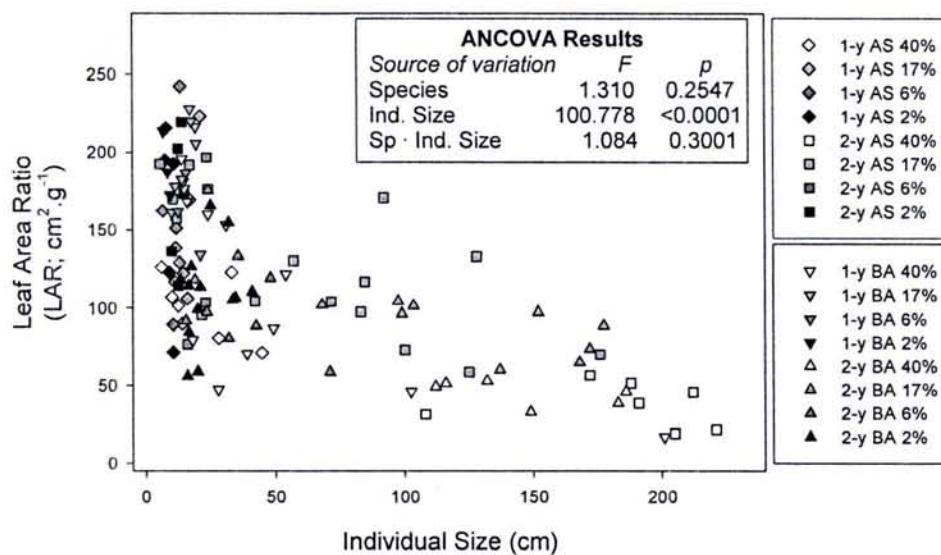


Figure 5.11. Relation between leaf area ratio (*LAR*; $\text{cm}^2 \cdot \text{g}^{-1}$) and individual size (cm) for *A. saccharum* and *B. alleghaniensis* seedlings grown in a nursery at Nancy, France. 1- and 2-year-old seedlings of *A. saccharum* and *B. alleghaniensis* are represented by squares, diamonds, up-triangles and down-triangles, respectively. The models used in the ANCOVA were $y = 231.09 - 75.62 \log(x)$ ($r^2 = 0.44$) for *A. saccharum* and $y = 261.09 - 93.12 \log(x)$ ($r^2 = 0.50$) for *B. alleghaniensis*.

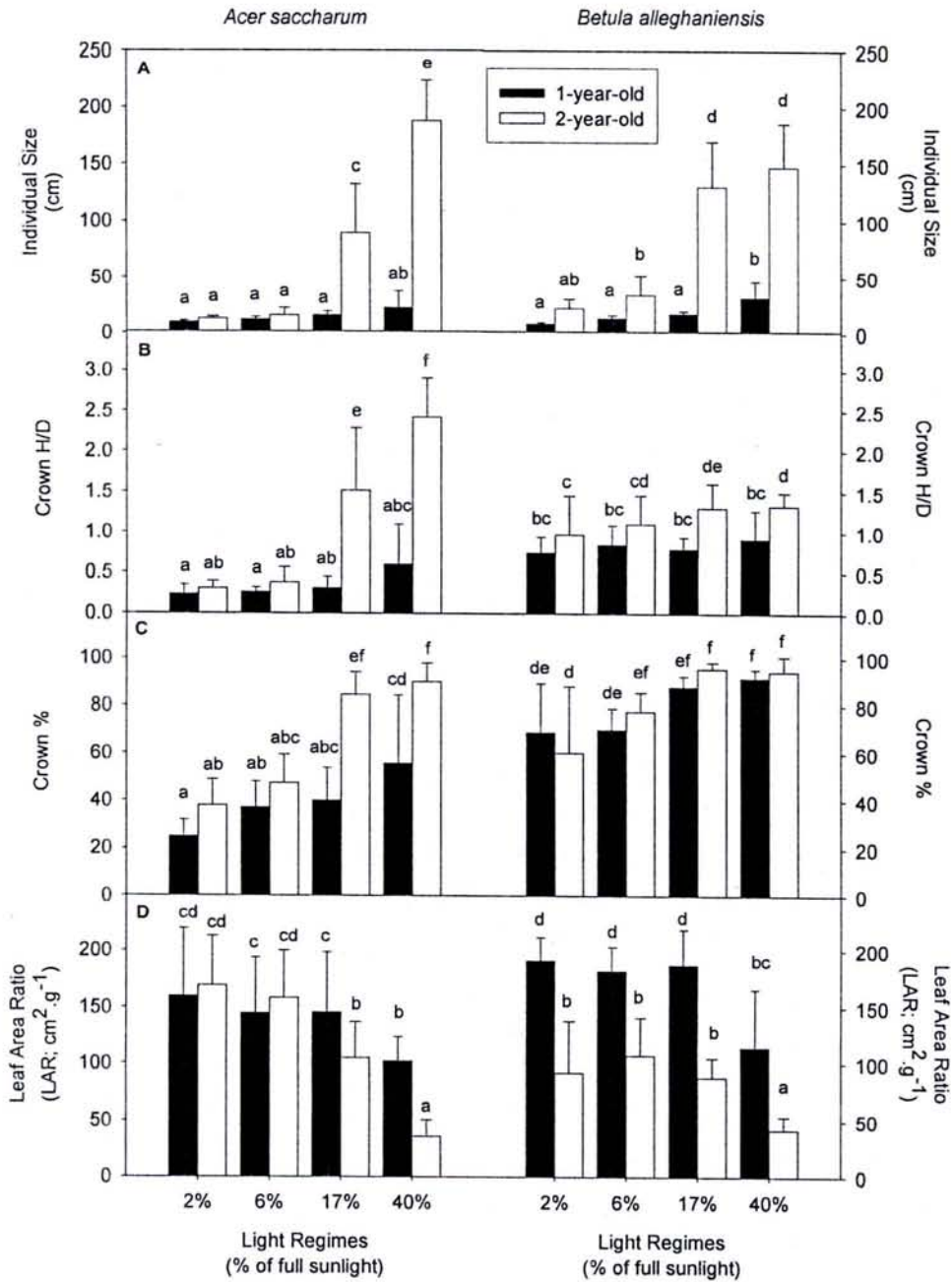


Figure 5.10. Mean values and standard deviations for individual size and crown morphology for 1- (filled bars) and 2-year-old (open bars) *A. saccharum* and *B. alleghaniensis* seedlings grown in a nursery at Nancy, France. Results for A: individual size (cm), B: crown height over crown diameter ratio (Crown H/D), C: live crown proportion (Crown%) and D: Leaf Area Ratio (LAR; $\text{cm}^2 \cdot \text{g}^{-1}$) are presented as a function of light regimes (40, 17, 6 and 2% of full sun light). Depending on classes, n ranged from 5 to 8. Contrasting letters correspond to significant differences at $\alpha = 5\%$.

5.2.4.2. Leaf organisation within crowns

Acer saccharum and *B. alleghaniensis* showed contrasting patterns of variation in the frequency (Figure 5.12) and mean (Table 5.6) of leaf inclination and rolling angles with light regimes and ages. Mean leaf inclination angle of *A. saccharum* was relatively constant among light regimes while *B. alleghaniensis* showed a slight increase of mean leaf inclination angle with increasing light regimes for both the 1- and 2-year-old seedlings (Table 5.6). For both species, mean leaf rolling angles were not significantly different from zero (data not shown). Mean leaf inclination angles were higher for *A. saccharum* than *B. alleghaniensis* but differences between species were less pronounced for the 2-year-old seedlings and under higher light regimes (Table 5.6). In addition, Figure 5.12 clearly illustrates a narrower range of leaf inclination and rolling angles (with higher frequency) in the 1- compared to 2-year-old seedlings.

Table 5.6. Summary of the mean, standard error (SE) and ANOVA results (F ratios and p values) for leaf inclination angle of 1- and 2-year-old *A. saccharum* and *B. alleghaniensis* grown under four contrasting light regimes (40, 17, 6 and 2% of full sun light). Mean values with contrasting letters are significantly different at $\alpha = 5\%$. In ANOVA results, values in bold are significant at $\alpha = 5\%$.

		Leaf Inclination Angle (θ)	
		Mean	\pm (SE)
Acer <i>saccharum</i>	1 year	40%	-19.56 <i>d</i> (2.87)
		17%	-24.44 <i>e</i> (2.43)
		6%	-19.46 <i>d</i> (1.59)
		2%	-14.20 <i>cd</i> (3.63)
	2 years	40%	-21.42 <i>de</i> (1.49)
		17%	-18.93 <i>d</i> (1.90)
		6%	-24.11 <i>e</i> (1.74)
		2%	-21.61 <i>de</i> (4.58)
<i>Betula</i> <i>alleghaniensis</i>	1 year	40%	-12.94 <i>cd</i> (3.98)
		17%	-3.71 <i>b</i> (1.23)
		6%	2.41 <i>a</i> (2.24)
		2%	2.68 <i>a</i> (2.60)
	2 years	40%	-30.84 <i>f</i> (0.75)
		17%	-17.46 <i>d</i> (1.30)
		6%	-16.03 <i>d</i> (1.57)
		2%	-10.60 <i>c</i> (3.12)
ANOVA RESULTS		Leaf Inclination Angle (θ)	
<u>Source of variation:</u>		<i>F</i>	<i>p</i>
<i>Species</i>		28.889	<0.0001
<i>Light Regimes</i>		6.725	0.0002
<i>Age</i>		27.915	<0.0001
<i>Species x Light Regimes</i>		6.108	0.0004
<i>Species x Age</i>		15.336	<0.0001
<i>Light Regimes x Age</i>		0.106	0.9567
<i>Species x Light Regimes x Age</i>		0.895	0.4432

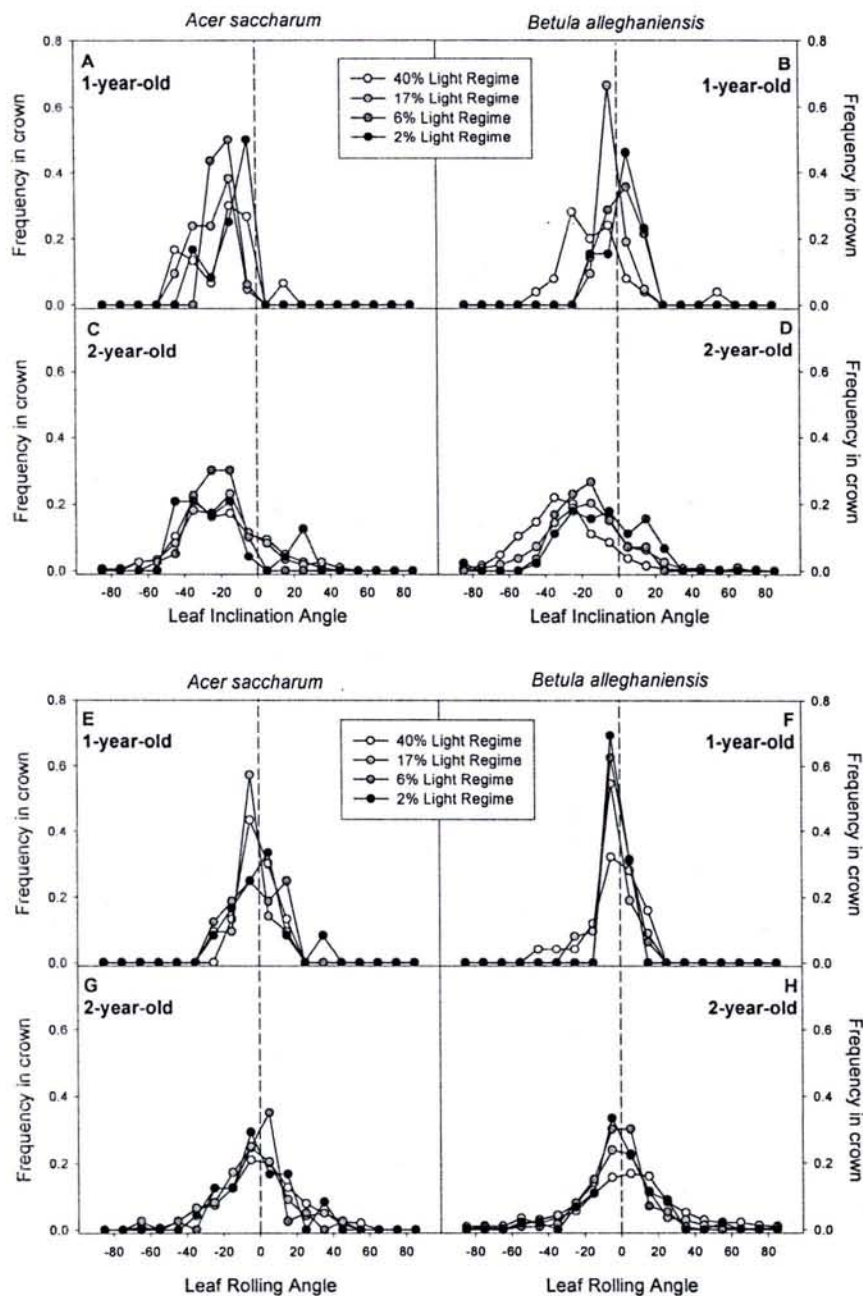


Figure 5.12. Frequencies of leaf inclination (A, B, C and D) and leaf rolling (E, F, G and H) for 1- and 2-year-old seedlings of *A. saccharum* and *B. alleghaniensis* grown under contrasting light regimes in a nursery at Nancy, France. For each graphic, the 40, 17, 6 and 2% light regimes correspond to white, grey, dark grey and black symbols.

5.2.4.3. Seedling light interception

For each of the 32 digitised individuals, general linear model analyses showed that Silhouette to Total leaf Area Ratio (*STAR*) was highly dependent on the elevation angle but independent of sight azimuth angle (data not shown). Azimuth was therefore removed from further analyses while elevation was categorized into four classes: 0 to 20°, 21 to 40°, 41 to 65° and 66 to 90°. Since the quadruple and triple interactions and species factor explained relatively little of the variation in *STAR* (Table 5.7, Figure 5.13), we focused on the effect of elevation, light regimes, ages and interaction between these factors. *STAR* decreased rapidly with decreasing elevation for both species, both ages and the 4 light regimes. However, this decrease was higher for 1- compared to 2-year-old seedlings. For the lowest elevation class (0 to 20°), *STAR* was higher in 2- compared to 1-year-old seedlings and increased with light regime. *STAR* measured for the higher elevation class (66 to 90°) was higher in 1- compared to 2-year-old seedlings and decreased with increasing light regimes. *STAR* of the middle elevation classes (21 to 40° and 41 to 65°) showed less changes with age and light regime (Table 5.7, Figure 5.13). Leaf orientation and leaf overlap effects on *STAR* were both highly dependent on elevation class (Figure 5.14). Leaf orientation was mostly responsible for changes in *STAR* values all along elevation classes while leaf overlap effect was more important only for the highest elevation class (Figure 5.14). Species, age and light had little importance in the pattern of variation of leaf inclination or overlap effect in *STAR* determination, except that decreasing light regimes decreased the elevation at which both curves intercept (Data not shown).

$STAR_{int}$ as well as LCC_s and LCC_o were strongly affected by ages and light regimes but not by species (Figure 5.15, Table 5.8). For both species, $STAR_{int}$, LCC_s and LCC_o were lower for 2- compared to 1-year-old seedlings and decreased with increasing light regimes. However, the decrease of $STAR_{int}$, LCC_s and LCC_o with increasing light regime was larger in the 2-year-old especially for LCC_s (Figure 5.15, Table 5.8). It is noteworthy to mention that LCC were higher during totally overcast compared to sunny conditions and that this increase raised with increasing light regime (Figure 5.15). When plotted as a function of individual size, variations in $STAR_{int}$, LCC_s and LCC_o were highly dependent on individual size variations while no differences between species were found (Figure 5.16, results are not presented for LCC_s and LCC_o since they followed exactly the same pattern as $STAR_{int}$).

Table 5.7. ANOVA results (F ratios and p values) for individual Silhouette to Total Area Ratio ($STAR$) variations in relation to Species (*A. saccharum* and *B. alleghaniensis*), Light Regimes (40, 17, 6 and 2% of full sun light), Age (1- and 2-year-old seedlings), line sight Elevation classes (0-20°, 21-40°, 41-65° and 66-90°) and their interactions. Values in bold are significant at $\alpha = 5\%$.

STAR		
<i>Source of variation:</i>	F	p
Species	16.310	<0.0001
Light Regimes	104.087	<0.0001
Age	345.487	<0.0001
El	1712.547	<0.0001
Species x Light Regimes	17.219	<0.0001
Species x Age	0.056	.8132
Species x El	23.192	<0.0001
Light Regimes x Age	25.340	<0.0001
Light Regimes x El	38.721	<0.0001
Age x El	160.103	<0.0001
Species x Light Regimes x Age	6.386	0.0003
Species x Light Regimes x El	8.818	<0.0001
Species x Age x El	2.926	0.0332
Light Regimes x Age x El	3.113	0.0011
Species x Light Regimes x Age x El	0.895	0.0621

Table 5.8. ANOVA results for individual crown light interception parameters (i.e. Silhouette to Total Area Ratio integrated for 46 line sights ($STAR_{int}$), Light Capture Coefficient calculated under totally overcast (LCC_o) and sunny (LCC_s) conditions). F ratios and p values are presented for relations between species (*A. saccharum* and *B. alleghaniensis*), Light Regimes (40, 17, 6 and 2% of full sun light), Age (1- and 2-year-old seedlings) and their interactions and parameters variation. Values in bold are significant at $\alpha = 5\%$.

<i>Source of variation:</i>	$STAR_{int}$		LCC_o		LCC_s	
	F	p	F	p	F	p
Species	1.965	0.1813	2.068	0.1710	2.071	0.1706
Light Regimes	9.771	0.0008	19.891	<0.0001	10.779	0.0005
Age	34.042	<0.0001	43.485	<0.0001	35.279	<0.0001
Species x Light Regimes	1.740	0.2018	1.963	0.1630	1.980	0.1603
Species x Age	0.097	0.7599	0.028	0.8688	<0.001	0.9854
Light Regimes x Age	2.381	0.1103	4.283	0.0226	3.246	0.0517
Species x Light Regimes x Age	0.817	0.5045	0.560	0.6493	0.969	0.4332

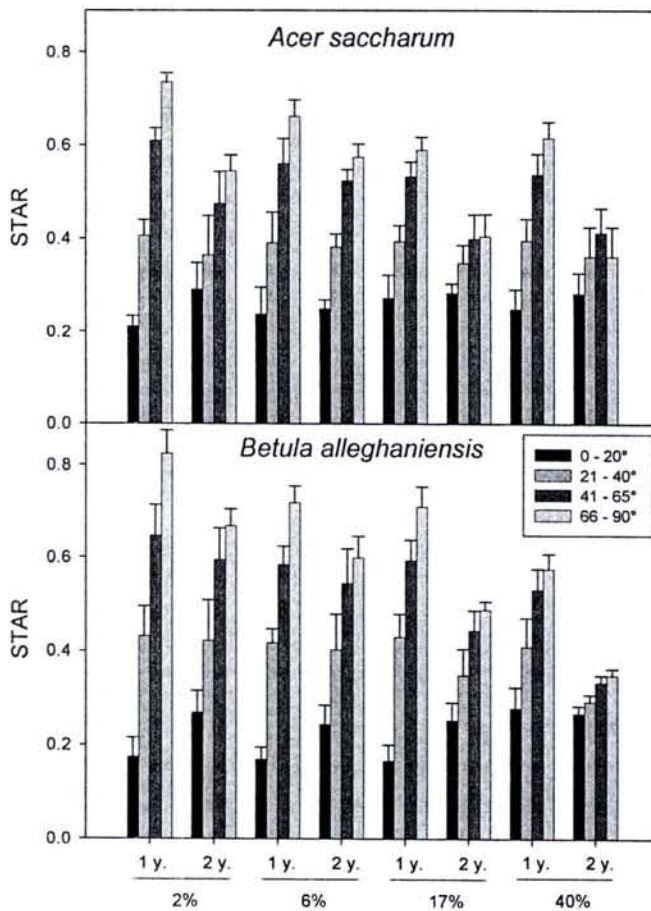


Figure 5.13. Mean values and standard deviations for Silhouette to Total leaf Area Ratio (STAR) for 1- and 2-year-old *A. saccharum* and *B. alleghaniensis* seedlings (open bars) grown in a nursery under 4 contrasting light regimes (40, 17, 6 and 2% of full sun light) at Nancy, France. Results are presented as a function of line sight elevation classes (0-20°, 21-40°, 41-65° and 66-90°).

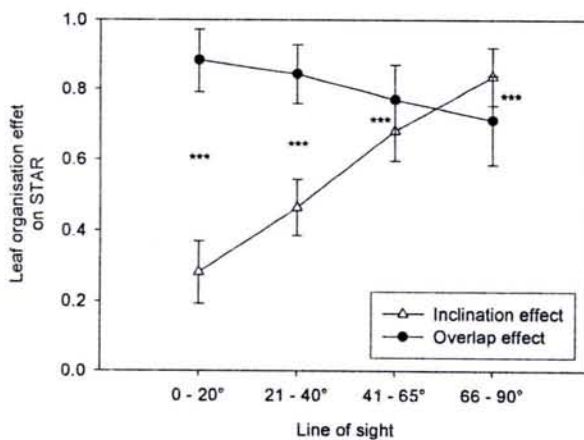


Figure 5.14. Relation between leaf orientation (black circles) and leaf overlap (white triangles) effect on STAR determination as a function of line of sight elevation classes. Species, ages, and light regimes were pooled together since variation due to these factors was of a little importance compared to the one induced by the elevation of line of sight (data not shown). Values close to 1 have little impact on STAR value whereas those close to 0 critically reduce it.

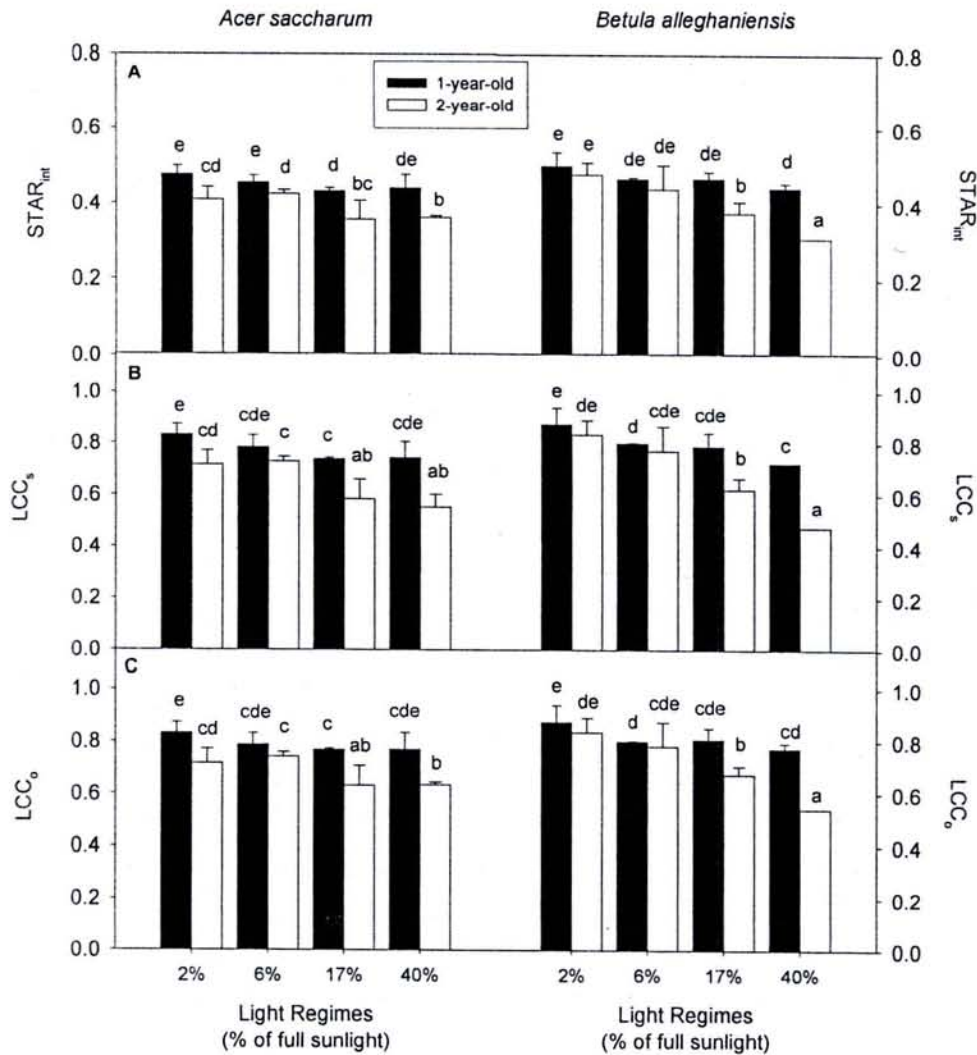


Figure 5.15. Mean values and standard errors for crown light interception parameters of 1- (filled bars) and 2-year-old (open bars) *A. saccharum* and *B. alleghaniensis* seedlings grown in a nursery at Nancy, France. Results for A: Silhouette to Total Area Ratio integrated for 46 line of sights ($STAR_{int}$), B: Light Capture Coefficient calculated under overcast conditions (LCC_o) and C: Light Capture Coefficient calculated under sunny conditions (LCC_s) are presented as a function of light regimes (40, 17, 6 and 2% of full sun light). Contrasting letters correspond to significant differences at $\alpha = 5\%$.

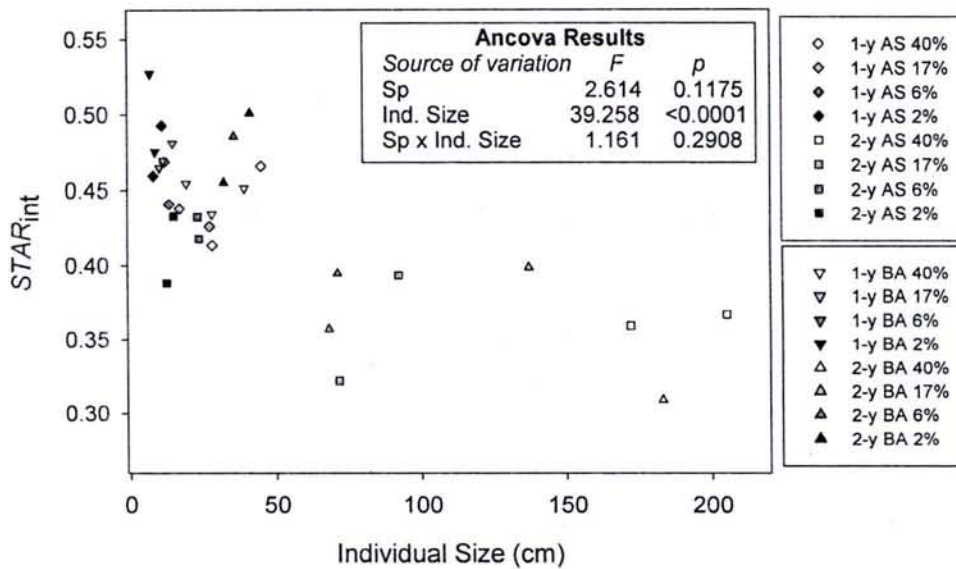


Figure 5.16. Relation between silhouette to total area ratio ($STAR_{int}$) and individual size (cm) for *A. saccharum* and *B. alleghaniensis* seedlings grown in a nursery at Nancy, France. 1- and 2-year-old seedlings of *A. saccharum* and *B. alleghaniensis* are represented by squares, diamonds, up-triangles and down-triangles, respectively. For both species, the 40, 17, 6 and 2% light regimes correspond to white, grey, dark grey and black symbols. The models used in the ANCOVA were $y = 0.53 - 0.08 \log(x)$ ($r^2 = 0.53$) for *A. saccharum* and $y = 0.60 - 0.11 \log(x)$ ($r^2 = 0.64$) for *B. alleghaniensis*.

5.2.5. Discussion

5.2.5.1. Variation in light capture efficiency

Static observations and descriptions of individual shape and fine-scale tree traits generally show a wide diversity of crown morphology and architecture among tree species (e.g. Hallé et al. 1978, Sterck 1997, Millet et al. 1998, Claveau et al 2002). In this study, numerous differences in crown morphology, leaf angles and resulting light interception efficiency were observed between ages, light regimes, species and the interaction of two or more of these factors. In both species, the observed reduction in $STAR_{int}$, LCC_s and LCC_o with age and increasing light regimes was related to an increase in leaf area that undoubtedly induced higher leaf overlap and self shading independently of species specific architecture. Nevertheless, seedlings with higher leaf area (i.e. 2-year-old seedlings and seedlings grown under higher light regimes) showed higher leaf inclination and rotation angles which increased their interception in all directions, especially at lower elevation. This increase in multi-directional light interception (i.e. diffuse and direct light interception) with increasing leaf area might compensate for the reduction of interception in the vertical direction (Farque et al. 2001). Indeed, leaf re-orientation has been seen to greatly improve light interception with the advantage of a lower carbon cost than investment in longer internodes (Galvez and Percy, 2003). In contrast, the greater number of horizontal leaves and relatively low leaf overlap of shaded and/or 1-year-old seedlings causes very efficient light interception in more vertical directions which resulted in higher $STAR_{int}$. These shaded and/or 1-year-old seedlings were thus more efficient in the interception of radiation at angles corresponding to periods of potential high and direct sunlight. These results highlighting contrasting patterns of light interception between ages or light regimes may explain the significantly higher LCC observed in 2-year-old and less shaded seedlings under overcast (i.e. diffuse light) rather than sunny conditions since they are more adapted to multidirectional interception. However, for older seedlings, this result may also be partially related to a longer acclimation of their crown to the specific light environment created by the nets (i.e. a large reduction in direct light and an increase in diffuse light).

In regard to species differences, *A. saccharum* exhibited a higher crown plasticity with light regimes and ages and higher mean inclination and rolling angles, whereas *B. alleghaniensis* showed a wider and generally longer crown among both ages and almost all light regimes. Since light capture efficiency has been seen to be critically influenced by traits such as leaf inclination and rolling angles (Farque et al 2001, Niinemets and Fleck 2002, Valladares et al. 2002, Galvez and Percy 2003) or branching pattern (Sipe and Bazzaz, 1994), differences in light interception efficiency were expected between *A. saccharum* and *B. alleghaniensis*. However, despite these distinctive fine-scale differences, resulting $STAR_{int}$ or LCC_s and LCC_o of both species were comparable under similar light environment or seedling age. In addition, no species benefited more than the other from variation in light environmental conditions (i.e. sunny or totally overcast conditions), demonstrating no significant differences in species adaptations to preferentially intercept diffuse or direct light. This may partially be due to the fact that leaf orientation is only critical for interception in lines of sight of lower elevation while it becomes less important than leaf overlap in lines of sight of higher elevation where most of radiations comes from (Figure 7). These small species differences in $STAR_{int}$ or LCC might also concur with the idea of a variety of fine-scale trait associations to achieve a given large-scale function (Givnish 1988, Reich et al. 1998). Such large-scale crown form and function convergences between species have been already pointed out for tropical

woody species (Poorter and Werger 1999, Valladares et al. 2002). These authors associated this convergence to the result of comparable crown history during development and/or comparable pressure of other crown functions such as hydraulic conduction and reproduction. Here mean *LCC* values found under sunny and overcast conditions (0.71 [± 0.10] and 0.73 [± 0.08] respectively for *A. saccharum*, and 0.75 [± 0.11] and 0.77 [± 0.09] for *B. alleghaniensis*) fit well within the range reported by Valladares et al. (2002) for the same coefficient calculated for numerous understorey tropical woody species.

Thus, even if our results highlighted numerous small-scale differences in crown morphology and leaf orientation between *A. saccharum* and *B. alleghaniensis* seedlings, variation in light interception efficiency with age, light regime and the interaction of these factors were usually greater than variation found between species.

5.2.5.2. Importance of individual size

As demonstrated by several previous studies, individual tree size is an important factor in above-ground morphological and allocational modifications, alone or in interaction with numerous environmental conditions (Messier and Nikinmaa 2000, Naumburg et al. 2001, Claveau et al. 2002, Delagrange et al. 2004). Here, when comparing groups of equivalent size in Figure 3a (e.g., 2-year-old seedlings under 8% and 1-year-old seedlings under 18% for *A. saccharum* or 2-year-old seedlings under 8% and 1-year-old seedlings under 40% for *B. alleghaniensis*, or 1-year-old seedlings under 40% for *A. saccharum* and 2-year-old seedlings under 3% for *B. alleghaniensis*), little or no differences in mean trait values were observed (Figure 3b, c and d). In addition, since the 2 ages and the contrasting light regimes also included a size effect (i.e. older seedlings and those grown under higher light regimes reached taller sizes), we compiled these results as a function of individual size. With such approach, individual size was responsible of most of the variation in *LAR* or in *STAR_{int}*, *LCC_s* and *LCC_o*, whereas differences between species totally disappeared. This concurs with the critical importance of size-dependent variation of several seedling and sapling traits (Messier and Nikinmaa 2000, Sterck and Bongers 2001, Naumburg et al. 2001, Claveau et al. 2002, Delagrange et al. 2004).

However, precautions have to be taken with such assumptions since we only studied two species and because dissimilar size gradients under each light regime did not allow the complete comparison of the importance of light, age and size on trait variation in a single analysis (e.g. an ANCOVA with species, age and light regimes as factors and individual size as co-variable). Furthermore, this result does not totally exclude some possible direct effects of light availability or ontogeny on trait variations since they surely both impose a degree of variation in traits (i.e. some plasticity) at any given individual size. Indeed, Kawamura and Takeda (2003) already reported the control of light and ontogeny on phyllotaxic and architectural traits in addition to the size dependence of numerous crown dimensional traits. Finally, such a convergence in species traits along a size gradient was mostly established for large-scale tree traits such as *LAR*, *LIE* (i.e. *STAR_{int}*) or *LCC*. This result thus underscores the necessity to take individual size into account when comparing contrasting species development and functional ecology.

5.2.5.3. Light interception and seedling functional ecology

Parallel conclusions describing little or no species differences in light interception abilities under similar environment (Poorter and Werger, 1999, Valladares et al. 2002) or

at equivalent size (this study) are not ruling out the supposed importance of LIE in species functional ecology or shade tolerance. Indeed, small differences between species in instantaneous or daily light capture may add up to involve rather large differences in final carbon gain over the whole growing season. In addition, differences in light use efficiency (LUE) are common between woody species (e.g. Kitajima 1994, Lei and Lechowicz 1997, Dreyer *et al.* 2001, Whitehead and Gower 2001). Thus, a small increase in light capture for species investing in higher photosynthetic capacities (i.e. higher leaf nitrogen concentration and/or higher atmospheric CO₂ conductance), may result in significant gains in carbon uptake and thus to large differences in growth abilities over the whole growing season.

Tree species also usually show contrasting patterns of carbon allocation which may have a critical importance in their light interception efficiency and resulting functional ecology. Species allocating carbon preferentially to growth even in shaded environment may reduce their *LAR* and *LIE* since they are increasing their size and leaf area, whereas species holding lower growth rates under shaded conditions might increase their survival by maintaining a more efficient leaf display with a low carbon cost. These specific differences may partially help explaining the better shade tolerance of *A. saccharum* compared to *B. alleghaniensis* in forest understorey. Indeed, small seedling of *B. alleghaniensis* showed at least equivalent LIE and LCC as *A. saccharum* (Figure 8, Table 4) since helical phyllotaxy is surely more efficient to avoid self-shading than the opposite decussate phyllotaxy of *A. saccharum* (Valladares *et al.* 2002, Gálvez and Pearcy 2003). However, during its development, *B. alleghaniensis* rapidly allocates biomass to height and lateral growth of crown even in shaded environments (Delagrange *et al.* 2004, this study) which is likely to dramatically increase carbon costs and self-shading. In contrast, the ability of *A. saccharum* to control apical and especially lateral meristem development when suppressed (Sipe and Bazzaz 1994, Goulet *et al.* 2000, Delagrange *et al.* 2004) allows this species to stay small and maintain higher *LAR* with relatively efficient interception at low construction and support costs owing to long petioles and higher leaf re-orientation (Ackerly and Bazzaz 1995a, Niinemets and Fleck 2002, this study). So the relatively better tolerance of *A. saccharum* over *B. alleghaniensis* does not stem from a better light interception efficiency for a similar size, but rather its ability to stay smaller in shade.

Finally, another essential factor associated with light interception abilities and possibly linked to species functional ecology is the potential partitioning between direct and diffuse light capture among species. Although this study did not reveal significant differences between both species in their daily light capture under the artificial shading nets using realistic simulated sunny or overcast conditions, it pointed out to the generally better diffuse light interception capability of *A. saccharum* owing to a better leaf orientation than *B. alleghaniensis*. In addition, several studies already reported the ability of some tree species seedlings to preferentially intercept direct (Muraoka *et al.* 2003) or diffuse light (Ackerly and Bazzaz 1995b, Valladares *et al.* 2002). However to estimate the advantage of enhancing diffuse light compared to direct light interception (or the reverse) and conclude on its impact on the survival of those species in forest understorey, more research is needed to (i) develop long term light capture modelling using realistic and highly variable cloudy/sunny conditions and (ii) improve our understanding of sun-fleck use (i.e. photosynthetic apparatus activation and de-activation) of *A. saccharum* and *B. alleghaniensis*.

5.2.6. Conclusion

Light interception efficiency was found to significantly decrease when seedlings increase in size because of aging, higher light regimes or interaction of both. However, this relative reduction in light capture, especially in more vertical directions, was also associated with a better interception in other lines of sight due to higher leaf re-orientation. Under the particular light environment created by our shading nets (i.e. high proportion of diffuse light), this result, as well as the better estimated *LCC* when light is only composed of diffuse radiation, suggests a multidirectional light interception in older and/or less shaded seedlings to compensate for the decrease in potential direct light interception associated with the increasing self-shading that occurs during seedling development.

In addition, in agreement with several other studies (Poorter and Werger, 1999, Valladares et al. 2002, Muraoka et al 2003), results showed little differences in *A. saccharum* and *B. alleghaniensis* efficiencies of light interception when comparing seedlings in similar light environments or equivalent ages. However, depending on species light use efficiency, and since these little differences were likely to be due to differences in individual size, other factors such as contrasting carbon allocation patterns (e.g. allocation to growth versus reserve storage) or contrasting leaf dynamic are expected to play a key role in species survival under low light environment.

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*"Les hommes ? Il en existe, je crois, six ou sept.
Je les ai aperçus il y des années. Mais on ne sait
jamais où les trouver. Le vent les promène. Ils
manquent de racines, ça les gêne beaucoup."*

*Antoine de Saint-Exupéry,
Le Petit Prince, 1946*

"Plant roots: The hidden half."

*Waisel Y. and Eshel A.
1991*

5.3. Chapitre 3: *In vivo* and *in situ* below-ground respiration in *Acer saccharum* and *Betula alleghaniensis* seedlings grown under contrasting light regimes.

5.3.1. Abstract

A 'perfusive' method was used to assess below-ground respiration of potted *Acer saccharum* (sugar maple) and *Betula alleghaniensis* (yellow birch) seedlings. Set to contain 8L pots filled with coarse sand, the open system chamber allowed *in vivo* and *in situ* long term (several days or weeks) monitoring of autotrophic rhizosphere respiration[ED1]. We compared root respiration of both species for individuals grown under three contrasted light regimes (40, 18 and 8% of full sun light). Q_{10} (calculated in a temperature range from 15 to 21°C) was constant among the three light regimes. Mean Q_{10} , estimated at 3 and 3.4 for *A. saccharum* and *B. alleghaniensis* respectively, were used to normalise respiration measurements at 15°C. Contrasting light regimes did not affect rhizosphere respiration except under the 8% light regime for *A. saccharum*. However, under this light regimes seedlings were smaller and showed higher fine roots proportion in total roots. Indeed, specific rhizosphere respiration of both species was closely associated to fine roots fraction. Consequently, variations in rhizosphere respiration may be directly related to variations in fine roots fraction that vary with environmental conditions. This suggests that trees modify their below-ground uptake capacity through adjustments in fine root biomass allocation and possibly fine root architecture plasticity rather than fine roots activity modifications on a mass basis. Both species showed similar response of specific rhizosphere respiration with light regime variations, however the very low growth of *B. alleghaniensis* on the poor neutral substrate needed for the below-ground respiration measurements possibly reduced its rhizosphere respiration compared to *A. saccharum*.

Key Words: Fine roots, Nursery, Open gas chamber, Q_{10} , Shading nets, Sugar maple, Temperature, Yellow birch.

5.3.2. Introduction

It seems critical when studying or modelling tree growth or productivity to describe respiration as adequately as photosynthesis (Amthor, 1984). Indeed, several studies indicate that over a one year period, whole plant respiration may consume over 50% of the carbon assimilated by leaf photosynthesis (Mogensen, 1977; Waring *et al.*, 1998). Theoretical models of plant respiration (*cf.* McCree, 1970; Thornley, 1970) separated this total respiration in growth (i.e. new tissue production; R_g) and maintenance (i.e. tissue repair and functioning; R_m) components. Recently reviewed by Amthor (2000) and Thornley and Cannell (2000), this model, if simple, remains flexible and fits well with reality in many predictive situations.

At individual tree scale, roots represent a large fraction of total tree biomass and correspond to a very active tree compartment due to their growth, storage function and below-ground resources uptake activity (Amthor, 1986; Larcher, 1995). Roots are consequently thought to be one of the major sinks of carbon in trees mainly because of a permanent respiratory carbon cost but also because of fine roots turnover, root exudation and carbon allocation to mycorrhizae. Root respiration may consume between 30 and 60% of the carbohydrates produced annually by the leaves (Ryan *et al.*, 1996; Bouma *et al.*, 1997). In a young Scots pine carbon budget study, 63% of the photosynthetic production was allocated to below-ground organs (Ågren *et al.*, 1980), and in boreal forest stands, $\frac{3}{4}$ of the carbon allocated to roots was estimated to be respired whereas the rest was assumed to be used for growth (Högberg *et al.*, 2001). However, our understanding of root overall activity and its variability with contrasting environmental conditions is just beginning. Even if the importance of tree roots as structural, mechanical, storage and physiological active tissues is more and more recognised in the literature, root processes are still often neglected or oversimplified in models such as carbon based tree growth models (LeRoux *et al.*, 2001). This lack of representation is probably linked to technical difficulties associated with below-ground studies. Indeed, studying roots structure or functioning usually generates large perturbations (i.e. trenching, digging, root excision) which in turn probably induce errors in measurements and a large variability in the available data.

However, several studies that measured soil respiration, agreed on the important seasonal contribution of roots in total soil CO₂ efflux (Epron *et al.*, 1999; 2001; Widen and Majdi, 2001). The higher root contribution during summer compared to winter, was mainly attributed to higher soil temperature in summer and to root growth which is thought to be maximal during this period. Indeed, numerous studies showed the critical dependence of rhizosphere respiration rates on soil temperature (e.g. Burton *et al.*, 1998; Atkin *et al.*, 2000; Pregitzer *et al.*, 1998). However, several concurrent factors have also been found to act on rhizosphere respiration, such as soil humidity, root volume, soil depth and nitrogen concentration in roots (e.g. Zogg *et al.*, 1996; Bouma *et al.*, 1997; Davidson *et al.*, 1998; Pregitzer *et al.*, 1998; Burton *et al.*, 2002). Increasing soil CO₂ concentration was suspected to reduce (Qi *et al.*, 1994) or to have no real impact on root respiration rates (Bouma *et al.*, 1997; Burton and Pregitzer, 2002).

In order to correctly compare rhizosphere respiration in response to changes of any factor (such as light regimes or species) without the confounding effect of temperature, a temperature correction using Q_{10} (coefficient by which reaction rate is multiplied when temperature rise of 10°C) is essential. Often supposed to be constant and very close to the theoretical value of 2, Q_{10} is widely used to explain or model temperature dependence of biological processes such as root decomposition, nitrogen mineralisation or tissues respiration (Kirschbaum, 1995; Chen *et al.*, 2000). However, there is a large variability of

rhizosphere or root respiration Q_{10} values in literature (e.g. Kirschbaum, 1995; Davidson *et al.*, 1998; Buchmann, 2000; DesRochers *et al.*, 2002) which still requires to be clarified.

Therefore, to improve our understanding of root respiration variations with contrasting environmental conditions, we proposed in this study:

- (1) to calculate the species specific temperature dependence coefficient Q_{10} for rhizosphere respiration of *Acer saccharum* and *Betula alleghaniensis* seedlings and discuss the variation in Q_{10} coefficient and precautions that have to be taken when measuring or using such parameter,
- (2) to detect potential differences in rhizosphere respiration between seedlings of both species grown under contrasting light regimes.

5.3.3. Material and methods

5.3.3.1. Plant material and growth conditions

Acer saccharum, Marsh. (sugar maple) and *Betula alleghaniensis*, Britton (yellow birch) are two co-existing species in eastern North-American temperate deciduous forest. *A. saccharum* is considered as a very shade tolerant tree species whereas *B. alleghaniensis* is rather known as an intermediate shade tolerant species (Baker, 1949; Forcier, 1975). For both species, seeds were provided by the Natural Resources Ministry of Quebec from the Duchesnay forest station (46°55' N, 71°40' W). During spring 2002, they were germinated in a green house at Champenoux (48°44' N, 6°14' E) near Nancy, France, using a cold storage pre-treatment for *A. saccharum* and adding a liquid fertiliser for *B. alleghaniensis*. Germinated seeds of each species were then planted into 8L pots filled with coarse sand. Substrate was topped by a layer of expanded clay balls in order to reduce direct sand evaporation. The use of coarse sand aimed at limiting heterotrophic respiration and at enabling adequate air circulation through the substrate. Seedlings were fertilised twice during the growing season (beginning of May and beginning of August) with 40 g (4 g.l⁻¹ of soil mixture) of a slow release fertiliser Nutricote 100 13/13/13 N/P/K also containing oligo-elements, buried in the substrate. Water was provided twice a day using a capillary previously buried deep in the pot to avoid algae development on the substrate surface. A total of sixty pots per species were then placed in a nursery under 3 contrasting light regimes (40, 18 and 8% of full sun light) in order to obtain 5 individuals per species under each light regime. Shading treatments were achieved by neutral aluminised nets that decreased light quantity without any modification of the spectral composition.

5.3.3.2. Below-ground respiration measurements

Based on a 'perfusive' method (Bouma *et al.*, 1997), the system used for below-ground CO₂ flux measurements has been developed at INRA Nancy by F. Huc, P. Gross, T. Barigah, JM. Gioria, D. Epron and E. Dreyer. In each pot, a perforated plastic tube was placed deep into the substrate before seedling establishment to allow air injection during measurements (Figure 5.17). To monitor rhizosphere respiration, 8 litre pots were placed in a closed and air-tight PVC chamber that only enclose the below-ground parts. Airtightness was obtained using malleable Terostat mastic (Teroson, Glastech Oy, Vaasa, Finland) at tubes and stem insertion and all around chamber cover. Outdoor air was pumped and driven over scrubs that removed CO₂ and reduced H₂O from the air. A controlled quantity of CO₂ was then injected into the CO₂ free air to reach a known and

stable concentration of 320ppm before injecting it into the reference cell of a differential CO₂ gas analyser (Infra-Red Gas Analyser, Analytical Development Company Limited, Hoddesdon, UK), and then deep inside the pot through the perforated tube (Figure 5.17). Such a CO₂ concentration is lower to what is expected in forest soils (Larcher, 1995; Widén and Majdi, 2001). However, recent findings showed that variation in CO₂ concentration did not affect root respiration in nine tree species including *A. saccharum* (Burton and Pregitzer, 2002). Air flow was set at 1L.min⁻¹ to obtain the replacement of air present in soil macro-pores and around the root system in less than 10 minutes. At chamber outlet, air was funnelled over another H₂O scrub that removed excess H₂O gained by the air during its course through the humid substrate. Finally, air flew into the sample cell of the differential CO₂ gas analyser to record outlet CO₂ concentration. The quantity of CO₂ produced by rhizosphere respiration was then calculated using equation 1:

$$R = F ([CO_2]_{out} - [CO_2]_{in}) \quad 1$$

R was the respiration, F the air-flow and [CO₂]_{in} and [CO₂]_{out} were the chamber incoming and out-coming air CO₂ concentration measured by the gas analyser. To reduce the time of measurements, 10 chambers (3 in each treatment plus 1 empty standard) were placed in parallel and recorded one after another during 60 minutes cycles. For each chamber, the 6 minutes period of measurement was divided into 3 minutes of gas replacement and system stabilisation followed by 3 periods of 1 minute during which CO₂ concentration and soil temperature (using a Copper/Constantine thermocouple) were averaged and stored in a Campbell 21X micro-logger (Campbell Scientific Inc.). Among several methods, 'perfusing' air through the soil has been described as the most efficient way to estimate root respiration of small potted seedlings (Bouma *et al.*, 1997). This open system also possesses the substantial advantage of a continuous measurement (from several days to several weeks or months) without any air pressure increase or any soil perturbation.

In our study, after 3 days of measurements, each plant was gently removed from the pot to minimise soil perturbation and the empty pot was replaced for 3 other days in the chamber to get the possible respiration of the substrate (R_{Substrate}) which was always very close to zero. Rhizosphere respiration (R_{Rhizosphere}) was thus calculated by subtracting R_{Substrate} from respiration measured before seedling harvest (R_{Rhizosphere + Substrate}). The use of coarse sand, confined environment and the removal of pot respiration after seedling harvest, allowed the measurement of a rhizosphere respiration obviously very close to autotrophic respiration.

For both species (n=13 for *A. saccharum* and n=6 for *B. alleghaniensis*), respiration measurements were performed during three consecutive weeks in the middle of the summer (starting at the end of July). As far as possible, at least one individual of each species was represented in each treatment during each week.

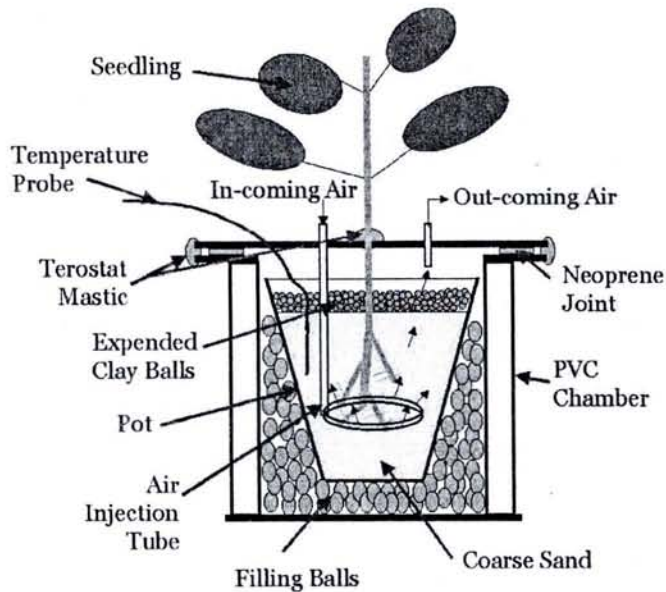


Figure 5.17. Scheme of the open system chamber used for rhizosphere respiration monitoring with potted seedlings. The air injection is achieved using a 'perfusive' methods that allows continuous measurements without any soil perturbations. The chamber is set to contain 8 litres pots.

5.3.3.3. Temperature correction of rhizosphere respiration

In order to compare the root respiration between species and light regimes, a temperature correction was applied using the temperature dependence coefficient Q_{10} . For both species, Q_{10} was computed using equations 2 and 3:

$$\ln(R_{\text{Rhizosphere}}) = a T_{\text{mes}} + b \quad 2$$

$$Q_{10} = e^{10a} \quad 3$$

where $R_{\text{Rhizosphere}}$ is the specific rhizosphere respiration ($\text{nmol CO}_2 \text{ g}^{-1}$ of total roots s^{-1}) at the corresponding soil temperature T_{mes} .

$R_{\text{Rhizosphere ref}}$ the respiration at the theoretical temperature T_{ref} was computed as:

$$R_{\text{Rhizosphere ref}} = R_{\text{Rhizosphere}} / Q_{10}^{(T_{\text{mes}} - T_{\text{ref}}/10)} \quad 4$$

In this study, T_{ref} was fixed at 15°C since this value was in the range of temperatures (min 15°C (± 1.5) and max 21°C (± 1.4)) we encountered during measurements and because it is within the range of summer values for a temperate deciduous forest soil (Larcher, 1995). For each individual, to obtain the biomass specific rhizosphere respiration, $R_{\text{Rhizosphere ref}}$ was divided by the dry mass of tissues contained inside the chamber during measurement.

5.3.3.4. Growth and tree morphological measurements

Seedlings were harvested immediately after root respiration measurements. Seedling dominant stem height and total leaf area using a planimeter (Delta T, Hoddesdon, UK)

were recorded. Tree biomass was divided into leaf, branches, stem, coarse root (> 2mm) and fine roots (< 2mm) and dried at 60°C for 48 hours and weighted. Leaf Area Ratio (LAR; $\text{cm}^2 \cdot \text{g}^{-1}$), Root Mass Ratio (RMR) and Fine Root fraction in total root dry mass (FR%) were then calculated.

5.3.3.5. Statistical analyses

All statistical analyses were performed using SYSTAT 8.0 (SPSS, Inc. 1998). As in the factorial design (2 species x 3 light regimes), one class was empty (i.e. *B. alleghaniensis* seedlings all died at the 8% light regime), a 2 factors ANOVA was impossible to complete. Statistical analyses of growth and seedling traits as well as respiration rates were thus realised using a 1 factor ANOVA where species and light regimes were including in the same factor ($df = 4$). Indeed, even if passing from a 2 way to a 1 way ANOVA is known to increase artificially the degree of freedom, we tested this effect by analysing light regimes effect and species effect separately and then species differences within each light regime separately (Data not shown). Results showed exactly the same significant patterns between light and species as in the 1 way analysis for all parameters tested. Thus in order to simplify data presentation we kept the 1 way ANOVA results which are presented in graphics by contrasting letters when differences were significant at $p=0.05$.

5.3.4. Results

5.3.4.1. Seedling growth

For both species, survival and initial growth were very low especially under the lower light regimes. No seedling of the intermediate shade tolerant species *B. alleghaniensis* survived under the 8% light regime. Height and total biomass at harvest time decreased with light availability and *B. alleghaniensis* was significantly smaller than *A. saccharum* under the 18% light regime (Figure 5.18a). In both species, LAR remained rather stable under the highest light regimes but it significantly increased under the lowest light availability (Figure 5.18b). In *A. saccharum*, low light reduced RMR whereas *B. alleghaniensis* showed constantly higher RMR that were significantly different under the 18% light regime (Figure 5.18c). FR% significantly increased under the 8% light regime. No significant differences in FR% could be detected between species under light regimes where both species were represented (Figure 5.18d).

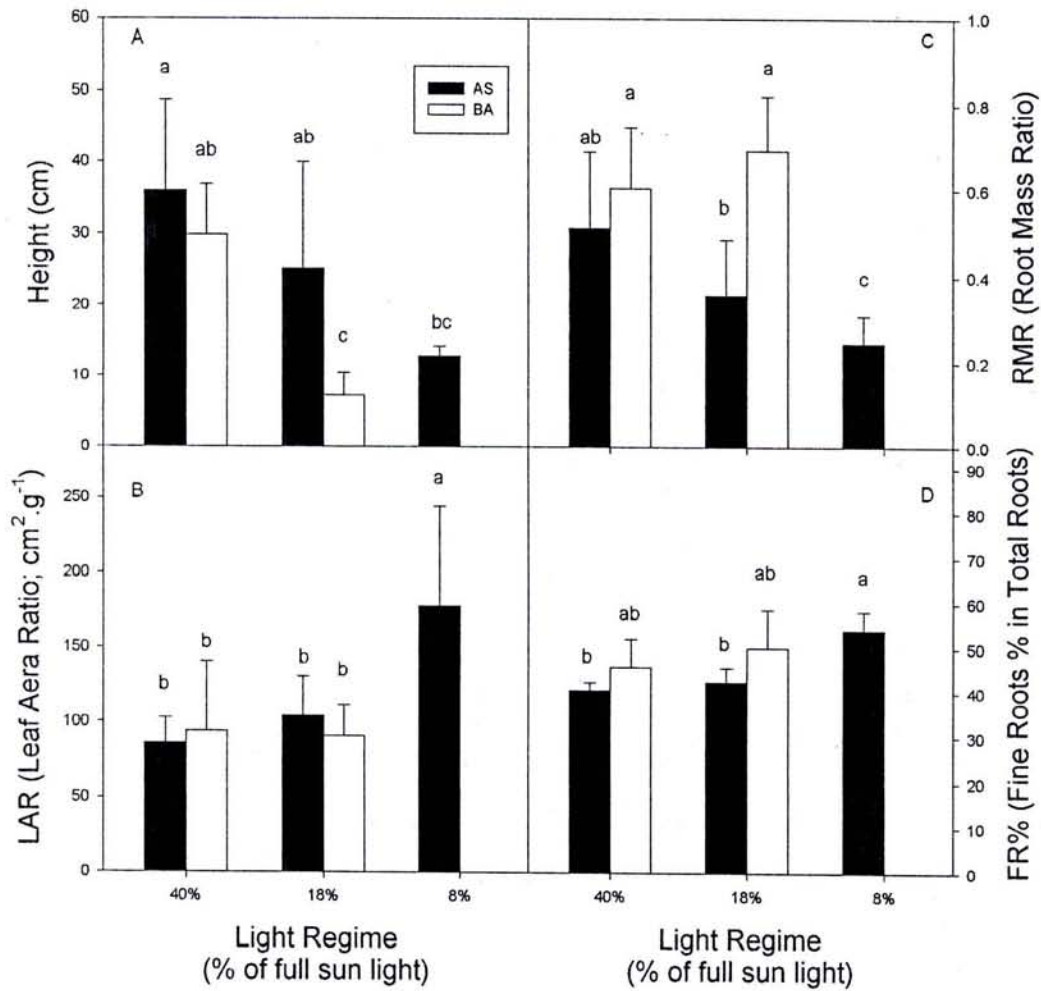


Figure 5.18. Height at harvest time (A), Leaf Area Ratio (B), Root Mass Ratio (C) and Fine Root fraction; FR% (D) in *A. saccharum* (filled bars) and *B. alleghaniensis* (open bars) seedlings grown in nursery under 3 contrasting light regimes (40, 18 and 8% of full sun light). Significant differences ($\alpha=0.05$) are represented by contrasting letters.

5.3.4.2. Temperature response

Q_{10} of rhizosphere respiration was calculated for each individual at temperatures ranging from 15°C (± 1.5) to 21°C (± 1.4). Mean values of Q_{10} under each light regime are presented in Table 5.9 for both species. No significant effect of light was detected as well as no species differences. Mean Q_{10} of *A. saccharum* and *B. alleghaniensis* were thus estimated at 3 and 3.4 respectively, and inter-specific differences were only significant at 10% ($p=0.0731$).

Table 5.9. Mean Q_{10} of *A. saccharum* (AS) and *B. alleghaniensis* (BA) seedlings grown under three contrasting light regimes in a nursery. No value is available for *B. alleghaniensis* under the 8 % light regimes since all seedlings died. Contrasting letters represent statistical differences at $\alpha=5\%$.

Light regimes	Sp	n	Mean Q_{10} (SE)
40%	AS	5	2.99 (0.18)a
	BA	3	3.47 (0.09)a
18%	AS	5	3.06 (0.21)a
	BA	3	3.29 (0.04)a
8%	AS	3	2.98 (0.42)a
	BA	-	- (-)

5.3.4.3. Rhizosphere respiration

Figure 5.19 represents a typical output of 3 consecutive days for substrate temperature, rhizosphere respiration measurements at substrate temperature and calculated rhizosphere respiration normalised at 15°C. For both species, specific rhizosphere respiration normalised at 15°C reached a value close to 7nmol CO₂.g⁻¹.s⁻¹ except under the 8% light regime where *A. saccharum* specific root respiration significantly increased to 11.8nmol CO₂.g⁻¹.s⁻¹ (Figure 5.20). In both species, a strong linear relationship was observed when plotting specific root respiration versus FR% (Figure 5.21). In this figure, due to the low number of repetition, light treatments were pooled to generate the regression line and equation of each species. In both *A. saccharum* and *B. alleghaniensis*, higher FR% induced higher rhizosphere respiration ($p=0.0012$) and along the FR% gradient, the relation was equivalent for both species ($p=0.1604$).

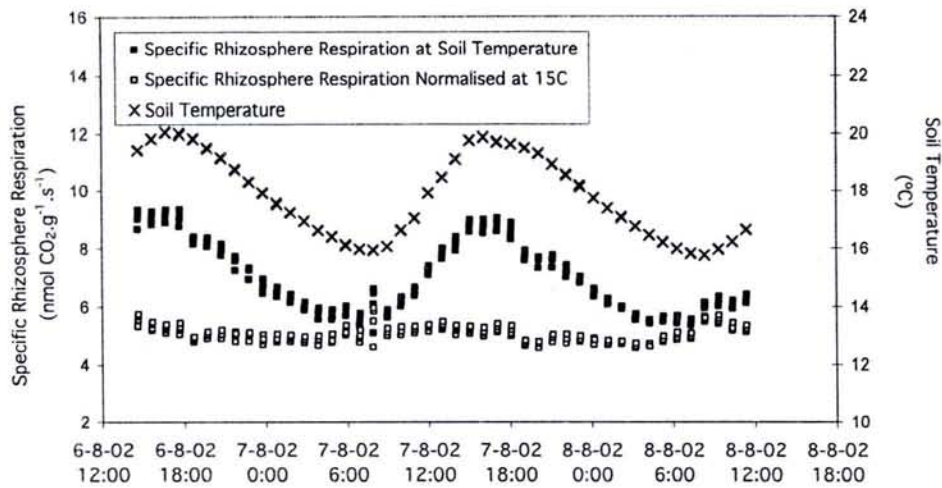


Figure 5.19. Representation of specific rhizosphere respiration at soil temperature (filled squares), specific rhizosphere respiration normalised at 15°C (open squares) and soil temperature (crosses) of a potted *A. saccharum* seedling grown under the 18% light regime in nursery over a 48h period at the beginning of August 2002.

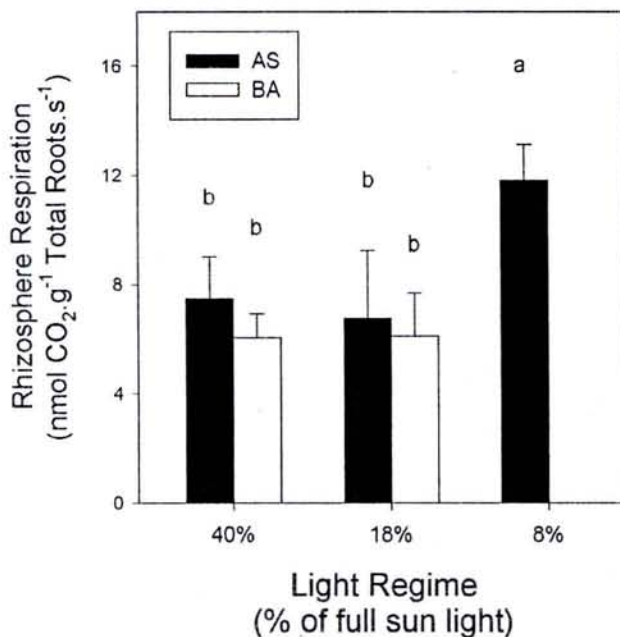


Figure 5.20. Rhizosphere respiration rates per gram of total root dry mass measured *in vivo* and *in situ* in *A. saccharum* (filled bars) and *B. alleghaniensis* (open bars) seedlings under 3 contrasting light regimes. Significant differences ($\alpha=5\%$) are represented by contrasting letters.

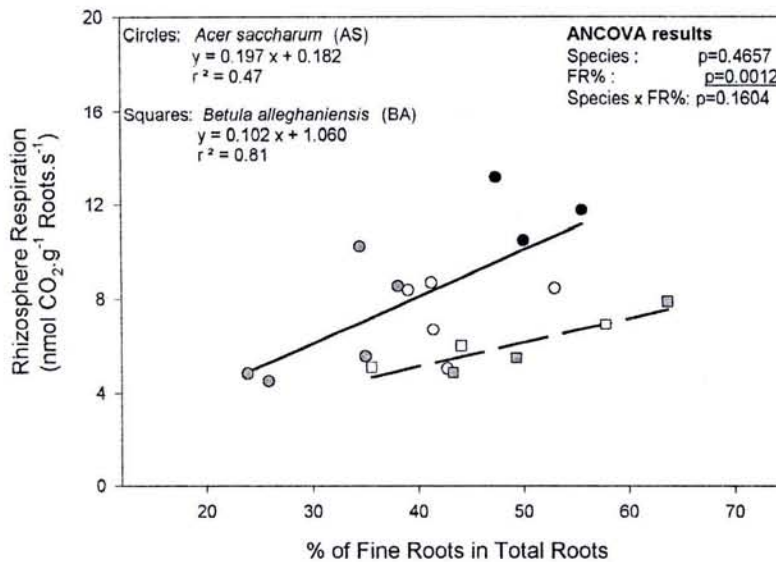


Figure 5.21. Relationship between fine root fraction in total root dry mass (FR%) and specific rhizosphere respiration normalised at 15°C in *A. saccharum* (circles) and *B. alleghaniensis* (squares) potted seedlings. Black, grey and white symbols represent the individuals grown under the 8, 18 and 40% light regime respectively. Plain and dotted lines represent the linear regressions (when light regimes are pooled) for sugar maple and yellow birch respectively.

5.3.5. Discussion

5.3.5.1. Temperature dependence and Q_{10} coefficient

In this study, Q_{10} was computed over a narrow range of temperatures (from 15 to 21°C). The observed stability of Q_{10} with light regime (Table 5.9) tends to support the assumption that temperature response of root respiration is more dependent on species ($p=0.0731$) than the light environment under which they grow. The mean Q_{10} values of 3 and 3.4 calculated for *A. saccharum* and *B. alleghaniensis*, respectively, are in the range of Q_{10} reported in other studies for total root respiration (Table 5.10). Care has to be taken when comparing Q_{10} coefficients coming from contrasting studies since there are no experimental evidence of its often supposed invariability. Q_{10} coefficient has been found to differ among tree species (Burton *et al.*, 2002) and even between organs (Ryan *et al.*, 1996). Root respiration Q_{10} may also vary with the period of the year because of contrasting root turnover and root uptake and/or growth activities. Indeed, seasonal variations in the contribution of growth (R_g) and maintenance (R_m) respiration in total root respiration probably imply dissimilar responses to temperature since contrasting biological processes are involved. Finally, root respiration Q_{10} itself is not independent of temperature as it has already been shown for soil respiration, N mineralization and dead roots decomposition Q_{10} coefficients (Kirschbaum, 1995; Winkler *et al.*, 1996; Davidson *et al.*, 1998, Chen *et al.*, 2000). If absolute respiration rates obviously increase with temperatures, the relative increase of the reaction rate is higher at lower temperatures. **Consequently, the range of temperatures for which Q_{10} is calculated and the size of the range are decisive.** A range in low temperatures is likely to generate higher Q_{10} value

whereas lower Q_{10} are expected at higher temperature ranges (see Kirschbaum, 1995; Huc, 2000; DesRochers *et al.*, 2002 and Table 5.10). In addition, larger ranges of temperatures will provide an approximate mean Q_{10} while shorter ranges will allow the calculation of precise Q_{10} but only accurate within this short range of temperatures.

Thus, the theoretical and constant Q_{10} value of 2 sometimes cited in literature for biological processes may not have any real ecological meaning for tree tissue respiration. So, even if the simplified Arrhenius model using Q_{10} coefficient (see equations 1 to 3 in *Material and Methods*) is a simple and satisfying method to describe the temperature dependence of tissue respiration, precautions have to be taken particularly in the range of temperature chosen to measure and apply Q_{10} coefficient. Indeed, little variations in Q_{10} has already been seen to induce large differences in final results of some respiration modelling exercises (Atkin *et al.*, 2000).

Table 5.10. Summary of a literature review of the temperature dependence coefficients (Q_{10}) of soils respiration and/or rhizosphere or root respiration in contrasting tree species. The table includes: author(s) of the study, Q_{10} , range of temperature within Q_{10} was calculated and species or soil types for which Q_{10} was calculated. References (a non-exhaustive list) were ranked from highest to lower Q_{10} values for soil and then tree species.

Study Reference	Soil (with roots)	Soil (without roots)	Total Roots	Coarse Roots	Fine Roots	Temperature range used for calculation	Species	
Lessar et al 1994*	4.5					5 – 15°C	Cultivated and forest soils	
Epron et al 2001*	3.9					2 – 18°C	Beech Forest (<i>Fagus sylvatica</i>)	
Davidson et al 1998*	3.4 – 5.6					1 – 20°C	Mixed temperate forest	
Boone et al 1998*	3.5	2.5				3 – 22°C	Mixed temperate forest	
Buchmann 2000*	2.39 – 4.11					2.5 – 17°C	<i>Picea abies</i> stands	
Psarras et al 2000*	2.3					-	Aple tree stand (<i>Malus sylvestris</i>)	
Thierron and Laudelout 1996*	2.2					0, 13, 20, 25°C	Oak-Hornbeam forest	
Widén and Majdi 2001* and †	2.1					6 – 15°C	Mixed Norway Spruce and Scot pine Forest	
Winkler et al 1996†	1.7-1.9					4, 15, 22 and 38°C	Mixed temperate forest	
Kirschbaum 1995*	1 – 12.9 review	From 12 contrasting measured terrestrial biomes with and without roots and a literature						
Boone et al 1998*			4.6			3 – 22°C	Mixed temperate forest	
DesRochers et al 2002			3.9			5 and 15°C	Aspen (<i>Populus tremuloides</i>)	
Psarras et al 2000*			3.1			-	Aple tree (<i>Malus sylvestris</i>)	
Burton et al 2002†			2.4 – 3.1			6, 18 and 24°C	9 sp.	
Huc 2000†			2.4			15 – 22°C	Common oak (<i>Quercus robur</i>)	

Table 5.10 continued

Study Reference	Soil (with roots)	Soil (without roots)	Total Roots	Coarse Roots	Fine Roots	Temperature range used for calculation	Species
DesRochers et al 2002			2.19			15 and 25°C	Aspen (<i>Populus tremuloides</i>)
Maier and Kress 2000 [‡]			2*			-	Loblolly pine (<i>Pinus taeda</i>)
Huc 2000 [†]			1.9			19 – 31°C	Common oak (<i>Quercus robur</i>)
Widén and Majdi 2001* and ‡				1.5 [^]	5	9 – 17°C	Mixed Norway Spruce and Scot pine Forest
Gansert 1994*					2.8 – 2.9	1 – 15°C	Beech Forest (<i>Fagus sylvatica</i>)
Burton et al 1998 [‡]					2.1 – 3	6 and 24°C	Sugar maple forest (<i>Acer saccharum</i>)
Epron et Badot 1997 [‡]					2.2	5, 10, 15 and 20°C	European Beech (<i>Fagus sylvatica</i>)
Bouma et al 1997 [†]					2.1	22 – 31°C	Volkamer lemon (<i>Citrus volkameriana</i>)
Ryan et al 1996 [‡]				1.5	2	5 – 25°C	Pine (<i>Pinus radiata</i>)
Zogg et al 1996 [‡]					1.95	6 – 19°C	4 Sugar maple stands (<i>Acer saccharum</i>)

‡ : Measurements made on excised roots.

* : Measurements made *in situ*, in field conditions.

† : Measurements made *in situ*, in controlled conditions.

* : Theoretical value.

^ : Value coming from Ryan *et al.* (1996).

5.3.5.2. Continuous *in situ* and *in vivo* below-ground respiration

Root respiration (i.e. autotrophic respiration) is very difficult to measure and even to estimate. In natural conditions, root respiration measurement is usually associated with respiration of (1) rhizosphere micro-organisms that use exudates, (2) mycorrhizae using plant produced carbon and (3) the heterotrophic respiration (i.e. soil micro-organisms that use soil organic mater). The method we used to measure below-ground respiration tried to prevent this heterotrophic respiration by using coarse sand, semi-controlled environment and the correction for soil with respiration values obtained after seedling harvest. However, as it remains impossible to avoid any microbial or mycorrhizal activity in the rhizosphere, the respiration we measured was labelled rhizosphere respiration rather than root respiration. Nevertheless, when compared to other methods such as root excision, this open system removes the difficulties surrounding the short range of time available for accurate measurement after root harvest. It also possesses the critical advantage to allow continuous measurements for several hours, days or even weeks without any perturbation what may be of a critical importance in long term or seasonal root activity studies.

5.3.5.3. Interspecific differences in rhizosphere respiration

A. saccharum specific rhizosphere respiration (Figure 5.20) was in the lower part of the range from 5 to 16 nmol CO₂.g⁻¹.s⁻¹ reported for excised fine root respiration of this species (Zogg *et al.*, 1996; Burton *et al.*, 1998; Comas *et al.*, 2002; Burton *et al.*, 2002; Burton and Pregitzer, 2002). However, for both species, specific rhizosphere respiration was much lower than the root respiration recorded after whole seedling excavation by Walters and Reich's work (Walters *et al.*, 1993a; 1993b; Reich *et al.*, 1998). On one hand, measuring excised fine roots or excavated seedlings may overestimate root respiration due to heating and stress induced by mechanical injury. On the other hand, we calculated the whole specific rhizosphere respiration which must be lower than fine root respiration measurements because the high mass but low activity (Gansert, 1994; Ryan *et al.*, 1996; Pregitzer *et al.*, 1998) of larger root tissues are taken into account in such calculations. Realistic comparisons with previous studies remain thus difficult to establish when they were performed using dissimilar principle-based measurement methods and contrasting result expressions.

No inter-specific differences were observed between the two species under each light treatment despite the known potentially higher growth of *B. alleghaniensis* compared to *A. saccharum*. Indeed, Comas *et al.* (2002) reported in three tree families that species with slow growth had lower root respiration rates than those with rapid growth supporting the hypothesis that species with rapid growth hold higher root activity in order to respond to higher water and nutrients demands. However, Burton and Pregitzer (2002) already reported superior root respiration of *A. saccharum* compared to more intolerant and fast growing species. In our study, *B. alleghaniensis* showed extremely low growth and high mortality compared to *A. saccharum* under all three light regimes (40, 18 and 8%). This low growth was attributed to the neutral sandy substrate used in this study which appears less appropriate for *B. alleghaniensis* than *A. saccharum*. Punctual comparison between species rhizosphere respiration may also be altered by contrasting root activity during the measurement period (i.e. contrasting phenology). However, correlation between rhizosphere respiration and root nitrogen concentrations or root phenology remain difficult to report for our species since (i) nitrogen concentration were not measured in this study and (ii) more research is needed concerning root seasonal activity of both species.

A. saccharum and *B. alleghaniensis* specific rhizosphere respiration was also correlated to the proportion of fine roots in total root biomass (Figure 5.21). Indeed, fine root nitrogen concentration by unit of dry mass and fine root respiration rates have been shown to largely exceed that of other root tissues in contrasting tree species (Gansert, 1994; Ryan *et al.*, 1996; Pregitzer *et al.*, 1998). This is not surprising when considering the numerous energy-dependant reactions linked with growth, soil exploration, micro-organisms association and active resources uptake that take place in this compartment, whereas larger root tissue activity is, to some extent, limited to storage and passive transports. Thus, when considering this result in a carbon balance point of view, variations in fine root fraction in root biomass or total tree biomass should play a key role in the proportion of carbon released by below-ground respiration.

5.3.5.4. Rhizosphere respiration under contrasting light regimes

In our study, light regimes did not affect rhizosphere respiration of both species, except under the 8% light regime where respiration of *A. saccharum* was higher (Figure 5.20 and 5.21). However, it is rather difficult to conclude on a direct effect of low light

regime on rhizosphere respiration since under lower light regimes, seedlings of *A. saccharum* reached smaller size which, in turn, induced a higher proportion of fine roots in root dry mass (Figure 5.18a and 5.18d). Under the 8% light regime, higher respiration of *A. saccharum* may thus be the consequence of smaller size (i.e. higher proportion of fine root in total roots) rather than the result of higher root activity in low light. Those findings are in agreement with Walters *et al.* (1993b)'s results that already reported decreasing root respiration with ontogeny. Thus, with increasing seedling size (because of time or higher light regime), biomass specific root respiration is likely to decrease due to fine roots dilution in total roots dry mass. In addition, Reich *et al.* (1998) showed no apparent differences in seedling root respiration of nine tree species including *B. alleghaniensis* between 5 and 25% of full sunlight. In another experiment, fine root respiration of European beech saplings was found to be slightly higher in an understory compared to a gap environment (Gansert, 1994), however, this observation was not associated with saplings light environment but with a higher mycorrhizal infection of understory saplings compared to gap saplings. Thus, no real experimental evidence exists to corroborate the theoretical assumptions reporting that higher growth rates (expected in higher light regimes) require a higher water and nutrient demand which in turn, require higher active uptake by fine roots (Chapin, 1980; Amthor, 1986). To support higher nutrient demands under higher light regimes, tree seedlings probably increase their uptake capacity by producing higher quantity of roots during root growth periods instead of increasing their activity per mass unit. Trees may also increase their uptake capacity through root architecture plasticity that has been shown to exist with contrasting soil types (Bauhus and Messier, 1999).

5.3.6. Conclusion

Contrasting light regimes had no effect on *A. saccharum* and *B. alleghaniensis* Q_{10} coefficient and had no clear and direct influence on both species rhizosphere respiration. No statistical differences in rhizosphere respiration were observed between the two species but *B. alleghaniensis* showed very low growth on the neutral sandy substrate which probably affected its below-ground activity. Ours results also highlighted the substantial relationship between fine roots fraction in total root dry mass and rhizosphere respiration. Consequently, factors influencing the proportion of fine roots in tree dry mass will be of a critical importance in the proportion of CO_2 released by below-ground parts, which have been seen to represent a large part of crown carbon gains (Ryan *et al.*, 1996; Bouma *et al.*, 1997).

The open system chamber used in this study allowed accurate *in vivo* and *in situ* measurements of seedling below-ground respiration. Nutrient and water supply might need to be improved in order to get better growth, especially for such species as *B. alleghaniensis*. Such continuous and non-destructive measurement system also opens numerous possibilities in understanding linkages between root activity and seasonal above- and/or below-ground phenology.

5.3.7. References

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"Il n'existe pas de petite économie."

Proverbe français

"Rien ne sert de courir...."

*Jean de la Fontaine
Le lièvre et la tortue*

5.4. Chapitre 4: Biomass partitioning, leaf photosynthetic capacity and whole crown gas exchanges in *Acer saccharum* and *Betula alleghaniensis* juveniles grown under contrasting light regimes.

5.4.1. Abstract

Biomass partitioning, leaf photosynthetic capacity (V_{cmax} , J_{max} , R_d and N_a) and whole crown gas exchanges using a plant bag system of *Acer saccharum* March. (sugar maple) and *Betula alleghaniensis* Britton (yellow birch) seedlings were studied in relation to contrasting light environments (2, 6, 17 and 40% of full sun light) in a nursery at Nancy, France. For both species, light-driven acclimation of leaf functioning resulted in a significant decrease in photosynthetic capacity and leaf respiration as light regime decreased through a decrease in N_a . Results also showed a greater photosynthetic capacity, R_d and steeper $V_{\text{cmax}}-N_a$ and $J_{\text{max}}-N_a$ relationship for the less shade tolerant *B. alleghaniensis* species as compared to the more shade tolerant *A. saccharum* species. As a result, *B. alleghaniensis* had a slightly higher daytime A_{crown} and night time A_{crown} (i.e. above-ground night respiration) on an area basis than did *A. saccharum* ($p = 0.0365$ and $p = 0.0680$, respectively). Higher dry biomass accumulation of *B. alleghaniensis* was related to its slightly higher daily A_{crown} but differences between species in daily A_{crown} were not significant at $\alpha = 5\%$. However, dry biomass partitioning clearly differed between both species, especially under lower light regimes. Under low light regimes, *B. alleghaniensis* allocated more biomass to stem and branches which dramatically increased its NPT/PT ratio as compared to *A. saccharum*. Given the approximately equal daily A_{crown} found in both species under this low light regimes, the higher biomass investment of *B. alleghaniensis* in above-ground foraging through perennial tissues construction may represent a disadvantage in its shade tolerance ability since such allocation are competitive with other carbon sink such as reserve storage.

Key words: Allocation, Carbon balance, Functional ecology, Leaf nitrogen, Plant bag, Respiration, Sugar maple, Yellow birch

5.4.2. Introduction

"Positive carbon balance allows trees to grow and survive, negative carbon balance leads them to death".

Based on this dual assumption, estimating individual carbon balance under varying environment should help in the study of species adaptation to their surrounding environment. Indeed, trees develop numerous structural (architectural) and functional (physiological) traits that allow them to capture light and use it to acquire carbon (Givnish, 1988; Walters and Reich, 1998). Under any given environmental conditions, an efficient combination of traits will provide carbon gains superior to carbon losses and excess in carbon (i.e. net primary production) can then be used to produce new tissues and/or store reserves. On the contrary, non-adapted combinations of traits are likely to lead to (i) superior losses as compared to gains, (ii) depletion of reserves, (iii) reduction of seedling vigour in response to stresses and (iv) higher probability of individual mortality (cf. Waring 1987).

At the individual scale, the assessment of tree carbon balance could be achieved by measuring or estimating whole individual CO₂ gas exchange which is indicative of the sum of carbon gained through photosynthesis and carbon release by the respiration of all living tissues (Baldocchi and Amthor 2001, Amthor and Baldocchi 2001). Over the last decades, many researchers have focussed on evaluating variations in leaf photosynthesis (Bazzaz and Carlson 1982, Walcroft et al. 1997, Dreyer et al. 2001, Lovelock and Feller 2003) and plant tissue respiration (Amthor 1986, Ryan 1990, Ryan et al. 1996, Lusk and Reich 2000, Bosc et al. 2003) in response to environmental factors. According to McCree, Thornley and Penning de Vries' paradigm (cf. Amthor 2000, Thornley and Cannell 2000), tissue respiration is governed by the combination of growth (i.e. the production of new tissues) and maintenance (i.e. processes of reparation and function) respiration. In their models, growth respiration is dependent on specific growth rates and thus on the overall carbon gain, whereas maintenance respiration is related to total accumulated biomass. Concurrently, models of leaf photosynthesis (Farquhar et al. 1980, von Caemmerer 2000) associated aspects of leaf function with specific leaf parameters such as carboxylation (V_{cmax} ; maximal rubisco carboxylation rate), bioenergetics (J_{max} ; maximal electron transport rate), light capture (Chl; leaf chlorophyll content) and leaf respiration (R_d ; leaf dark respiration). These parameters are all dependent on structural or functional proteins (enzyme, reactional complex or pigment) which make them highly dependent on leaf nitrogen content (Niinemets 1997, LeRoux et al. 1999a, Hikosaka et al. 2002, Warren et al. 2003). This is of particular importance when modelling photosynthesis at the whole-crown level since nitrogen partitioning within the crown is not homogenous (Ellsworth and Reich 1993, LeRoux et al. 1999b).

However, individual carbon gain is also greatly influenced by morphological and allocational traits. Indeed these traits determine the pattern of biomass partitioning into photosynthetic tissues (PT) and non photosynthetic tissues (NPT) but also the efficiency of PT display for light interception (cf. Givnish 1988, 1995). Patterns of biomass partitioning are dependent on resources availability (Tilman 1988, Gleeson and Tilman 1992, Canham et al 1999, King 2003). However, allocational and morphological traits are also changing during plant development (McCanaughay and Coleman 1999, Sterck and Bongers 2001, Claveau et al. 2002), which can affect species competitive abilities (Messier and Nikinmaa 2000, Delagrange et al. 2004).

Furthermore, differences in the association and interaction of physiological, morphological and allocational tree traits as well as differences in the plasticity of these traits may explain the wide diversity of shade tolerances observed in forest tree species

(Baker 1949, Forcier 1975, Burns and Honkala 1990). Integrated studies (Valladares et al. 2000, Gratani et al. 2003, Coll et al. 2004) are needed to understand such whole-tree levels mechanisms (Vester 2001, Meinzer 2003).

In this study, we assessed the variation of leaf photosynthetic capacity, daily crown carbon assimilation and biomass partitioning in plant compartment in seedlings grown under contrasting light regimes for two temperate deciduous tree species that differ in shade tolerance; *Acer saccharum* March. (sugar maple) which is a shade tolerant species that maintains very low growth rates when suppressed but is capable of relatively high growth when light availability increases (Canham 1988, Godman et al. 1990) and *Betula alleghaniensis* Britton (yellow birch) which is an intermediate shade tolerant species that generally shows good growth rates under all light conditions (Forcier 1975, Erdmann 1990). Whole daily crown gas exchanges were measured using a CO₂ gas analyser linked to a plant-bag system (PIAF, Clermont-Ferrand, France). This allowed the continuous measurement of spatially and temporally integrated gas exchange for seedlings ranging from 20 cm to 200 cm tall.

The main objective of this study was to investigate the relationships of leaf photosynthetic capacity and whole crown gas exchanges with that of the overall growth and biomass partitioning of *A. saccharum* and *B. alleghaniensis*. This was done to better assess the adaptative significance of these traits in differentiating their shade tolerance.

5.4.3. Material and methods

5.4.3.1. Growing conditions

Seeds of both species were provided by the Natural Resources Ministry of Quebec from the Duchesnay forest station (46°55' N, 71°40' W). During early spring, seeds were germinated in a green house at Champenoux (48°44' N, 6°14' E) near Nancy (France), using a pre-treatment in cold room for sugar maple and by adding a liquid fertiliser for yellow birch. Then, 80 germinated seeds of each species were planted into ten litre pots filled with a mixture of peat and sand (1/3, v/v). All pots were placed in a nursery under 4 contrasting light regimes; 40, 17, 6 and 2% of external global radiations. Shading treatments were applied using neutral aluminised nets that decreased light quantity without modification of the spectral composition. Twice a year, seedlings were fertilised (beginning of May and beginning of August) with 40 g (4 g.l⁻¹ of soil mixture) of a slow release fertiliser (Nutricote 100 13/13/13 N/P/K with oligo-elements). All pots were watered to field capacity twice a day using drip irrigation.

5.4.3.2. Leaf gas exchanges and photosynthetic capacity

Leaf gas exchanges were measured during 3 contrasting periods of the second year of acclimation of seedlings; end of June (early summer), end of July (middle summer) and beginning of September (late summer). A total of 61 *Acer saccharum* and 77 *Betula alleghaniensis* fully developed leaves distributed under each of the four light regimes were used to generate A/C_i curves. Measurements were achieved using a Li-Cor 6400 gas exchange chamber (Li-Cor, Nebraska, USA) with leaf temperature set at 25°C, relative humidity kept between 60 and 75% and light was chosen to be saturating (relative to the light regime where leaves were acclimated). A/C_i curves started with a period of photosynthetic apparatus activation (about 30 min with saturating light and ambient CO₂).

Then, CO₂ concentration was increased to 1800 ppm for the first record and then reduced to 50 ppm in 12 steps. At each CO₂ concentration, a 2-minute period was used to reach photosynthesis stabilization which was followed by 3 measurements spaced by 1 minute interval. Each measurement compiled net photosynthesis (A), estimated intercellular CO₂ concentration (C_i), stomatal conductance, leaf temperature and air pressure. At the end of each A/C_i curve, leaf dark respiration (R_d) was assessed by turning off the light in the chamber and injecting ambient CO₂ concentration. Respiration was recorded after at least 5 minutes in order to get leaf temperature and gas exchanges stabilisation. Measured leaves were then collected and their areas recorded (Planimeter, Delta T, Hoddesdon, UK). Leaves were then oven-dried at 60°C for 48h in order to measure their dry biomass. Leaf nitrogen content (N_a) was evaluated using an elemental NCS 2500 analyser (ThermoQuest, Milan, Italia). From each A/C_i curve, V_{cmax} (maximal carboxylation rate) and J_{max} (maximal light driven electron flow) were estimated by fitting the Farquhar et al. (1980) photosynthetic model with the measured data (for more details on the curves fitting see Dreyer et al. 2001).

5.4.3.3. Whole crown gas exchange measurements

Whole crown gas exchange measurements were completed during August 2002 on 16 individuals (2 species, 4 light regimes and 2 repetitions) using plant-bag chambers (PIAF, Clermont-Ferrand, France). Crown net assimilation (A_{crown}) was recorded during 3 consecutive days for each individual by injecting outdoor air into 4 plant-bag chambers simultaneously using a compressor that controlled air flow. For each chamber, differences in CO₂ between incoming and outgoing air were analysed by a differential infra-red gas analyser (IRGA). Every 6 minutes, the air analysis automatically shifted from one bag to another but each first minute was not recorded to allow the complete replacement and stabilisation of the air in the whole system. Every hour, the sequence was interrupted in order to obtain a zero reading (incoming air pass through both cells of the analyser) and a air flow estimation. During the whole measurement periods, a line quantum sensor (LI-191, Li-Cor, Nebraska, USA) and a thermocouple recorded light and temperature closed to the measured seedlings. For each measurement, the plant-bag chamber was adjusted to seedlings shape to minimise dead volumes and improve the sensitivity of the system to CO₂ changes.

5.4.3.4. Growth and tree biomass partitioning measurements

At the end of the second growing season, 33 *A. saccharum* and 42 *B. alleghaniensis* seedlings distributed under each of the 4 light regimes (minimum and maximum repetitions taken under a light regime were 5 and 10, respectively) were harvested to measure biomass partitioning. Main stem length (individual size; cm) was measured and roots (fine: <2mm, coarse: >2mm), stem, branches, petiole and leaves were separated, dried at 65°C for 48h, and weighed. Using these measurements, the percentage of dry mass allocated to each tree compartment and the ratio of non photosynthetic tissues to photosynthetic tissues (NPT/PT) were calculated.

5.4.3.5. Statistical analyses

All data analyses were performed using StatView software version 5 (SAS Institute Inc., Cary, North Carolina, USA). Statistical significance of trait variation in relation to species, light regime, and interaction of both factors if required were achieved using one and two way analyses of variance (ANOVA). Relationships between leaf parameters and leaf nitrogen content as well as the relationship between NPT/PT ratio and individual size were realised using an analysis of covariance (ANCOVA) where light regimes were pooled, species was the factor and N_a or individual size were the cofactor respectively. In the analysis of NTP/PT ratio variation, the model used to achieve normality of the residues and homogeneity of the variance was: $y = a \log(x) + b$. In all analyses, differences were considered statistically significant at $p < 0.05$.

5.4.4. Results

5.4.4.1. Growth and biomass partitioning

For both species, higher light regimes increased seedling size and total dry biomass (Figure 5.22, Table 5.11). Under all light regimes, *B. alleghaniensis* showed greater total dry mass accumulation than *A. saccharum*, but differences were not significant under the 2 and 40% light regimes. *Betula alleghaniensis* also showed larger final size as compared to *A. saccharum* (species differences were not significant under the 2% light regime) except under the 40% light regime where *A. saccharum* was larger (Figure 5.22, Table 5.11). Overall, *A. saccharum* showed higher height growth enhancement with increasing light regimes than *B. alleghaniensis*. Indeed, *A. saccharum* showed almost no growth under the lower light regimes and very good growth under higher light regimes, whereas *B. alleghaniensis* showed good growth under all light regimes and a lower increase in height growth with increasing light regimes (Figure 5.22, Table 5.11).

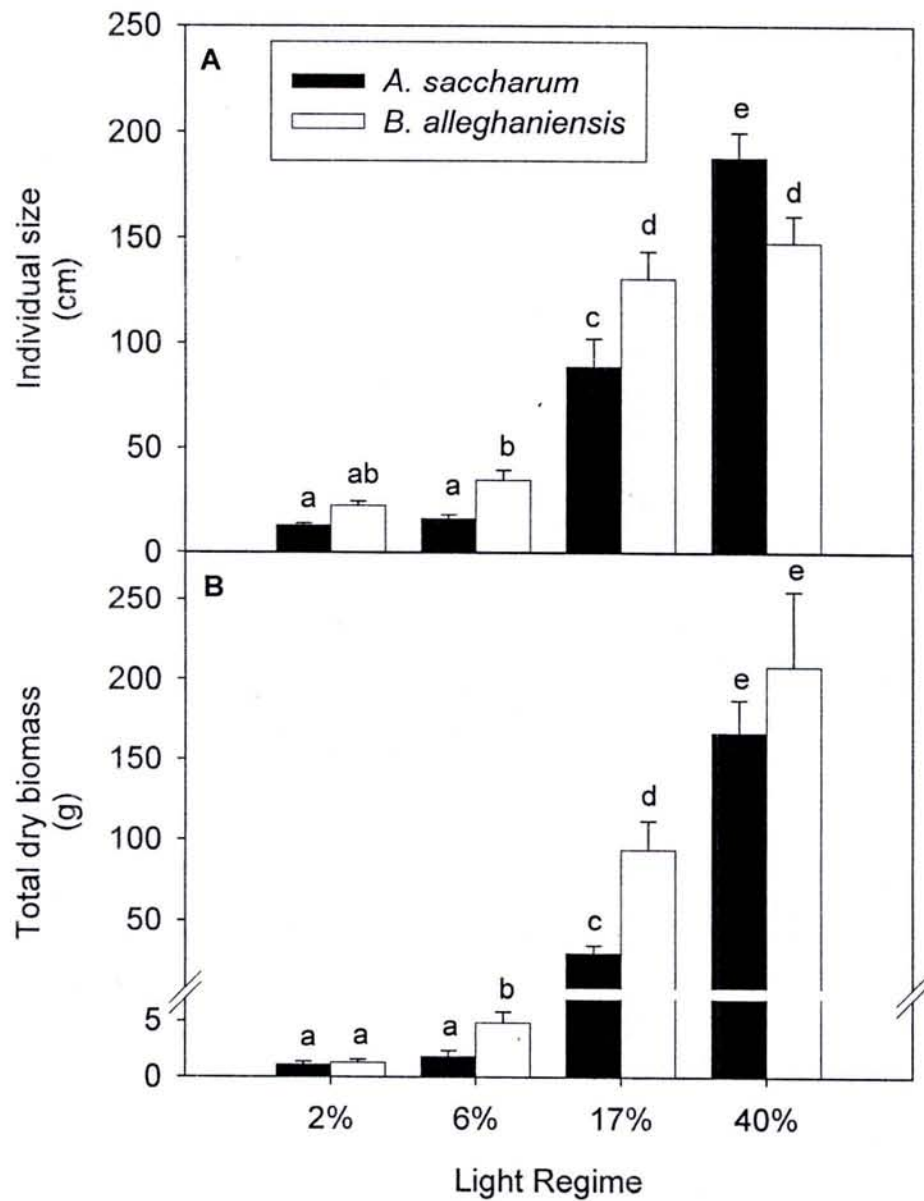


Figure 5.22. Mean values and standard error for (A) individual size and (B) total plant dry mass for *A. saccharum* (filled bars) and *B. alleghaniensis* (open bars) seedlings grown in a nursery at Nancy, France under four contrasting light regimes (40, 17, 6 and 2% of full sun light). Contrasting letters correspond to significant differences at $\alpha = 5\%$.

Both species showed contrasting biomass partitioning (Figure 5.23A and 5.23B, Table 5.11). *Acer saccharum* generally allocated a higher proportion of biomass to its leaves and petiole, especially under lower light regimes whereas *B. alleghaniensis* allocated more biomass to its branches and coarse roots (Figure 5.23A and 5.23B, Table 5.11). However, for both species, the proportion of dry biomass allocated to leaves decreased with increasing light regimes, whereas the proportion of dry biomass allocated to trunk, branches and coarse roots increased (Figure 5.23). This increase in non photosynthetic tissues (NPT) with increasing light regimes (Figure 5.24) was also related to increasing individual size (Figure 5.25). A particularly high NPT/PT ratio was observed for a few small *B. alleghaniensis* individuals grown under the 2 and 6% light regimes (Figure 5.25), which explain the relatively low leaf biomass and high NPT/TP ratio reported for those seedlings in Figure 5.23B and 5.24.

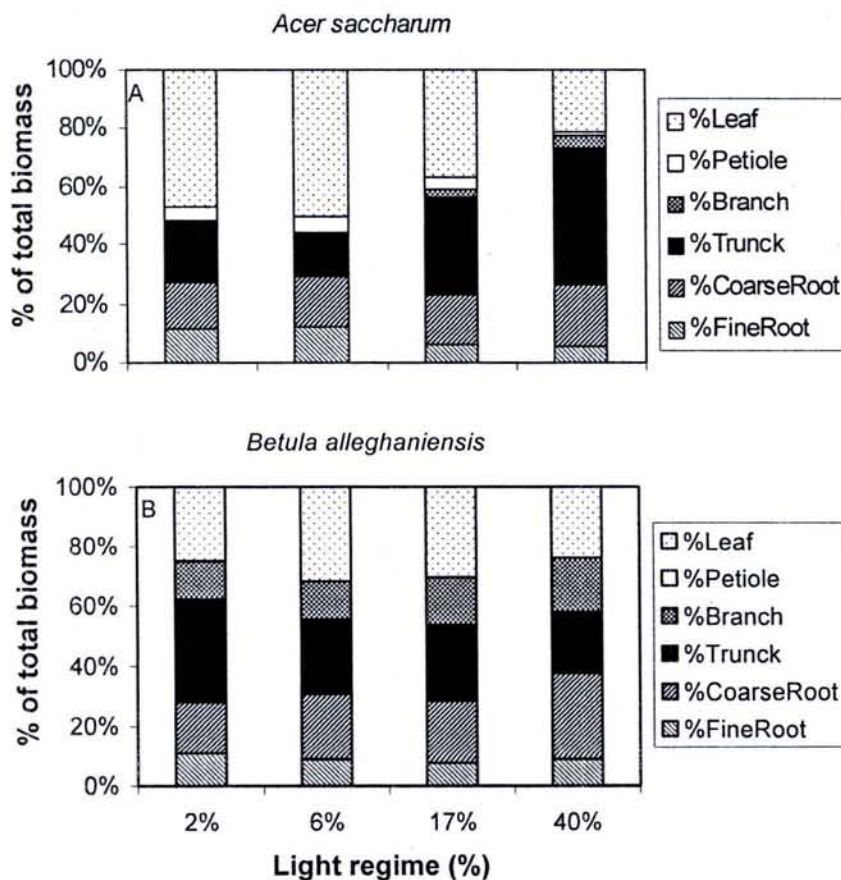


Figure 5.23. Mean values of dry biomass partitioning in contrasting plant compartments. Results are presented as proportion (%) of total plant dry mass allocated to leaves, petioles, branches, stem, coarse roots and fine roots for (A) *A. saccharum* and (B) *B. alleghaniensis* seedlings grown in a nursery at Nancy, France under four contrasting light regimes (40, 17, 6 and 2% of full sun light).

Table 5.11. ANOVA results for Individual size, total tree dry biomass and biomass partitioning in tree compartments parameters (i.e. leaves, petiole, branches, stem, coarse roots and fine roots). F ratios and p values are presented for relations between species (*A. saccharum* and *B. alleghaniensis*), Light Regimes (40, 17, 6 and 2% of full sun light) and their interactions and parameters variation. Values in bold are significant at $\alpha = 5\%$.

	Sp.		Light regime		Sp. x Light Regime	
	F	p	F	p	F	p
Individual size	1.170	0.2834	104.915	<0.0001	6.291	0.0008
Total dry biomass	4.707	0.0336	45.540	<0.0001	1.603	0.1970
% of leaves	21.841	<0.0001	10.316	<0.0001	5.577	0.0506
% of petiole	82.506	<0.0001	2.898	0.0414	2.731	0.0018
% of branches	21.110	<0.0001	0.625	0.6012	0.017	0.9969
% of stem	1.883	0.1745	6.184	0.0009	14.551	<0.0001
% of coarse roots (>2mm)	10.220	0.0021	5.083	0.0031	0.480	0.6972
% of fine roots (<2mm)	0.022	0.8817	1.598	0.1981	0.691	0.5609

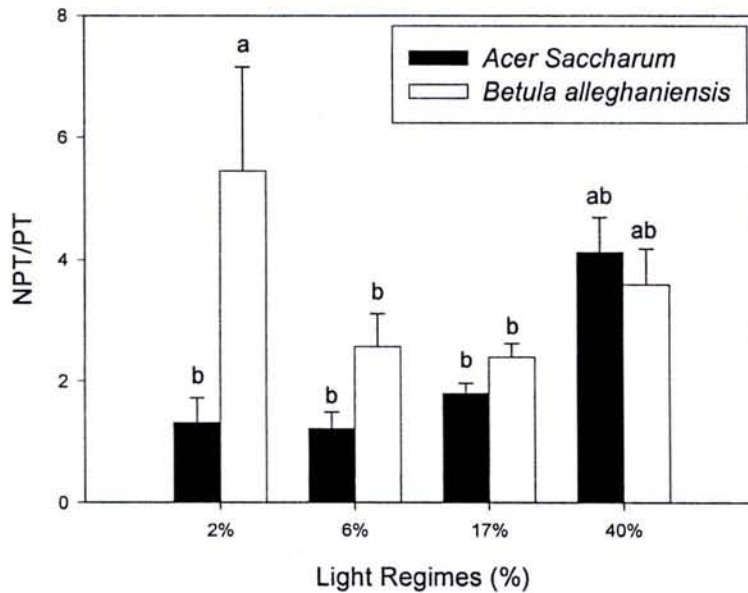


Figure 5.24. Mean values and standard error of NPT/PT ratio for *A. saccharum* (filled bars) and *B. alleghaniensis* (open bars) seedlings grown in a nursery at Nancy, France under four contrasting light regimes (40, 17, 6 and 2% of full sun light). Contrasting letters correspond to significant differences at $\alpha = 5\%$.

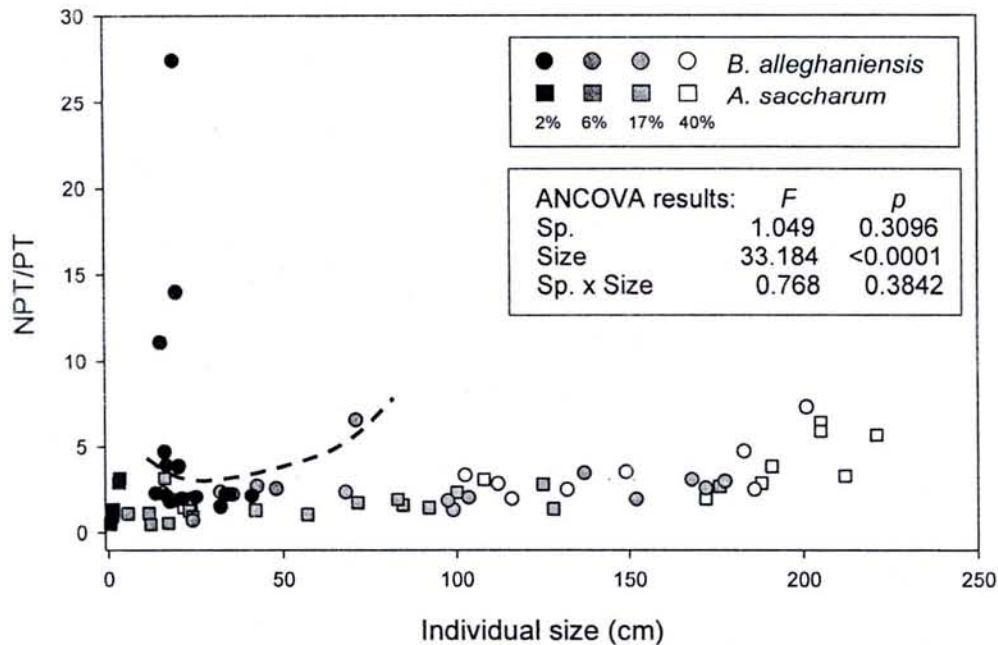


Figure 5.25. Relationship between NPT/PT and individual size (cm) for *A. saccharum* (squares) and *B. alleghaniensis* (circle) seedlings grown in a nursery at Nancy, France. The models used in the ANCOVA were $y = a \log(x) + b$ and the seven *B. alleghaniensis* seedlings separated by the dotted line were removed from the ancova. Individuals coming from contrasting light regimes were pooled together.

5.4.4.2. Photosynthetic capacity

For both species, a significant increase in maximal rubisco carboxylation rate (V_{cmax}), maximal light driven electron flux (J_{max}), leaf dark respiration rate (R_d) and leaf nitrogen content (N_a) was observed with increasing light regimes (Figure 5.26, Table 5.12). However, while both species responded to light regime increase, *B. alleghaniensis* showed higher photosynthetic capacity under all light regimes as compared to *A. saccharum* (Figure 5.26, Table 5.12). Photosynthetic capacity tended to increase from early summer (June) to middle summer (July) and then decrease during late summer (September). However, these variations were only significant in V_{cmax} and J_{max} and were more pronounced for *B. alleghaniensis* as compared to *A. saccharum* and under higher light regimes (Figure 5.26, Table 5.12).

Increases in V_{cmax} , J_{max} and R_d were clearly related to increases in per-area leaf nitrogen content (N_a), and slight differences appeared between species for these relationships (Figure 5.27, Table 5.13). Relationships were slightly steeper for *B. alleghaniensis* than for *A. saccharum* except in the case of R_d as shown by the Sp. x N_a interaction (Table 5.13).

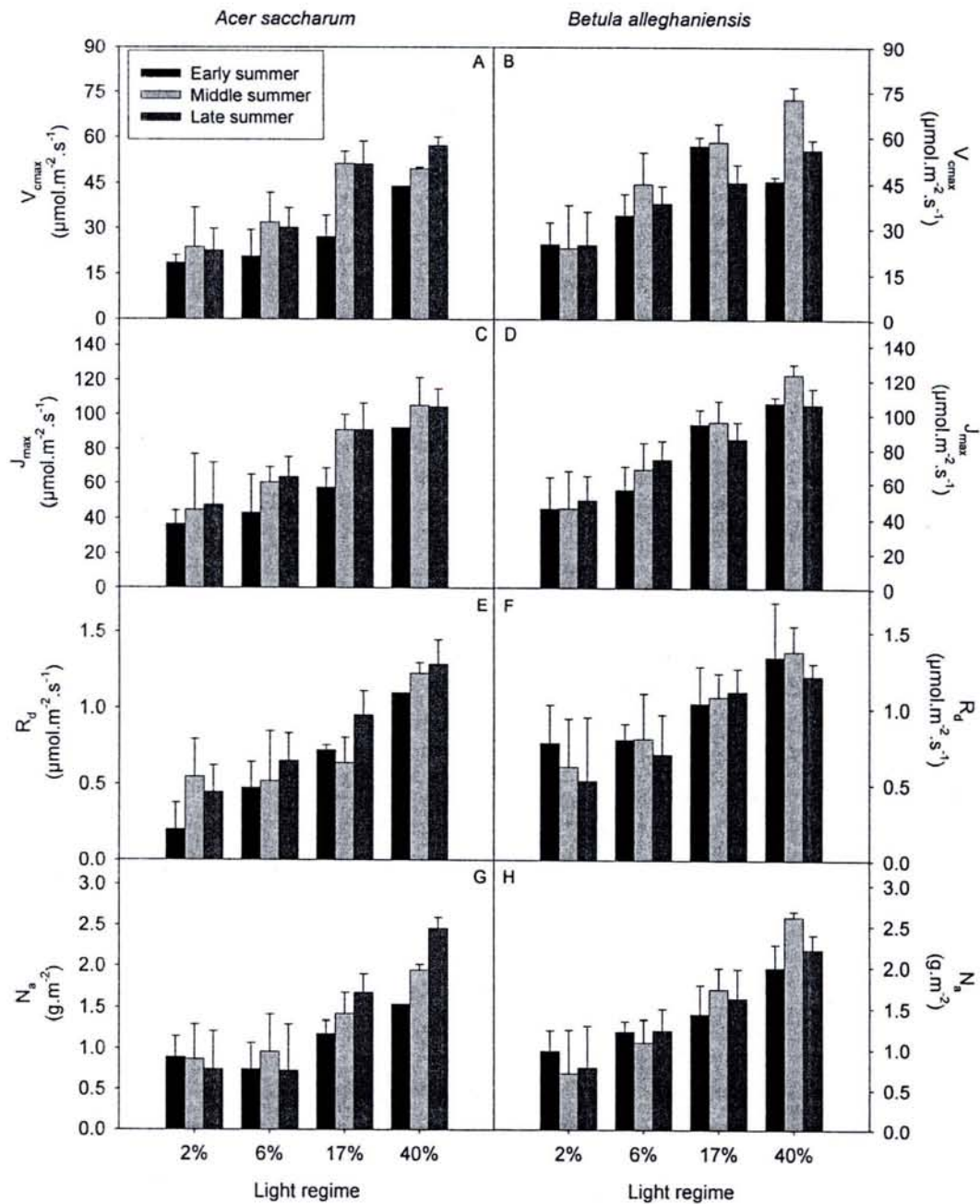


Figure 5.26. Mean values and standard error of maximal rubisco carboxylation (V_{max} ; $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$), maximal electron transport (J_{max} ; $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$), leaf dark respiration (R_{d} ; $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) and leaf nitrogen content (N_{a} ; $\text{g}\cdot\text{m}^{-2}$) for *A. saccharum* (A, C, E and G) and *B. alleghaniensis* (B, D, F and H) seedlings grown under contrasting light Regimes (40, 17, 6 and 2% of full sun light). Results are presented for early (black bars), middle (gray bars) and late (dark gray bars) summer periods.

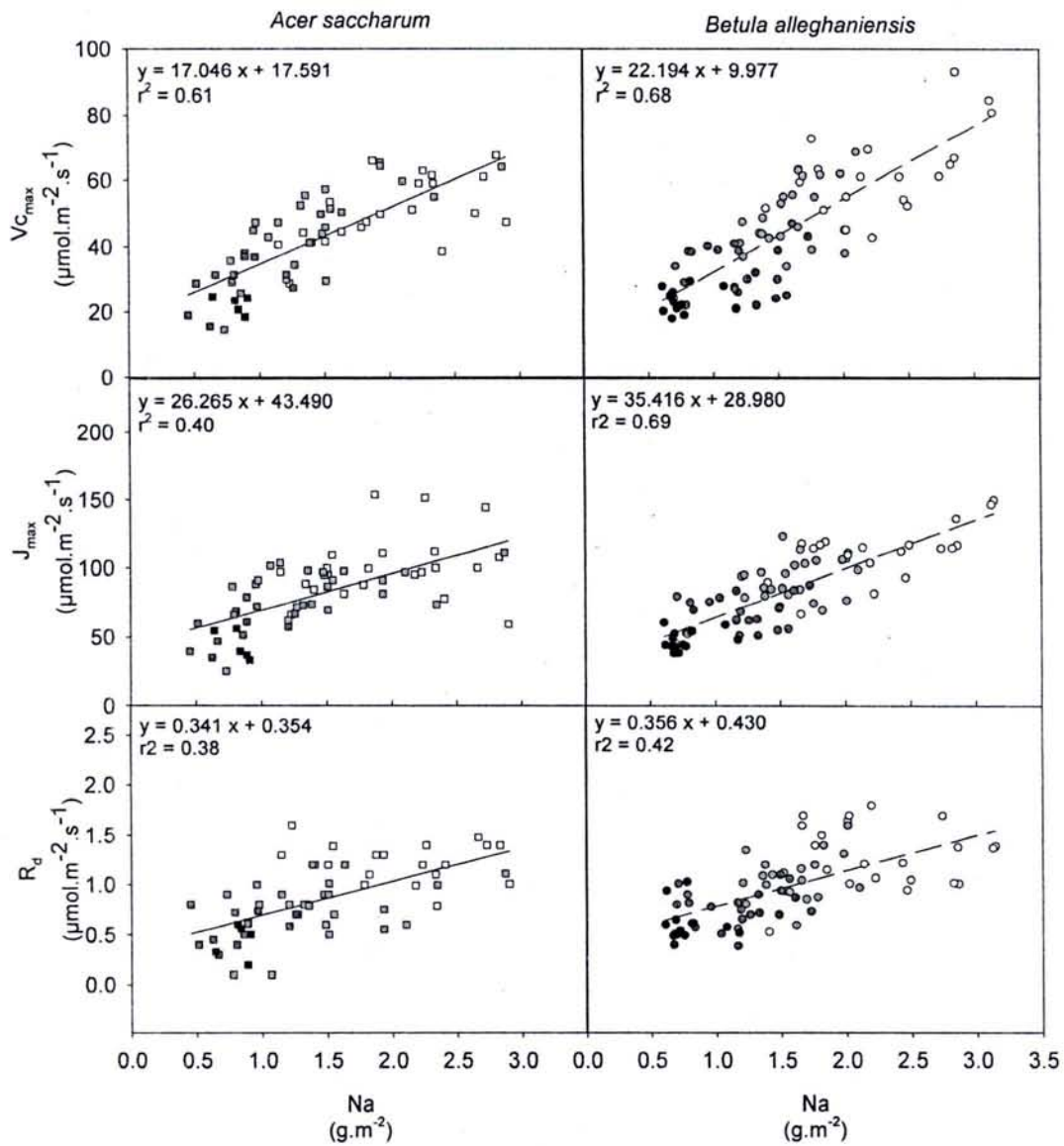


Figure 5.27. Relationship between leaf physiological traits and leaf nitrogen content (N_a ; $g \cdot m^{-2}$) for *A. saccharum* (squares) and *B. alleghaniensis* (circle) seedlings grown in a nursery at Nancy, France. In the analysis, individuals coming from contrasting light regimes were pooled together.

Table 5.12. ANOVA results for leaf physiological parameters. F ratios and p values are presented for relations between maximal rubisco carboxylation (V_{cmax} ; $\mu\text{mol m}^{-2} \text{s}^{-1}$), maximal electron transport (J_{max} ; $\mu\text{mol m}^{-2} \text{s}^{-1}$), leaf dark respiration (R_{d} ; $\mu\text{mol m}^{-2} \text{s}^{-1}$) and leaf nitrogen content (N_{a} ; g.m^{-2}) and species (*A. saccharum* and *B. alleghaniensis*), Light Regimes (40, 17, 6 and 2% of full sun light) and their interactions and parameters variation. Values in bold are significant at $\alpha = 5\%$.

	V_{cmax}		J_{max}		R_{d}		N_{a}	
	F	p	F	p	F	p	F	p
Sp.	13.4	0.0004	8.9	0.0034	20.1	<0.0001	7.2	0.0082
LR	91.7	<0.0001	72.9	<0.0001	51.3	<0.0001	72.4	<0.0001
Season	14.4	<0.0001	5.2	0.0066	0.4	0.6581	2.0	0.1304
Sp. x LR	1.8	0.1419	0.2	0.8884	1.2	0.3121	0.9	0.4030
Sp. x Season	2.9	0.0582	1.8	0.1663	3.3	0.0373	1.0	0.3474
LR x Season	1.5	0.1804	0.7	0.6474	0.7	0.5738	1.7	0.1053
Sp. x LR x Season	3.1	0.0068	1.2	0.3076	0.4	0.8289	1.9	0.0758

Table 5.13. ANCOVA results for variation of maximal rubisco carboxylation (V_{cmax} ; $\mu\text{mol m}^{-2} \text{s}^{-1}$), maximal electron transport (J_{max} ; $\mu\text{mol m}^{-2} \text{s}^{-1}$), leaf dark respiration (R_{d} ; $\mu\text{mol m}^{-2} \text{s}^{-1}$) as a function of leaf nitrogen content (N_{a} ; g.m^{-2}) and species (*A. saccharum* and *B. alleghaniensis*). In this analysis, data from the four light regimes were pooled. Values in bold are significant at $\alpha = 5\%$.

	Sp.		N_{a}		Sp. x N_{a}	
	F	p	F	p	F	p
V_{cmax}	3.463	0.0649	242.923	<0.0001	4.181	0.0428
J_{max}	3.359	0.0690	160.313	<0.0001	3.528	0.0625
R_{d}	0.394	0.5311	88.106	<0.0001	0.043	0.8356

5.4.4.3. Whole crown gas exchanges

Measurement of daily gas exchanges for each light treatment were made one after the other over consecutive 3-days periods and then averaged for these periods. The mean incoming light and mean daily temperature measured during the 3-days periods are also presented (Figure 5.28A) and compared to allow a better interpretation of the observed variations in crown assimilation between light regimes. Mean incoming light and mean daily temperature were not significantly different during each 3-day periods except for

the 40% light regime measurement when the mean daily temperature was higher ($p < 0.01$), and for the 2% light regime measurements where mean incoming light was lower ($p < 0.005$) (Figure 5.28A). Even if *B. alleghaniensis* tended to have slightly greater mean daily A_{crown} per m^2 than *A. saccharum*, no significant differences between species were found. However, mean daily A_{crown} significantly decreased for both species with decreasing light regime, ranging from 132 mmol per m^2 per 24h under the 40% light regime to 66 mmol per m^2 per 24h under the 2% light regime (Figure 5.28B, Table 5.14). When the whole crown mean daily assimilation (A_{crown}) was separated between daylight and night time assimilation, mean A_{crown} during daylight was found to decrease with decreasing light regimes whereas no clear patterns of variation were observed for mean A_{crown} measured during the night time with light regime (Figure 5.29, Table 5.14). In addition, significant differences between species were observed when daily A_{crown} was decomposed into night time and daylight. Under all light regimes, *B. alleghaniensis* showed higher mean A_{crown} during daylight ($p = 0.0365$) and significantly higher mean A_{crown} measured during night time at $\alpha = 10\%$ ($p = 0.0680$) than *A. saccharum* (Figure 5.29, Table 5.14). Finally, the proportion of carbon incorporated during daylight that is then released during night time increased from 24 to 61% from the 40 to 2% light regime for *B. alleghaniensis* whereas it remained approximately the same at around 27% for *A. saccharum* (Figure 5.30). However, differences between species were not significant (Table 5.14).

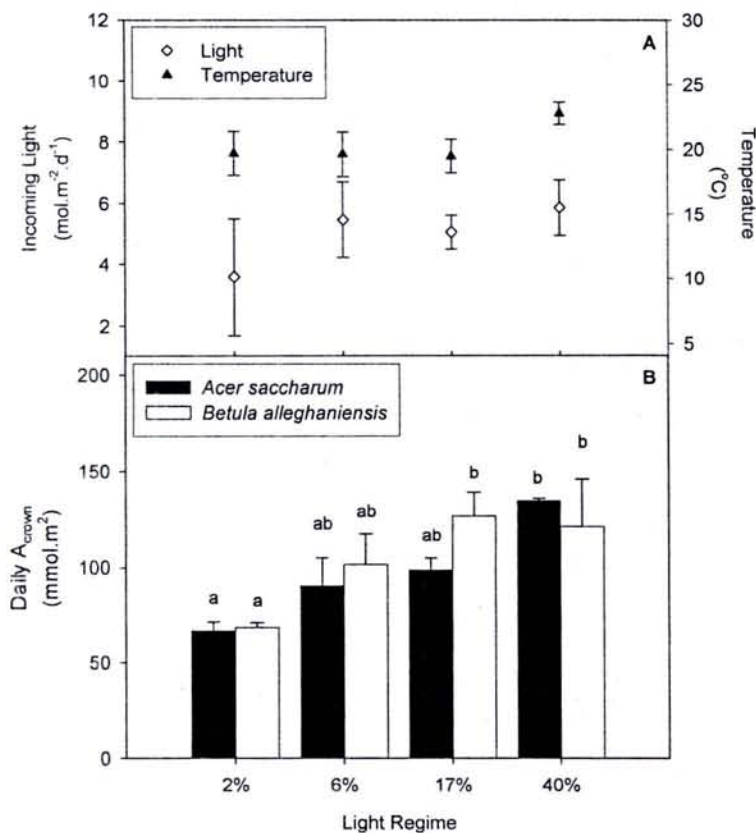


Figure 5.28. Mean values and standard error of A; mean incoming light ($\text{mol m}^{-2} \text{d}^{-1}$, open diamonds) and mean temperature ($^{\circ}\text{C}$, filled triangles) during the three days of crown assimilation measurements and B; mean daily crown assimilation (A_{crown} , mmol m^{-2}) for *A. saccharum* (filled bars) and *B. alleghaniensis* (open bars) seedlings grown in a nursery at Nancy, France under four contrasting light regimes (40, 17, 6 and 2% of full sun light). Contrasting letters correspond to significant differences at $\alpha = 5\%$.

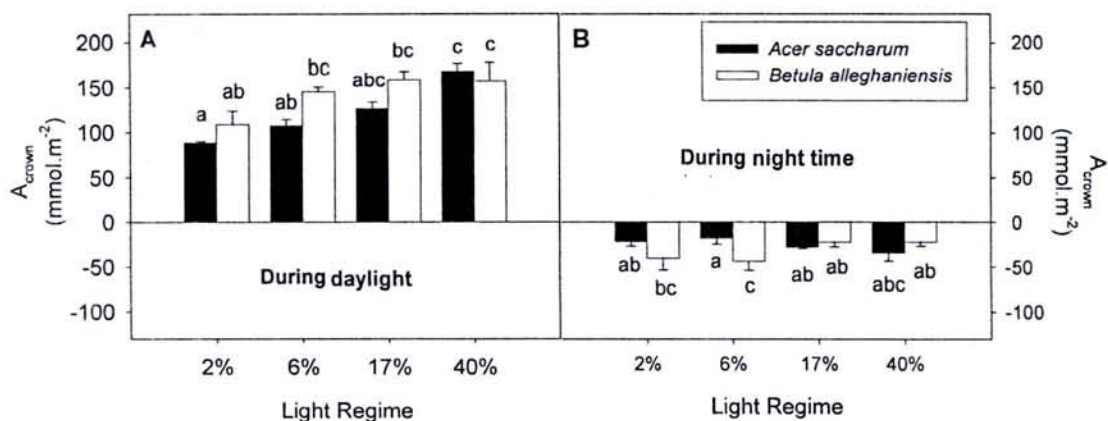


Figure 5.29. Mean values and standard error of A; mean crown assimilation (A_{crown} , mmol m^{-2}) during daylight and B; mean crown assimilation (A_{crown} , mmol m^{-2}) during night time for *A. saccharum* (filled bars) and *B. alleghaniensis* (open bars) seedlings grown in a nursery at Nancy, France under four contrasting light regimes (40, 17, 6 and 2% of full sun light). Contrasting letters correspond to significant differences at $\alpha = 5\%$.

Table 5.14. ANOVA results for above-ground assimilation measurements. F ratios and p values are presented for relations between light-time, night-time and daily crown assimilation (A_{crown}) and species (*A. saccharum* and *B. alleghaniensis*), Light Regimes (40, 17, 6 and 2% of full sun light) and their interactions and parameters variation. Values in bold are significant at $\alpha = 5\%$.

	Sp.		Light regime		Sp. x Light Regime	
	F	p	F	p	F	p
A_{crown} during light time	6.287	0.0365	12.605	0.0021	2.673	0.1184
A_{crown} during night time	4.447	0.0680	0.021	0.9954	2.008	0.1915
Daily A_{crown}	0.625	0.4521	8.431	0.0074	0.975	0.4510
% of CO_2 respired during night	3.088	0.1169	1.831	0.2196	1.304	0.3383

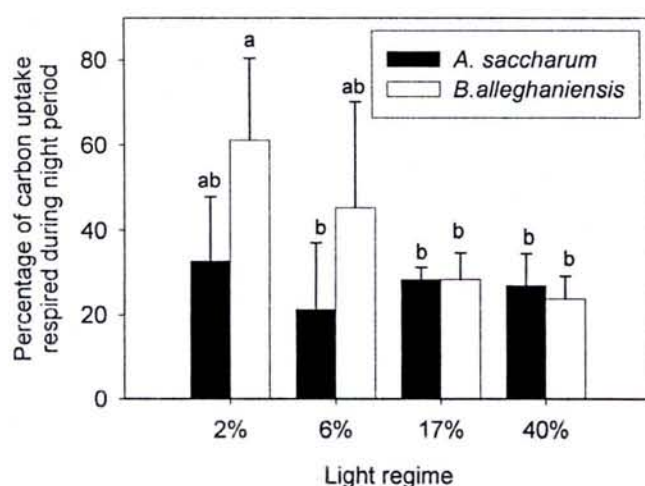


Figure 5.30. Mean values and standard error of the percentage of carbon assimilated during light-time that was respired during night time for *A. saccharum* (filled bars) and *B. alleghaniensis* (open bars) seedlings grown in a nursery at Nancy, France under four contrasting light regimes (40, 17, 6 and 2% of full sun light). Contrasting letters correspond to significant differences at $\alpha = 5\%$.

5.4.5. Discussion

5.4.5.1. Leaf photosynthetic capacity and whole crown gas exchanges

The acclimation potential of leaf photosynthetic capacity to various light environments has already been reported for several hardwood and coniferous species (e.g. Sullivan et al. 1996, Wilson et al. 2000, Robakowski et al. 2003). This light driven variation of V_{cmax} and J_{max} is usually linked to variation in leaf dry mass or nitrogen content (Niinemets 1997, Niinemets and Tenhunen 1997, Walcroft et al. 1997, LeRoux et al. 1999a, Robakowski et al. 2003). In some cases, however, it is also related to the partitioning of nitrogen into different leaf functions (i.e. carboxylation, electron transport and light absorption) (Evans 1989a, Naidu and DeLucia 1998, Frak et al. 2001, LeRoux et al. 2001). Here, the decreases in maximal carboxylation rate (V_{cmax}) and maximal electron flux (J_{max}) with decreasing light regime were similar to the decreases reported by Robakowski et al. (2003) from 100 to 8% of full sun light for *Abies alba*, but values were slightly higher for our two hardwood species under comparable light environment. On the other hand, values of V_{cmax} and J_{max} measured under the 40% light regime were consistent with those reported at 25°C by Dreyer et al. (2001) for seven other European hardwood species under an equivalent light regime. For both species, increasing light regime resulted in higher leaf abilities for carbon uptake as well as higher leaf respiration rates (cf. Niinemets et al. 1998, Reich et al. 1998, Walters and Reich 1999). In addition, it is noteworthy to mention that light acclimation of deciduous leaf respiration is linked not only to a reduction in leaf biomass but also to a reduction of respiration rates on a mass basis (Lusk and Reich 2000).

Comparison between our species leads to an association between higher shade tolerance and lower photosynthetic capacity, lower respiration rate and less steep relationships between V_{cmax} , J_{max} and N_a (cf. also Walters and Reich 1999, Lusk and Reich 2000). Indeed, *B. alleghaniensis* showed higher V_{cmax} and J_{max} values under all light regimes and a greater increase in photosynthetic capacity with increasing N_a than *A. saccharum*. Species differences in photosynthesis-nitrogen relationship have been previously reported (Evans 1989b, Hikosaka et al. 2002) and according to Niinemets (1997) a shift in photosynthetic performance is expected under lower light regimes between tolerant and intolerant species due to the generally lower slope but higher intercept of tolerant species (cf. Figure 5.27). However, no shift was found between *A. saccharum* and *B. alleghaniensis* even under the lowest light regime (2% of full sun light). Our results rather highlighted a convergence in leaf photosynthetic capacity for lower leaf N_a , which in turn implies a convergence of this function under lower light regimes. Such a decrease in species differences under limiting environmental factors, has been already reported in several studies for similar or other leaf and tree functions (Reich et al. 1998, Hikosaka et al. 2002, Meinzer 2003, Valladares et al. 2002, Delagrangé et al. 2004) and is likely to fit with the hypothesis of a limited number of functional solutions under a stressful environment.

On the other hand, *B. alleghaniensis* tended (not significantly) to be more responsive to seasonal changes (i.e. changes dependent on leaf age) in photosynthetic capacity and N_a than *A. saccharum* especially under higher light regimes. This might be due to the possible lower leaf life span and thus lower duration of leaf activity found in more shade intolerant species and/or more sunny leaves (Ackerly and Bazzaz 1995, Atkin et al. 1996, Givnish 1988). However, more research is needed concerning species specific-seasonal pattern of N_a and species specific seasonal variation in nitrogen partitioning in leaf functions to verify these hypotheses. Results of some experiments have shown that

nitrogen partitioning in carboxylation, bioenergetics, light absorption (Wilson et al. 2000, Frak et al. 2001) and N storage (Warren et al. 2003) is likely to change during leaf aging.

The higher leaf photosynthetic capacity of *B. alleghaniensis* as compared to *A. saccharum* suggested a much higher carbon gain for this species, especially under higher light regimes. However, if *B. alleghaniensis* showed higher whole crown carbon gain, differences between species in their A_{crown} during daylight periods were small and became insignificant when integrated over a 24h period (i.e. when crown night respiration was added). This result was attributed to the higher R_d experienced by *B. alleghaniensis* as compared to *A. saccharum* which resulted in higher leaf respiration during the night period. The higher leaf respiration rates of the less shade tolerant species *B. alleghaniensis* were likely related to higher leaf metabolic activity (i.e. higher photosynthetic capacity and N_a) which would induce higher leaf maintenance respiration costs (Niinemets et al. 1998, Walters et Reich 1999). Higher leaf respiration rates in lower shade tolerance species has also been associated with higher respiration activity per leaf dry biomass or leaf N content (Lusk and Reich 2000). However, it should be noted that our daily A_{crown} measurements included the above-ground non photosynthetic tissue (NPT). Even if stem and branch respiration is thought to be much lower than leaf respiration (Ryan et al, 1996), above-ground NPT respiration of *B. alleghaniensis* might have increased its total above-ground respiration. Indeed, the continuous growth and higher allocation to NPT even in lower light regimes of *B. alleghaniensis* likely implies higher growth and maintenance respiration in above-ground parts (Amthor 2000, Thorney and Cannell 2000). In our growing experiments, the above-ground tissue respiration of *B. alleghaniensis* accounted for up to 60% of the carbon assimilated during the daytime under the 2% light regime. In contrast, *A. saccharum* respired an approximately constant percentage of 30% of daytime assimilated carbon under all light regimes which demonstrates the superior ability of this species to save carbon under low light conditions. This result highlights the critical importance of tissue respiration in concurrence to photosynthetic abilities in daily individual gas exchange estimation. It also clearly demonstrates the necessity to take this process into account in tree growth modelling since it could consume a large part of day time assimilated CO_2 .

5.4.5.2. Growth, biomass partitioning and species functional ecology

As for the physiological leaf traits we measured, seedlings of *A. saccharum* and *B. alleghaniensis* showed a large growth and biomass partitioning acclimation to variation in light availability. For both species, biomass accumulation was greatly reduced under the lower light regimes because of lower whole-crown carbon gain. The observed pattern of increasing PT proportion with decreasing light regimes concurs with many previous studies (e.g. Tilman 1988, Gardiner and Hodges 1998, Poorter and Nagel 2000, Lusk 2002, King 2003). However, many recent studies have suggested that this pattern was more linked to changes in individual size associated with different light regimes than with light itself (McConnaughay and Coleman 1999, Claveau et al. 2002, Delagrangé et al. 2004) Thus, the ability to allocate a large proportion of biomass to leaf may be more a question of staying small rather than an ability to modify biomass partitioning in contrasting environments.

With respect to species differences, *B. alleghaniensis* tended after two growing seasons to accumulate more total dry biomass and reach larger final size than *A. saccharum* when compared under equivalent light regimes. If differences in dry biomass accumulation were obviously related to the slightly higher A_{crown} (even if not significant)

of *B. alleghaniensis* under all light regimes, higher final size of *B. alleghaniensis* were associated with its higher allocation to height growth compared to *A. saccharum* (Bellefleur and Larocque 1983a, 1983b, Beaudet and Messier 1998, Ricard et al 2003). *Betula alleghaniensis* also allocated more dry mass to branches and less to petioles than *A. saccharum*. This particularly important allocation to branches was responsible of the lower final size of *B. alleghaniensis* under the 40% light regime, since dry biomass was distributed between stem and branches whereas *A. saccharum* mainly allocated biomass to main stem. Under lower light regimes, *B. alleghaniensis* allocated also higher proportion of dry biomass to stem compared to *A. saccharum*. This, in addition to a greater allocation to height growth in low light environment, might represent a disadvantage in shade. Indeed, given the fact that carbon uptake was not significantly different between both species under the 2 and 6% light regimes, the allocation of assimilated carbon to new branches, leaves and height growth will result in relatively higher respiration costs (in maintenance and growth) and also comparatively lower opportunities of reserve storage. In contrast, *A. saccharum* tends to avoid branch formation (Sipe and Bazzaz 1994, Goulet et al. 2001) as well as height growth (Canham 1985) under low light environment. Assimilated carbon is thus preferentially allocated to the production of new leaves, maintenance of standing biomass and new leaves and possibly to reserve storage (Gougeon 2000). In addition, owing to its smaller size, *A. saccharum* may also keep higher light interception efficiency (LIE) than *B. alleghaniensis* as LIE is known to decrease as seedlings increase in size (Chapter 2, Farque et al. 2001).

5.4.5.3. Future utilizations of plant bag measurements

An increasing demand for daily as well as daytime A_{crown} measurements is occurring for the purposes of growth modelling validation. Predicted individual carbon balance on daily, seasonal or annual time step (e.g. Beaudet et al. 2000, Pertunnen et al 2001, Naumburg et al. 2001, Muraoka et al. 2003) usually have a lack of accurate and relevant validation measurements of total gas exchange, especially under contrasting environmental conditions and for diverse periods of the growing season. Indeed, such integrated measurements of individual assimilation might provide the opportunity to test important aspect of whole individual carbon balance that remains not well known such as the spatially and temporally dynamic distribution of N_a within the crown of an individual (Ellsworth and Reich 1993, Niinemets 1997, Le Roux et al. 1999b, Wilson 2000, Frak et al. 2001) or the contrasting activation and sunfleck use by photosynthetic apparatus (Sipe and Bazzaz, 1994, Valladares et al. 1997, Naumburg and Ellsworth 2000).

5.4.6. Conclusions

Decreasing photosynthetic capacity at lower light regimes caused by lower leaf nitrogen investment greatly decreased daily whole crown carbon uptake of both species. However lower leaf nitrogen content also induced a reduction in leaf respiration rates. This reduction allowed seedlings to maintain the proportion of carbon release by above-ground parts during the night period constant (30%) except in the case of *B. alleghaniensis* under the lowest light regime (2% of full sun light) where this proportion goes up to 60%. Indeed, despite having higher photosynthetic capacity under all light regimes and thus, higher crown carbon gain during daylight, *B. alleghaniensis* did not have significantly higher daily carbon gain than *A. saccharum* because of higher carbon

release by above-ground parts during night (especially under lower light regimes). This was in part imputable to the greater height growth and greater allocation to non photosynthetic tissues (NPT) of *B. alleghaniensis*. Consequently, given equivalent biomass accumulation in lower light regimes, *B. alleghaniensis* accumulated structural (perennial) tissue, whereas *A. saccharum* with no production of new structural tissues surely accumulated reserves. These findings thus underscore (i) no evidence of carbon uptake maximization under low light environments for shade tolerant species and (ii) the importance of allocational patterns of assimilated carbon in addition to other tree traits in species functional ecology.

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6. CONCLUSION GÉNÉRALE

6.1. Une approche novatrice

L'étude du bilan carboné et de la tolérance à l'ombre des semis forestiers représente des domaines de recherche, qui du fait de leur importance, ont fait et font encore l'objet de nombreuses études. Cependant, l'approche généralement morcelée des mécanismes qui les gouvernent dessert la compréhension de leur implication au niveau de la performance des individus (Vester 2001, Meinzer 2003). L'objectif de ce travail résidait donc dans l'adoption d'une approche nouvelle et intégrée considérant à la fois différentes échelles de processus (physiologie, morphologie et allocation) et l'échelle de l'individu. L'intérêt de ce travail consistait également à étudier ces mécanismes en relation avec le tempérament écologique des espèces afin d'essayer d'en éclaircir les mécanismes et cela durant les premiers stades de développement des individus.

De plus, la combinaison d'un site établi en milieu naturel et d'un site offrant des conditions plus contrôlées (pépinière) a rendu possible l'étude précise des composantes du bilan carboné tout en gardant le contact avec la réalité de la régénération naturelle des semis en sous couvert. En effet, l'excavation méticuleuse de semis et de gaulis allant jusqu'à 5 mètres de hauteur en milieu naturel ainsi que l'utilisation d'ombrières appliquées directement en sous couvert (chapitre 5.1) ont permis l'acquisition de données qui n'avaient encore jamais été mesurées chez des individus de cette taille vis-à-vis de leur développement en sous couvert. Parallèlement, l'utilisation en milieu plus contrôlé de la digitalisation en 3 dimensions associée à un modèle d'interception de lumière (chapitre 5.2), ainsi que de techniques novatrices (enceintes de respiration racinaire, sacs d'assimilation de la cime) de mesure des échanges gazeux *in vivo* et *in situ* (chapitres 5.3 et 5.4) ont rendu possible l'étude pointue de l'interception de lumière, de l'assimilation et de la respiration à l'échelle de l'individu. L'intérêt non négligeable de ces techniques résidait dans le fait qu'elles permettaient ces mesures intégrées en évitant le recours aux changements d'échelles ou à la modélisation dont l'utilisation peut être parfois problématique (*cf.* Beaudet et al. 2000, Baldocchi et Amthor 2001).

6.2. Principaux résultats

En milieu naturel (chapitre 5.1), l'étude de semis et gaulis en régénération a permis la mise en évidence de l'importance de la taille, de la disponibilité en lumière et de l'interaction des deux facteurs dans la variation des paramètres internes des individus d'érable à sucre et de bouleau jaune. En effet, la taille était un facteur d'une importance capitale dans la variation de la répartition de biomasse à l'intérieur des différents compartiments de l'arbre alors que la disponibilité en lumière influençait principalement la physiologie de la feuille. La morphologie de la cime quant à elle, était principalement dirigée par la variation en taille des individus, mais l'implication de la lumière en interaction avec la taille était significative. De plus, si certaines différences entre l'érable à sucre et le bouleau jaune étaient visibles au niveau de paramètres physiologiques (assimilation de carbone et respiration plus faibles), morphologique (cime plus plate) ou d'allocation (moins de branches), ces différences tendaient à disparaître avec la diminution de lumière, avec l'augmentation de la taille, ou encore à taille égale. En plus de prouver que les différences entre les espèces sont loin d'être constantes, ce résultat démontre l'impossibilité d'extrapoler les connaissances acquises chez les semis pour les stades ultérieurs de croissance. D'un autre côté, l'ombrage imposé en sous couvert a de

façon surprenante peu affecté les gaulis qui pourtant ne possédaient pas une architecture adaptée à d'aussi faibles disponibilités en lumière. Malgré une meilleure plasticité de leurs caractères, les semis semblaient moins capables de supporter un ombrage imposé pendant 4 années que les gaulis. L'explication d'un tel résultat fut alors associée à la possibilité que les gaulis possédaient, comparativement aux semis, plus de réserves dans leur tissus de soutien, ce qui leur auraient permis de survivre à cet ombrage drastique de 4 ans. Finalement, sous cet ombrage, l'érable à sucre a été moins affecté que le bouleau jaune, ce qui est explicable grâce à sa capacité de demeurer de petite taille et donc de conserver ses caractéristiques plus adaptées à l'ombrage (cime plate, peu de branches).

Par la suite, les études réalisées en milieu plus contrôlé, ont permis de démontrer une fois encore qu'il existait peu de différences entre l'érable à sucre et le bouleau jaune lorsque ceux-ci étaient comparés à taille équivalente ou sous des environnements lumineux similaires. En effet, en étudiant la capacité d'interception de lumière de semis de 1 et 2 ans ayant poussé sous différents environnement lumineux (chapitre 5.2), la plus grande source de différences entre l'interception les deux espèces ne résiderait pas dans les quelques différences visibles à petite échelle (ex : angle des feuilles), mais plutôt au niveau de la taille que les individus atteignaient dans un environnement lumineux donné. En effet, malgré une organisation spécifique des feuilles dans leur cime, les deux espèces ne différaient pas dans leur efficacité d'interception à l'échelle de l'individu. Toutefois, une perte de l'efficacité d'interception de lumière était clairement visible chez les deux espèces durant leur développement en taille. Ceci a d'ailleurs été relié à l'augmentation de l'auto-ombrage pendant le développement en taille du fait de l'augmentation de la surface foliaire. D'après ces résultats, l'intérêt à demeurer de petite taille en environnement ombragé était donc encore mis en évidence.

En ce qui concerne la mesure des échanges gazeux à l'échelle de la plante entière, l'utilisation d'une nouvelle technique de mesure de la production de CO₂ par les parties souterraines des semis (chapitre 5.3) n'a pas permis de réelle comparaison entre espèces du fait de la difficulté de croissance qu'a connu le bouleau jaune sur le milieu nécessaire à de telles mesures (sable grossier d'aquarium). Cela, en plus de souligner les efforts à faire dans l'apport de l'eau et des nutriments pour l'utilisation de cette technique, a tout de même permis de mettre en évidence une certaine constance de l'activité des racines des deux espèces en fonction de l'environnement lumineux. En effet, les résultats ont clairement démontré que la respiration des parties souterraines des deux espèces était intimement reliée à la quantité de racines fines contenues dans les racines totales. Par conséquent, les pertes en CO₂ des parties souterraines seront directement gouvernées par la quantité de biomasse allouée aux racines qui est un paramètre dépendant de la taille des individus (cf. chapitre 5.1).

Enfin, en comparant l'activité photosynthétique des feuilles d'érable à sucre et de bouleau jaune (chapitre 5.4), ce dernier a démontré de plus grandes capacités de photosynthèse que l'érable à sucre et cela quel que soit l'environnement lumineux testé. Cependant, en comparant l'assimilation de la cime entière, les différences entre les gains réalisés par le bouleau jaune et ceux réalisés par l'érable à sucre étaient très faibles durant la période de jour et non significatives lorsque intégrées sur une durée de 24 heures. En effet, les gains en carbone du bouleau jaune étaient grandement affectés par la forte respiration de ses tissus aériens pendant la période de nuit et cela particulièrement sous fort ombrage. Il existe donc un danger à comparer les espèces en fonction de paramètres foliaires isolés qui à l'échelle de l'individu perdent leur sens. Cependant, si peu de différences existaient entre les gains journaliers en carbone et l'accumulation de biomasse des deux espèces, leurs patrons d'allocation de cette biomasse étaient eux très différents.

En effet, à l'inverse du bouleau jaune, l'érable à sucre a alloué peu de carbone à sa croissance en hauteur et à ses tissus de structure (tige et branches), particulièrement sous fort ombrage. Par conséquent, plutôt que de fixer son carbone au sein de sa structure, il a été supposé que cette espèce allouait plutôt au stockage de réserves ce qui lui permettrait à la fois de minimiser ses coûts de construction et d'augmenter sa capacité à tolérer un stress.

6.3. Implications dans la régénération de l'érable à sucre et du bouleau jaune

Compte tenu des patrons de croissance, d'embranchement et d'allocation aux réserves de l'érable à sucre et du bouleau jaune, ainsi que de leurs capacités physiologiques (Bellefleur et LaRocque 1983a, 1983b, Walters et al. 1993a, 1993b, Wayne et Bazzaz 1993a, 1993b, Canham 1985, Ackerly et Bazzaz 1995a, Sipe et Bazzaz 1995, Kobe 1997, Beaudet et Messier 1998, Lei et Lechowicz 1998, Beaudet et al. 2000, Walters et Reich 2000, Gougeon 2000, chapitres 1, 2, 3 et 4), il est possible de mieux comprendre les mécanismes liés à leur tolérance à l'ombre respective mais également à leur mode de régénération en fonction de l'environnement lumineux.

En effet, il semble clair que l'érable à sucre en condition d'ombrage possède une dominance apicale forte évitant la production coûteuse de branches, mais également la possibilité de minimiser sa croissance en hauteur pour possiblement allouer son carbone accumulé au stockage de réserves. De plus, grâce à ses faibles taux de croissance sous ces conditions, l'érable à sucre semble pouvoir conserver de petites tailles associées avec une meilleure expression de ses caractéristiques propres et donc conserver une interception de lumière plus efficace. Ces avantages lui confèreraient donc une bonne tolérance à l'ombre lui permettant de supporter des périodes de suppression. Cependant, l'érable à sucre possède également la capacité de totalement modifier ces patrons d'allocation vers une forte croissance lorsque la disponibilité en lumière n'est pas limitante. Dans cette situation, les gains en carbone élevés permettent à la fois la production de tissus, leur maintien ainsi qu'une possible allocation aux réserves. Par la suite, ces réserves pourraient lui permettre, en cas de fermeture du couvert, de mieux tolérer une nouvelle période de suppression. Cette alternance de périodes de croissance et de périodes de suppression a déjà été observée sur les cernes de croissance d'individus adultes d'érable à sucre ayant atteint la canopée (Canham 1985). De plus, ceci s'accorde avec la description de la régénération de cette espèce lorsqu'étudiée sur de longues périodes. En effet, l'érable à sucre peut générer une importante banque de semis tolérants à l'ombre capables ponctuellement d'utiliser de petites trouées se refermant rapidement (McClure et al. 2000, Woods 2000).

D'un autre côté, si le bouleau jaune démontre des aptitudes parfois aussi performantes que l'érable à sucre, telles que dans l'interception de lumière (à taille égale), cette espèce semble perdre assez rapidement ces capacités en soutenant de forts taux de croissance en hauteur même sous ombrage. Bien que cette allocation à la croissance est parfois vue comme un avantage compétitif (Bellefleur et LaRocque 1983a), cette forte allocation de biomasse aux tissus de structure (tige et branches) malgré un environnement lumineux limitant et de faibles gains en carbone, pourrait se faire au détriment de l'allocation aux réserves. Si aucune ouverture du couvert ne survient, la diminution régulière des réserves et les coûts importants de construction et de maintenance engendrés chaque année diminueraient graduellement la possibilité de production de feuilles l'année suivante. *A terme, l'augmentation critique de la quantité de tissus non photosynthétiques par rapport aux tissus photosynthétiques deviendrait fatale pour l'individu.* Cependant,

sous un environnement lumineux non limitant, le bouleau jaune pourrait être capable d'allouer à la fois à sa croissance et partiellement à ses réserves ce qui lui permettrait de supporter temporairement une période d'ombrage en allouant le carbone de ses réserves à sa croissance en hauteur. Ce patron relativement dépensier du bouleau jaune par rapport à l'érable pourrait expliquer la faible capacité de cette espèce à supporter, après quelques années, la fermeture latérale des trouées qui avaient permis sa germination (McClure et al. 2000, Woods 2000).

De ce fait, la régénération de l'érable à sucre semble principalement gouvernée par l'association de caractéristiques internes avec un patron plastique d'allocation de biomasse aux différents puits (i.e. croissance, maintien, réserves) suivant l'environnement lumineux. En effet, la survie de cette espèce paraît peu dépendante de l'ouverture du couvert mais il est clair que cette ouverture influencera la vitesse de sa régénération. À l'inverse, la régénération du bouleau jaune apparaît totalement dépendante de la dynamique d'ouverture du couvert du fait de sa faible acclimatation à la variation de l'environnement lumineux au niveau de ses patrons d'allocation. En effet, la réussite de sa régénération par petits peuplements ou par individu isolé est possible grâce aux ouvertures importantes et durables (feux) ou plus petites mais très fréquentes (chute d'arbre(s) ou de branches) qui sont répertoriées dans les forêts feuillues d'Amérique du nord (Lorimer 1989) et qui lui permettent de soutenir son développement plus dépensier en carbone (Figure 6.1).

6.4. Une autre vision de la tolérance à l'ombre

Croître ou ne pas croître, une question de survie en sous couvert ?

Malgré le fait que l'érable à sucre et le bouleau jaune possèdent des degrés de tolérance à l'ombre finalement peu éloignés (i.e. tolérant et semi tolérant à l'ombre), l'étude de la littérature concernant les résultats mis en évidence dans les différents chapitres de ce travail permet de tisser quelques conclusions d'une portée plus étendue. En effet, il est clair qu'un grand nombre des paramètres internes des espèces sont influencés par l'accroissement en taille des individus (Givnish 1995, Niklas 1994, West et al. 1999, Messier et Nikinmaa 2000, Reich 2001, Naumburg et al. 2001, Claveau et al. 2002) et cela dans un sens qui pourrait diminuer les différences entre espèces dues à la pression de l'environnement et affecter leur tolérance à l'ombre (d'ailleurs souvent étudiée seulement au stade de semis).

En effet, s'il existe de nombreuses différences entre espèces au niveau de leurs paramètres propres, la majeure partie de ces différences diminuent ou même disparaissent avec l'augmentation de la taille (et/ou la diminution de la disponibilité en lumière). D'après certains auteurs, ceci correspond au phénomène de convergence des solutions physiologiques, morphologiques ou architecturales sous la pression grandissante de l'environnement (Niklas 1992, Meinzer 2003, Valladares et al. 2002). La diminution des différences inhérentes à chaque espèce avec l'augmentation en taille pourrait donc être en relation directe avec la modification de l'environnement physique de l'arbre (gravité, force du vent) qui s'effectue au cours de son accroissement (Niklas 1992, 1994, Hallé 1999). Cette hypothèse est supportée par le fait que certaines lois de croissance et certaines relations d'échelle semblent invariables parmi de nombreuses communautés d'organismes (West et al. 1999, 2001, Enquist et Niklas 2001). Par conséquent, la possibilité d'une variabilité des paramètres de l'arbre en fonction de l'environnement (*variation intra spécifique ou acclimatation*) ou entre espèces (*variation inter spécifique*) pourrait exister principalement lors des premiers stades de développement et posséder

relativement peu d'importance sur le fonctionnement général de l'individu pour des tailles plus importantes.

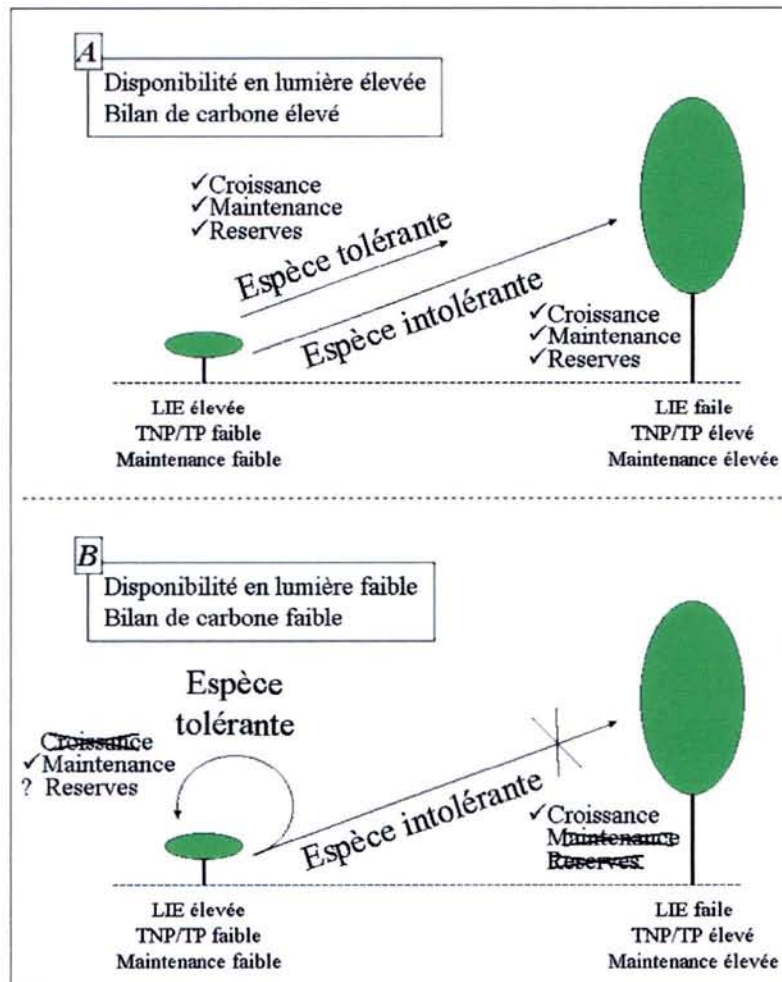


Figure 6.1. Schéma des patrons de croissance sous forte (A) et faible (B) disponibilité en lumière d'une espèce tolérante à l'ombre et d'une espèce intolérante à l'ombre. L'impact négatif sur l'allocation de carbone ou le potentiel de survie est indiqué par une croix.

Cependant, ces nombreuses convergences entre espèces ne vont pas contre la reconnaissance de différences entre le tempérament écologique des espèces. Bien au contraire, comme il a été mis en évidence pour le bouleau et l'érable à sucre, l'allocation ou non de biomasse vers la croissance en hauteur peut induire d'importantes différences entre espèces, particulièrement dans leurs possibilités de développement sous de faibles niveaux de lumière (Figure 6.1).

Croître en sous couvert fermé semble en effet très coûteux et même à plus long terme fatal. Ceci pourrait expliquer la relation entre la taille maximale des arbres en relation avec la disponibilité en lumière répertoriée chez un grand nombre d'espèces (Givnish 1988, Messier et al. 1999, Figure 6.2). De plus, les différences de taille apparaissant entre les espèces tolérantes et intolérantes à l'ombre pour un même niveau de lumière pourraient être le résultat de différences dans leur somme, plus ou moins efficace, de caractères internes (Figure 6.2).

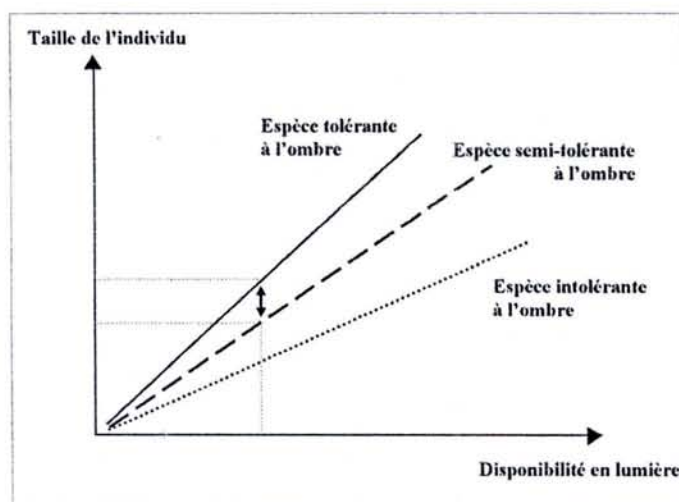


Figure 6.2. Relation entre la taille maximale et la disponibilité en lumière chez des espèces tolérantes, semi-tolérantes et intolérantes à l'ombre (D'après Messier et al 1999).

Par conséquent, si la réussite de la régénération d'un individu dans un environnement donné est grandement dépendante de la taille qu'il atteint et qu'il soutient dans cet environnement, sa performance résulte également de l'ensemble des paramètres physiologiques, morphologiques ou d'allocation qu'il exprime. Il est également clair que la performance à long terme d'un individu est conjointement déterminée par l'historique de la disponibilité en ressources telles que la lumière dans son environnement proche.

6.5. Perspectives de recherches

Si ce travail a permis de répondre à un certain nombre de questions, l'avancement des différents chapitres a soulevé l'importance de certains points mal connus ou non documentés qu'il faudrait explorer.

Par exemple, il est clair qu'au fil de ce travail, la dynamique de stockage et d'utilisation des réserves chez les arbres est apparue comme un point centrale de la performance des individus. En effet, les réserves possèdent une importance capitale dans leur développement et leur capacité de répondre à des variations de l'environnement. Pourtant peu de choses sont connues sur ce compartiment de l'allocation de carbone qui détient la propriété de pouvoir être un puit comme une source de carbone pour l'individu. Il serait donc nécessaire de développer nos connaissances en ce domaine, particulièrement en fonction du développement de l'arbre (i.e. différents stades de croissance) mais aussi en fonction de différentes conditions environnementales.

De même, la dynamique d'utilisation des taches de lumière par la cime des individus ainsi que leur utilisation pour la fixation du carbone (induction de la conductance stomatique, activation de l'appareil photosynthétique) sont encore mal connues. Pourtant là encore, ces mécanismes sont supposés primordiaux dans la performance des arbres, particulièrement en sous couvert où ces taches de lumière peuvent représenter une grande proportion de la lumière disponible. De plus, la capacité à utiliser ces taches de lumière est a priori très variable suivant les espèces, ce qui pourrait donc avoir une influence non négligeable sur le tempérament écologique de chacune.

Il serait aussi très intéressant d'étudier les relations qu'il peut exister entre l'activité phénologique des individus et leur performance, particulièrement si l'on cherche à établir un bilan carboné sur des périodes plus étendues qu'une journée (i.e. une saison, une année). En effet, le bilan carboné d'un individu est possiblement très affecté par la phénologie de croissance des différents compartiment de l'arbre. En période de croissance, les puits de carbone que représentent la construction de nouveaux tissus (activité respiratoire de construction et fixation de carbone dans la structure) ne sont pas négligeables. C'est pourquoi l'étude de la phénologie de compartiment très actifs tels que les racines fines ou les feuilles serait très utile, particulièrement sous différents environnements. En effet, la phénologie des espèces est potentiellement très variable selon les conditions environnementales (ex : nombre de flush, remplacement des racines fines), mais peu de documentation est disponible à ce sujet.

L'utilisation de la digitalisation en 3D pour décrire l'architecture précise des semis représente également une grande possibilité de future recherche. A partir de telles données, il est en effet possible de réaliser des tests de sensibilité (comme ceux utilisés pour tester les paramètres les plus importants d'un modèle) sur la plante elle-même. En modifiant par exemple la longueur des pétioles, l'angle des branches ou la forme de la feuille, il est alors possible grâce au modèle d'interception de définir l'importance relative de chaque paramètre de l'individu sur son interception de lumière ou même sur son bilan en carbone.

Enfin, une autre perspective serait, grâce à ce travail, de paramétrer (et valider) des modèles de croissance à l'échelle de l'individu pour ces deux espèces. Ceci permettrait en effet d'améliorer les possibilités de recherche et surtout de diminuer les coûts associés à l'étude de leur performance en fonction des conditions environnementales, qui sur le terrain sont des recherche toujours très coûteuses et parfois impossibles.

7. RÉFÉRENCES DE L'INTRODUCTION ET LA CONCLUSION GÉNÉRALE

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ANNEXES

 ANNEXE A : LE BOULEAU JAUNE: *Betula alleghaniensis* Britt.

Bouleau des Alléghanys, Merisier jaune.

Généralités: Le bouleau jaune est le plus grand et le plus tolérant à l'ombre des bouleaux de l'est de l'Amérique du Nord. Arbre d'envergure moyenne, il peut atteindre 25 à 30 mètres de hauteur, 60 à 100cm de diamètre et jusqu'à 300 ans. Son aire de distribution s'étend du sud de terre neuve au nord de la Caroline du Sud et de l'atlantique au Minnesota (Figure 1A). Le bouleau se trouve rarement en peuplements purs mais est fréquemment mélangé au hêtre, à l'érable à sucre, au tilleul, au sapin baumier au pin blanc et aux épinettes blanche et rouge. Le bois jaune doré de cette espèce est très apprécié commercialement dans l'est du Canada pour la fabrication de meubles, parquets et portes. Le bouleau jaune possède également une valeur ornementale notable du fait du jaune vif de ces feuilles en automne et de la couleur bronze ou cuivrée de son tronc. Le bouleau jaune fait partie intégrante du patrimoine Québécois dont il est l'arbre emblème.

Caractéristiques: L'architecture du bouleau jaune est basée sur une croissance orthotrope de la tige et des branches qui peut cependant devenir plagiotrope pour les branches durant le développement et plagiotrope pour la tige sous ombrage. Le patron d'embranchement est spiralé autour de l'axe principal. Toutefois, sous ombrage ce patron peut s'orienter vers une disposition plus alterne opposée. La phyllotaxie du bouleau jaune est alterne spiralée mais peut encore une fois devenir alterne opposé sous de faible niveau de lumière ou pour les rameaux secondaires. La feuille du bouleau possède un très petit pétiole et peu atteindre une longueur allant de 5 à 20 cm. La largeur de la feuille dépasse rarement $\frac{1}{4}$ de la longueur ce qui produit des feuilles moyennement effilée. Les feuilles de bouleau sont doublement dentelées mais ne possèdent pas de lobes. Le bouleau jaune est une espèce d'arbres possédant des associations symbiotiques ecto-mycorhiziennes pour la prise en charge des éléments minéraux du sol.

Autécologie:

Production de graines: Le bouleau jaune possède comme la majorité des arbres du genre *Betula* un comportement opportuniste de multiplication. Il produit en l'automne un grande quantité de graines (jusqu'à 18 000 graines/m²) très légères qui sont dispersées par le vent jusqu'à plusieurs centaines de mètre et même au delà si la couverture neigeuse est glacée. Cette stratégie permet une large dissémination de ses graines afin de coloniser les

milieux plus ouverts. Les bonnes années semencières reviennent environ tous les trois ans mais la durée de vie des graines dans le sol est assez courte (environ deux ans).

Germination: La germination du bouleau jaune nécessite généralement un substrat riche, minéral et très humide. En milieu naturel, le taux de germination du bouleau jaune est moyen (moins de 50%) et l'établissement des semis est très faible (moins de 1% des graines viable). La prédation, le broutage, les pathogènes et surtout l'épuisement des réserves de la graine, expliquent ce faible taux d'établissement. Lors de son installation, le semis ne produit que des racines de surface qui ne peuvent percer la couche de litière. La réussite de l'établissement de cette espèce est donc généralement associée à la présence d'un sol sans litière ou d'un sol perturbé où la couche minérale est exposée en surface. Le bouleau jaune s'établit également très bien sur le bois mort en décomposition car ces substrats représentent une importante réserve en eau et en nutriments. Cependant, le taux de mortalité des semis durant la première année peut atteindre plus de 90%.

Croissance: Le bouleau jaune possède une croissance monopodiale continue tant au niveau de la tige qu'au niveau des branches. Sous ombrage, la croissance orthotropique des semis peut se transformer en croissance plagiotropique (observation personnelle non retrouvée chez les gaulis). La position des feuilles sur les segments est alterne et spiralée. Généralement, le bouleau jaune est considéré comme une espèce semi-tolérante à l'ombre. Certaines études ont montré qu'un ombrage partiel est plus favorable à sa survie, à sa croissance en hauteur et au développement de sa large cime. Les conditions environnementales (vents, température, humidité de l'air, humidité du sol) plus sévères rencontrées en pleine lumière pourraient être en cause dans la meilleure performance du bouleau jaune sous ombrage partiel. En effet, le bouleau jaune supporte très mal les périodes de sécheresse en raison de son enracinement peu profond. Chez le bouleau jaune, la croissance optimale au dessus comme au dessous du sol a été observée autour de 50% du rayonnement total.

Patron de succession et régénération: Le bouleau jaune est une espèce de milieu et de fin de succession. En effet, son établissement en milieu ouvert est réduit en raison de la forte compétition imposée par des espèces compétitrices plus agressives telles que le peuplier faux tremble, le bouleau blanc, le cerisier de Pennsylvanie ou le framboisier. En revanche, si un couvert totalement fermé ne lui permet pas d'atteindre la strate arborescente, le bouleau jaune peut se régénérer par petits peuplements grâce à des perturbations de petite et moyenne importance. En effet, de fortes densités de bouleau

jaune sont observées dans la composition des forêts où le diamètre moyen des trouées avoisine 20m, et où celles-ci restent ouvertes une dizaine d'année. Les trouées créées par la chute de branches ou les grandes perturbations telles que les feux ne sont donc pas favorables à sa régénération car elles amènent respectivement trop peu de lumière ou la présence d'espèces plus compétitrices. Grâce à sa longévité assez longue (en moyenne 200-250 ans), le bouleau jaune peut se retrouver au sein de vieilles forêts qui n'ont pas subi de perturbations majeures depuis plus de 150 ans.

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ANNEXE B : L'ÉRABLE À SUCRE: *Acer saccharum* Marsh.*Érable franc*

Généralités: L'érable à sucre est un arbre caractéristique des forêts feuillues tempérées de l'est de l'Amérique du Nord. Son aire de distribution s'étend du Minnesota à l'ouest, aux provinces maritimes de l'est du Canada, et au centre du Québec au nord jusqu'en Ohio au sud. L'érable à sucre peut se trouver en peuplements purs comme en peuplement mélangés. Les arbres généralement associés aux peuplements d'érable à sucre sont le hêtre à grandes feuilles, le bouleau jaune et le tilleul pour les feuillus et le sapin baumier et le pin blanc pour les conifères. L'érable à sucre atteint des hauteurs de 30 à 40m, des diamètres de tronc de 90 cm et un âge pouvant dépasser 400 ans. L'érable à sucre est une espèce à intérêts économiques importants tant pour son bois dur utilisé en menuiserie et pour la fabrication de d'articles façonnés que pour la production de sirop d'érable à partir de la sève. Il possède également un attrait touristique renommé du à la coloration flamboyante de son feuillage en automne. Représenté par une feuille stylisée sur le drapeau canadien, l'érable à sucre est l'arbre emblème du Canada.

Caractéristiques: L'érable à sucre est reconnu pour avoir une forte dominance apicale particulièrement sous ombrage ce qui minimise le nombre de bourgeons latéraux qui se développe en branches sous ces conditions. Sa phyllotaxie est opposée et décussée. Les feuilles possèdent de long pétiole et atteignent 5 à 11 cm de longueur suivant l'environnement lumineux et la position sur les tiges. Leur largeur est généralement équivalente à leur longueur ce qui en fait des feuilles relativement large. Les feuilles possèdent de 3 à 5 lobes peu dentelés et sont glabres. L'architecture de l'érable à sucre est basée chez les jeunes arbres sur une croissance orthotrope liée à un patron d'embranchement opposé et décussé. L'érable à sucre possède des associations endomycorhizienne qui peuvent l'aider lors de l'acquisition de ressource du sol. Cependant, les associations fortes établies par les endo-mycorhizes peuvent devenir parasitaires en cas mauvaises conditions environnementales.

Autécologie:

Production de graines: La production de semence de l'érable à sucre est très variable d'une année à l'autre mais s'améliore généralement lorsque les arbres atteignent un

diamètre supérieur à 30cm (plus de 70 ans). Au Canada, les bonnes années semencières sont espacées de 3 à 7 ans et correspondent à une production de près de 300 graines par mètre carré. La dispersion des graines s'effectue par le vent, mais du fait du poids élevé des graines, celle-ci est majoritairement inférieure à 50m. Bien que la viabilité des graines dans le sol puisse atteindre 5 années, la plupart germent le printemps suivant.

Germination: Le taux de germination des graines d'érable à sucre est généralement très bon (près de 95%). Optimale entre 1 et 4°C, la germination débute avant même la fonte complète de la couche neigeuse. Un couvert forestier fermé, ainsi que la présence d'une litière ne nuisent pas à sa germination. L'érable à sucre peut s'établir dans une grande variété de sols, mais il a déjà été remarqué que la présence de calcium et d'un bon drainage favorisaient sa survie. Il n'est donc pas rare de retrouver près de 350 000 semis à l'hectare, mais la mortalité est assez forte dans les 5 premières années.

Croissance: Au Canada, l'érable à sucre possède une croissance rythmique monopodiale orthotrope (2 ou 3 flush suivant les conditions climatiques) et la disposition des feuilles sur les segments est opposée décussée. Chaque année, la croissance de l'érable à sucre débute tôt au printemps ce qui lui permet de profiter d'intensités lumineuses plus élevées avant la sortie des feuilles de la strate arborescente. Cependant cette initiation précoce des feuilles le rend sensible aux gelées tardives et à la mort du bourgeon terminal. En cas de mort de la flèche terminale, les bourgeons latéraux peuvent rapidement produire de nouveaux axes. L'érable à sucre est une espèce tolérante à l'ombre qui peut supporter plusieurs années de suppression tout en possédant la capacité de répondre rapidement à l'ouverture de la canopée. Si, la survie de cette espèce est bonne sur un large spectre d'intensités lumineuses, sa croissance est meilleure entre 35% et 65% du rayonnement total. Chez l'érable à sucre, l'assimilation de CO₂ a déjà été observée comme maximale dès 25% du rayonnement total. L'érable à sucre possède souvent un enracinement profond dans la couche minéral qu'il installe dès les premières années de développement.

Patron de succession et régénération: L'érable à sucre est une espèce de fin de succession souvent associée aux vieilles forêts feuillues de l'est de l'Amérique du nord. Chez cette espèce, la réserve d'individus disponible pour la régénération se trouve sous forme de semis en sous couvert plutôt que sous forme de graines dans le sol. Pour atteindre la canopée, les semis profitent de la création de petites perturbations mais doivent généralement supporter plusieurs périodes de suppression. La régénération de cette espèce, peut également se faire par drageonnement et rejet de souche.

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ANNEXE C

Do understory sapling respond to both light and below-ground competition?: a field experiment in a north-eastern American hardwood forest and a literature review

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Abstract – A study was initiated in 1993 to evaluate the potential effects of both above- and below-ground competition exclusion on yellow birch (*Betula alleghaniensis* Britton), sugar maple (*Acer saccharum* Marsh.) and American beech (*Fagus grandifolia* Ehrh.) sapling growth along an understory light gradient ranging from 3% to 50% of full sunlight. We compared four different growth variables between a control and a treatment (trenching and manual removal of nearby vegetation). Height growth, diameter growth, height over stem diameter ratio, and crown area varied with light availability in all three species, whereas trenching treatment had no significant effect. Our results show that light is the main factor affecting understory sapling growth following a selection cut in this northern hardwood forest, at least up to 50% full sunlight. The unresponsiveness of these three species to below-ground competition is discussed in relation to a literature review in which both soil richness and species functional ecology are considered.

above- and below-ground competition / growth / light / northern hardwood species / trenching

Résumé – Les gaules en sous couvert répondent-ils à la fois à une compétition en dessous et au-dessus du sol ? Une expérience en forêt feuillue du Nord-Est de l'Amérique et une revue de littérature. En 1993, une étude a été entreprise afin de déterminer les effets éventuels de l'élimination de la compétition souterraine sur la croissance de gaules de bouleau jaune (*Betula alleghaniensis* Britton), d'érable à sucre (*Acer saccharum* Marsh.) et de hêtre à grandes feuilles (*Fagus grandifolia* Ehrh.) se trouvant sous un gradient de lumière allant de 3 % à 50 % du rayonnement solaire total. Quatre paramètres de croissance ont été comparés entre des gaules témoins et des gaules traitées (création d'une tranchée et enlèvement manuel des tiges avoisinantes). Pour les trois espèces, les croissances en hauteur et en diamètre, le ratio hauteur sur diamètre de la tige et la surface de cime ont varié avec la disponibilité en lumière, alors que l'élimination de la compétition n'a eu aucun effet. Nos résultats suggèrent donc que la lumière est le principal facteur limitant la croissance des gaules en sous-couvert après une coupe de jardinage dans cette forêt feuillue tempérée, au moins jusqu'à 50 % de pleine lumière. La faible réponse des trois espèces à l'élimination de la compétition est discutée à partir d'une revue de littérature dans laquelle la fertilité des sols et le comportement écologique des espèces sont comparés.

compétition au-dessus et en dessous du sol / croissance / lumière / espèces feuillues tempérées / élimination de la compétition souterraine

1. INTRODUCTION

In north-eastern American hardwood forests, understanding the response of understory trees to small canopy openings is important in order to carry out partial cutting that allows the regeneration and growth of a variety of tree species. Over the last decade, many studies have focussed on the relationship between light availability in gaps of various sizes and understory tree growth and physiology [3–6, 8, 11, 12, 14, 25, 26, 29, 36, 46, 47]. All of these studies have reported that increased light availability, as found in small to medium canopy openings, was a major factor affecting seedling and sapling growth.

However, below-ground resource availability is also believed to affect plant growth and species composition [18, 24, 31, 52, 55]. In a temperate oldfield, Putz and Canham [51] found that saplings of red maple (*Acer rubrum* L.) did not respond to canopy openings, but responded to a reduction in root competition. In another ecosystem, Christy [17] found that growth of understory western hemlock seedlings (*Tsuga heterophylla* Raf. [Sarg.]) was mainly affected by below-ground competition reduction and to a much lesser extent by an increase in light availability. While some studies have reported that root competition is a major factor affecting plant performance [23, 40, 41, 56], many others have found either

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Table I. Characteristics of sampled saplings prior to the experiment in 1993 at the Duchesnay experimental forest near Québec, Canada. Mean with standard errors in parentheses.

Species	Treatment	<i>n</i>	Sapling age in 1993	Initial height in 1993 (cm)	Initial diameter in 1993 (cm)
Yellow birch	control (NT)	39	7.9 (3.0)	124.9 (31.6)	1.27 (0.36)
	trenched (T)	36	7.7 (2.9)	112.4 (27.0)	1.37 (0.39)
Sugar maple	control (NT)	37	11.4 (2.5)	104.0 (25.0)	1.06 (0.30)
	trenched (T)	35	12.8 (3.9)	112.1 (26.0)	1.21 (0.31)
American beech	control (NT)	34	11.1 (3.3)	125.2 (33.4)	1.55 (0.54)
	trenched (T)	29	12.4 (3.4)	119.4 (29.6)	1.46 (0.59)

no real effect of trenching or fertilisation on plant growth [21, 22, 33, 51] or a better growth release when both above- and below-ground competition were removed [15, 22, 43, 50].

Studies that have investigated a large number of temperate and tropical tree species [18, 42] have also shown a variation in species response to increased above- and below-ground resources. These variations may be associated with the variation in shade tolerance: growth of shade intolerant species is affected by limited resource whereas growth of shade tolerant species is less affected owing to the slower growth rates and/or high storage capacities of these latter species [9, 16].

All of these studies and a recent review by Coomes and Grubb [19] seem to indicate that the relative importance of above- and below-ground competition for understory tree growth is very dependent on the site conditions and/or the species investigated. In fact, (1) understory trees growing on nutrient poor and dry sites tend to be more affected by below-ground competition than trees growing on sites that are not nutrient- or water-limited [19, 31, 45, 53], and (2) pioneer or shade intolerant species tend to be more sensitive to below-ground competition [16].

The objective of this study was to examine the relative importance of both above- and below-ground competition on the growth of well-established understory sugar maple (*Acer saccharum* Marsh.), American beech (*Fagus grandifolia* Ehrh.) and yellow birch (*Betula alleghaniensis* Britton) saplings which are found naturally coexisting in hardwood forests of north-eastern America. Of these three species, yellow birch is considered the most shade intolerant, whereas sugar maple and American beech are considered to be shade-tolerant and very shade-tolerant, respectively [1, 10, 13, 28, 30, 35, 54]. This study addresses three specific questions: (1) do understory vegetation and below-ground competition affect understory sapling height and diameter growth, (2) does this change with increasing gap size as measured by light availability, and (3) are shade intolerant species more affected by above- and below-ground competition? We then reviewed the results obtained in several studies done on this subject, as well as the conditions under which the studies were performed, to improve our understanding of the conditions under which exclusion of understory vegetation and below-ground competition may or may not be important for understory tree saplings.

2. MATERIALS AND METHODS

2.1. Study area

The study site was located at the Duchesnay experimental forest (46° 55' N, 71° 40' W) near Québec, Canada. The mean annual precipitation is approximately 1220 mm and mean daily temperature ranges from -12 °C in January to 28 °C in July [27]. Elevation ranges from 200 to 300 m, and slopes are generally gentle (2–20%). The humus layer was thin and of the moder type. Soils developed on a well-drained to imperfectly drained glacial till. Soil types ranged from drystic brunisols to humo-ferric podzols. The overstory canopy was dominated by sugar maple, American beech and yellow birch which respectively accounted for 60, 20 and 15%, respectively, of the merchantable volume. A selection cut was performed at the study site in 1989, where 30% of the total tree basal area was harvested. This cut created several gaps ranging in size from approximately 10 m² to 300 m². The main woody species present in the understory prior to the partial cut were Canadian yew (*Taxus canadensis* L.), striped maple (*Acer pensylvanicum* L.), mountain maple (*Acer spicatum* Lam.), sugar maple, American beech and yellow birch. Following the cut, early successional species such as red raspberry (*Rubus idaeus* L.) and pin cherry (*Prunus pensylvanica* L.f.) established in and around gaps.

2.2. Sapling selection and treatments

Fourteen gaps, with similar aspects and slopes, were selected in the partially cut area and in an adjacent undisturbed area of the stand to cover a wide gradient of canopy opening sizes and light availability (3 to 50% of above-canopy PPFD: Photosynthetic Photon Flux Density). Seventy-two (72) sugar maple, 63 beech, and 75 yellow birch saplings were selected. All selected saplings were dominant relative to the surrounding vegetation. Table I presents their average age, height and diameter at the start of the experiment. The removal of understory vegetation and trenching treatment was applied to half the saplings, by manually removing all above-ground vegetation and by trenching in a 1 m radius zone around each sapling to a depth of 30 to 40 cm. Trenching was carried out at the beginning of May 1993 and 1994, as well as in July 1993, 1994 and 1995 to avoid root incursion from adjacent understory vegetation and overstory trees. New growth or establishment of vegetation in the 1 meter radius zone was also manually eliminated as needed. This treatment was aimed at eliminating below-ground competition from both the overstory trees and non-shading understory vegetation. Non-shading understory vegetation was abundant around all selected saplings and composed mainly of tree seedlings and saplings (4 to 75 stems/m²), early and late successional shrubs (0 to 126 stems/m²) and various herb species (5 to 75% cover).

2.3. Growth and light measurements

All saplings were sampled at the end of the 1995 growing season, after three full years of growth following the initial treatment. Annual height growth for the three years following the treatment and the three years before the treatment was estimated from bud scars. Sapling stem diameter growth at the forest floor was measured under binoculars by measuring rings located on two perpendicular lines, from the centre of the stem to the bark. A mean was then calculated from both lines to avoid incorrect estimations resulting from irregular diameter growth. Sapling height over stem diameter ratio was calculated for each sapling, based on its dimension at the end of the 1995 growing season. At the same time, crown area was estimated in a quick way as the product of two perpendicular diameter measurements, one of which was the maximum crown diameter.

Understory percent PPFD was measured above all saplings using the method proposed by Messier and Puttonen [44] and tested by Parent and Messier [49] and Gendron et al. [32]. On three completely overcast days, three instantaneous light measurements were taken at 5–10 cm above each sapling (I_U), using a LI-189 light radiometer (LI-COR, Lincoln, Nebraska, USA). A quantum sensor linked to a LI-1000 datalogger (LI-COR) was placed in an adjacent clear-cut to record the overstory PPFD conditions (I_0). The datalogger was programmed to compute the mean PPFD ($\mu\text{mol m}^{-2} \text{s}^{-1}$) measured every 10 seconds over a one-minute period. The I_U value obtained at a certain time was divided by I_0 recorded at the same time (and multiplied by 100) to calculate the percent of above canopy PPFD (% PPFD) above each sapling. According to Messier and Puttonen [44], Parent and Messier [49] and Gendron et al. [32], such instantaneous measurements obtained under completely overcast sky conditions are highly related to the mean daily percent PPFD measured under both overcast and clear sky conditions.

2.4. Soil water, nutrient and temperature measurements

Soil water content, nutrient availability and temperature were measured in early August and late September 1993, at the end of the first growing season after treatment, in order to evaluate the effects of the understory vegetation removal and trenching treatment. Three to four subsamples of soil taken within 40 cm of each replicated sapling were bulked together into one sample. We sampled the soil around 15 treated and 15 untreated saplings selected at random in August and the same number in September 1993 among the 216 saplings used in this study. Soil samples were sifted in order to keep only the fine mineral soil. Water content (% of dry weight), soil temperature measured at 10 cm, nitrogen availability (NH_4^+ et NO_3^-) and total phosphorus (PO_4^{2-}) were measured for each soil sample. KCl was used for N extraction while Bray II (NH_4F et HCl) method was employed for P extraction.

2.5. Data analysis

Sapling height and diameter growth for the three years before the removal of understory vegetation and trenching treatment (1990 to 1992) initiation were investigated to test for any prior growth differences between the control and trenched treatments. No significant difference was found between treatments for any of the three species ($P > 0.60$). Consequently, equation (1) was used to calculate the relative height increment, and equation (2) was used for the relative diameter increment. These equations of relative increment allowed us to take into account the slight differences in initial height and basal stem diameter that were present among study saplings (see Tab. I).

$$\text{Relative height increment} = [(Height_{95} - Height_{92}) / Height_{92}] \times 100 \quad (1)$$

$$\text{Relative diameter increment} = [(Diameter_{95} - Diameter_{92}) / Diameter_{92}] \times 100 \quad (2)$$

where $Height_{92}$ and $Diameter_{92}$ are measurements before treatment, and $Height_{95}$ and $Diameter_{95}$ are measurements three growing seasons after treatment initiation.

Analysis of covariance (ANCOVA) using General Linear Models (SYSTAT v.8.0 [SPSS Science, Chicago, Illinois]) was performed to evaluate the effects of the treatment and species on sapling parameters (relative height increment, relative diameter increment, height/diameter ratio in 1995, and crown area in 1995). In all cases, %PPFD was used as a covariable whereas treatments and species were used as grouping factors. Slopes were considered significantly different when the probability associated to the interaction terms (%PPFD \times treatment, or %PPFD \times species) was lower than 0.05. A T-test with unequal variance was used to evaluate the effect of trenching on the various soil parameters.

Logarithmic transformation ($\log_{10}(x + 1)$) had to be performed on the four dependent variables and on the independent variable (PPFD) to meet statistical assumptions (residuals normality, homogeneity of variance and data linearity). Transformations were also used in some cases for the soil parameters to meet statistical assumptions.

3. RESULTS

Available nitrate (NO_3^-) was slightly higher for treated saplings (70.99 mg/L) compared to the control ones (58.53 mg/L), but these differences were not significant ($P = 0.1338$). Furthermore, we found no changes in ammonium (NH_4^+) (control = 281.87 $\mu\text{g/L}$, treated = 281.07 $\mu\text{g/L}$; $P = 0.9766$) and soil water availability (control = 52.35%, treated 51.07%; $P = 0.4393$) between treatments. Total phosphorus (P) was not influenced by the trenching and understory competition removal treatment (control = 0.151 $\mu\text{g/g}$, trenched 0.164 $\mu\text{g/g}$; $P = 0.4014$). Finally, soil temperature was slightly, but significantly higher near the treated compared to the untreated saplings.

The general linear model (Tab. II) indicated a few significant interactions between species and light for three variables (relative height and diameter increment, and height over diameter ratio). In all three species, relative height increment increased with increasing light, but the increase was the strongest for sugar maple and the weakest for American beech (Fig. 1A; Tab. II: interaction term $Sp \times L$). Also, in all three species, the relative diameter increment increased with increasing light, but the increase was clearly stronger for yellow birch compared to the other two species (Fig. 1B; Tab. II: interaction term $Sp \times L$). The height over stem diameter ratio decreased with increasing light in all three species, but the decrease was much stronger for American beech (Fig. 2A; Tab. II: interaction term $Sp \times L$). Finally, the crown area increased with increasing light and the slopes were parallel among the three species (Fig. 2B; Tab. II: interaction term $Sp \times L$ not significant). While light availability had a strong effect on all four growth variables, we did not find any effect of the below-ground exclusion treatment. The F values associated with the below-ground exclusion treatment effect and the interaction terms were all low (generally lower than 2) and the P values all higher than 0.125 (Tab. II).

4. DISCUSSION

Our three objectives were to determine if the exclusion of below-ground competition would affect sapling height and diameter growth, if the effect would vary depending on light

Table II. Summary (degree of freedom; *df*, *F* value and probability; *p*) of analysis of variance of relative height increment, relative diameter increment, height over stem diameter ratio, and crown area. Values in bold are significant at $\alpha = 0.05$.

Source of variation	Relative height increment			Relative diameter increment			Height/diameter ratio			Crown area		
	<i>df</i>	<i>F</i>	<i>P</i>	<i>df</i>	<i>F</i>	<i>P</i>	<i>df</i>	<i>F</i>	<i>P</i>	<i>df</i>	<i>F</i>	<i>P</i>
Species (Sp.)	2	13.39	< 0.001	2	0.79	0.457	2	0.71	0.493	2	0.68	0.507
Treatment (T)	1	1.83	0.178	1	0.11	0.744	1	1.18	0.279	1	0.14	0.714
Light (L)	1	186.52	< 0.001	1	142.26	< 0.001	1	37.90	< 0.001	1	37.95	< 0.001
Sp. × T	2	0.02	0.980	2	0.14	0.871	2	0.14	0.868	2	1.59	0.207
Sp. × L	2	6.69	0.002	2	7.61	0.001	2	3.16	0.045	2	0.43	0.650
L × T	1	1.77	0.185	1	0.03	0.866	1	2.38	0.125	1	0.61	0.434
Sp. × T × L	2	0.23	0.796	2	0.13	0.881	2	0.39	0.676	2	1.36	0.259
Error	175			179			166			193		

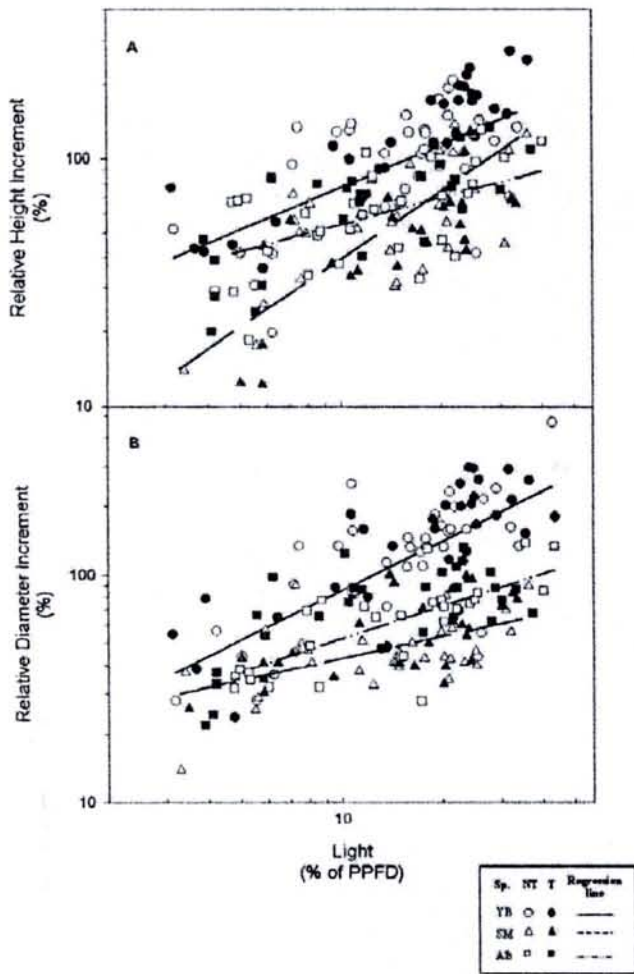


Figure 1. Linear relationships between mean daily percent PPFD and (A) relative height increment, and (B) relative diameter increment (logarithmic scale for both axes). Saplings of yellow birch (YB; circles), sugar maple (SM; triangles) and American beech (AM; squares) were separated in treated (T; filled symbols) and non-treated (NT; open symbols) saplings. As treatment had no effect on relative height growth of our three species, regression lines were drawn for each species after grouping treated and non-treated saplings in a single group.

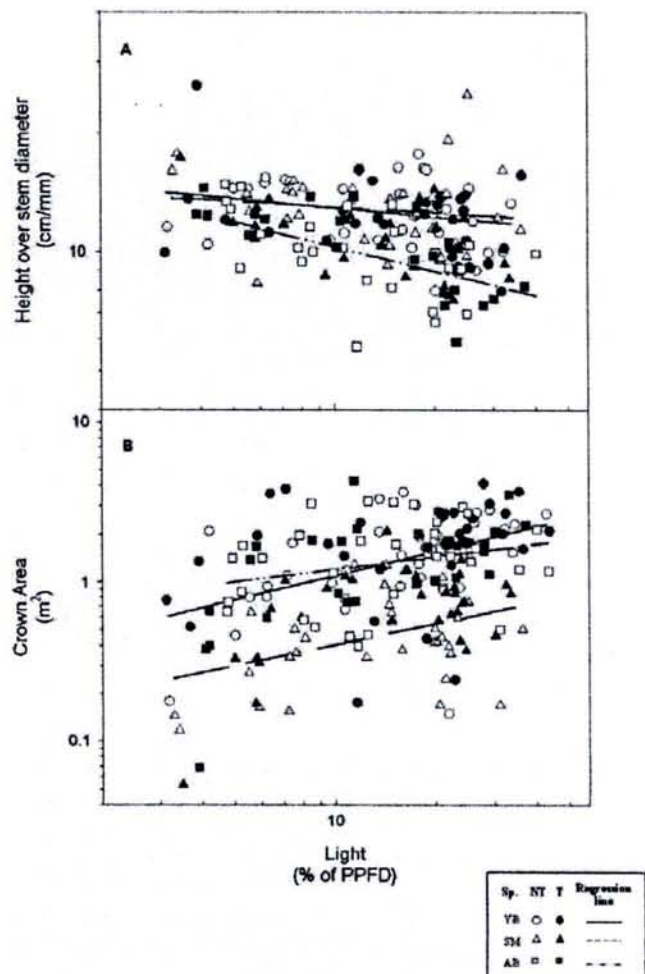


Figure 2. Linear relationships between mean daily percent PPFD and (A) height over stem diameter ratio and (B) crown area (logarithmic scale for both axes). Saplings of yellow birch (YB; circles), sugar maple (SM; triangles) and American beech (AM; squares) were separated in treated (T; filled symbols) and non-treated (NT; open symbols) saplings. As treatment had no effect, regression lines were drawn for each species after grouping treated and non-treated saplings in a single group.

availability and if less shade tolerant species would be more affected than more tolerant species. Our results showed that the below-ground exclusion treatment did not have any effect on height and diameter increment, height over diameter ratio or crown area, and that this was true under all light conditions (up to 50% light) and for all three species.

We expected that the exclusion of below-ground competition would increase nutrient and water availability through the elimination of below-ground competition for those resources. A more or less rapid decomposition of the trenched dead fine-roots could also have led to an increase in nutrient availability over time. Since we did not observe any effect of the below-ground exclusion treatment, we considered the possibility that the treatment may have had other effects than simply increasing nutrient and water availability. The elimination of the understory vegetation surrounding each treated sapling may have led to an increased exposure of the soil to solar radiation, to an increase in soil temperature, and an increased rate of evaporation. However, since precipitation are relatively abundant in our study area, and well distributed during the whole growing season, we think it is unlikely that the treatment led a water stress for treated saplings. The trenching treatment may also have destroyed some exploratory roots and mycorrhizal connections that normally expand beyond 1 m from those saplings. Although this remains possible, preliminary investigation on a few saplings of similar size indicated that roots longer than 1 m in length were very rare. Therefore, we feel very confident that our treatment should have increased the overall availability of below-ground resources, especially nutrient availability. This concurs with the review made by Coomes and Grubb [19].

Our findings therefore clearly demonstrate the overriding importance of the above-ground resource (i.e. light availability) for all four growth variables investigated in this study, for all three hardwood species, at least up to the sapling stage (between 50 and 200 cm in height), and for up to 50% light availability. It is possible, however, that at higher light levels as found in clearcut areas that below-ground competition may occur. This concurs with results reported in several other studies done in the same area [3, 5, 6]. However, the overall lack of responsiveness of our three species contradicts many studies that have found significant effects of understory vegetation and below-ground competition exclusion treatment [17, 18, 40, 41, 48, 56].

To improve our understanding of the conditions under which exclusion of understory vegetation and below-ground competition may or may not be important for understory tree saplings, we reviewed the results obtained in several studies done on this subject, as well as the conditions under which the studies were performed (Tab. III). From this literature review, it becomes evident that simultaneous growth limitation by both above- and below-ground competition ($A > B$, $A < B$, or $A = B$ in Tab. III) is not an exceptional situation, as proposed by Gleeson and Tilman [34]. However, except in a few studies [42, 43, 50], above- and below-ground competition usually do not equally affect growth, and their relative importance appears to be related to soil conditions. The results obtained in numerous studies done in very contrasting forest ecosystems (Tab. III) indicate a predominance for below-ground competition in sites with soils of low fertility, such as sandy arid soils [2, 41, 48], abandoned oldfield [51, 56], boreal [40], coniferous forest [17]

and disturbed tropical forests [18, 20]. On the other hand, in many tropical [21, 22, 38, 46] and hardwood temperate ([37, this study] forests, where the soils are rich and where precipitation is abundant, above-ground competition (i.e. light availability) is clearly the main factor affecting understory sapling growth (A; no B in Tab. III). Interestingly, very similar conclusions were obtained independently by Coomes and Grubb [19] in their recent review of the impacts of root competition in forests.

In this review, we have also looked for a possible pattern of response in relation to the successional or tolerance status of the tree species investigated. Such a pattern, if it exists, is not completely clear from this review. However, there appears to be a slightly greater response to below-ground competition [22, 39, 46], and more globally a higher growth response to both above- and below-ground competition removal [22, 39, 42, 43], for early successional and rather shade intolerant species [19]. According to Chapin [16], this could be due to the higher growth rates of shade intolerant species which require more resources to grow and develop. However, a lack of growth response in shade tolerant species when below-ground resources increase do not necessarily mean that such trees did not respond to an increase in those resources. Burslem et al. [9] and Coomes and Grubb [18] have observed that such species could increase nutrient storage, number of leaves or branch length after trenching without any critical growth response.

Therefore, considering that precipitation in our study area is fairly high (i.e. approximately 1220 mm/year) and well distributed throughout the growing season, and that the soil is relatively nutrient rich (dystric brunisol to humo-ferric podzol), it is not surprising that our understory vegetation and below-ground competition exclusion treatment did not produce any strong growth response. Bellefleur and Pétillon [7], who studied the growth of the same three species, but at the seedling stage, following the elimination of understory vegetation over 3 years in the same area, also reported that soil moisture was not a limiting factor for the growth of these same three species.

5. CONCLUSION

Our results suggest that the exclusion of the understory vegetation and below-ground competition in this northern hardwood forest does not improve the understory soil conditions enough to trigger any significant changes in growth for any of the three species investigated in this study. Furthermore, we did not find any measurable threshold of light availability (up to 50% light availability) at which the effects of the treatment became significant (i.e. no light \times treatment interaction). A thorough review of the literature on this subject also indicated that understory tree saplings respond to the elimination of below-ground competition only in relatively nutrient poor and/or dry sites. Therefore, given the relatively nutrient rich soil and wet conditions in this study, light is the overriding factor limiting understory tree growth, at least up to the sapling stage and up to 50% light availability.

Table III. Literature review of the relative importance and strength of the effects of both above- and below-ground competition on the growth response of understory trees in various forest ecosystems and soil conditions. The table includes: authors, types of treatment applied to separate the below-ground effects from the above-ground effect, types of forest and soil conditions of the study, tree species investigated with a rough classification of their shade tolerance level, and a summary of (1) the relative response to both above (A)- and below (B)-ground competition and, (2) the overall strength of the response. References were ranked in a decreasing importance of above-ground competition importance (column 5).

Reference	Treatment applied	Forest and Soil conditions *	Species	Relative and strength of the response #
Ricard et al. (this study)	Trenching and Gradient of light regimes	Temperate hardwood forest (Quebec, Ca)	Tol (<i>Fagus grandifolia</i> , <i>Acer saccharum</i>) Mid (<i>Betula alleghaniensis</i>)	A: (no B) – Low A: (no B) – Medium
Denslow et al., 1990	Fertilisation and Contrasting location in forest (gap centre, gap edges and adjacent understory)	Tropical wet forest (Costa Rica)	Tol (<i>Miconia gracilis</i> , <i>Piper arieianum</i> , <i>Piper urostachyum</i>) Mid (<i>Miconia nervosa</i>) Int (<i>Miconia barbinervis</i> , <i>Piper sancti-felices</i> , <i>Piper culebratum</i>)	A: no B – Medium A: no B – Medium A: no B – Medium
Denslow et al., 1998	Fertilisation and Gaps	Tropical wet forest (Costa Rica)	Tol (<i>Miconia multispicata</i> , <i>Miconia gracilis</i>) Mid (<i>Miconia nervosa</i>) Int (<i>Miconia affinis</i>)	A: no B – Low A: no B – Low A = B – Medium
Ostertag, 1998	Trenching and Gaps in medium and poor soils	Tropical wet forest (Costa Rica) Tropical residual forest (Costa Rica)	Int (<i>Hampea appendiculata</i>)	A: no B – Medium A > B – Medium
Putz and Canham, 1992	Trenching and Gaps	Temperate abandoned rich area (New York, USA)	Tol (<i>Acer rubrum</i>)	A: no B – Low
Gerdel et al., 2002	Fertilisation and Above-ground clearing	Temperate heath (Italy)	Int? (<i>Vaccinium myrtillus</i> , <i>Vaccinium uliginosum</i>)	A: no B – Medium
Grubb et al., 1996 ^	Rich and poor soil samples and 4 contrasting light regimes (from 0.3 to 63% PFD)	Temperate scrubland (Rich-fertile) Temperate grassland (Poor: low P and N)	Tol (<i>Euonymus europaeus</i> , <i>Rhamnus cartharticus</i> , <i>Viburnum opulus</i> , <i>Viburnum lantana</i> , <i>Fagus sylvatica</i>) Mid (<i>Cornus sanguinea</i> , <i>Crataegus monogyna</i> , <i>Ligustrum vulgare</i> , <i>Juniperus communis</i> , <i>Rosa canina</i>)	A > B – Medium A > B – Medium
Holl, 1998	Trenching and Above-ground clearing	Tropical abandoned pasture (Costa Rica)	Int (<i>Calophyllum brasiliense</i>)	A > B – Medium
Canham et al., 1996	Fertilisation and Contrasting light regimes	Temperate substrate	Tol (<i>Acer saccharum</i>)	A > B – Medium
Dalling and Tanner, 1995	Fertilisation in rich-closed site	Tropical rain forest (Jamaica)	Int (<i>Alchornea latifolia</i> , <i>Clethra occidentalis</i> , <i>Vaccinium meridionale</i>)	A > B – Medium
Lewis and Tanner, 2000	Trenching and Gaps	Tropical central Amazonian forest (Brazil)	Tol (<i>Aspidosperma carapanauba</i>) Int (<i>Dinizia excelsa</i>)	A = B – Medium A = B – High
Peace and Grubb, 1982 ^	Fertilisation and 4 light regimes	Temperate woodland forest (England, U.K.)	Int (<i>Impatiens parviflora</i>)	A = B – Low
Putz and Canham, 1992	Trenching and Gaps	Temperate abandoned medium area (New York, USA)	Tol (<i>Acer rubrum</i>) Mid (<i>Fraxinus americana</i>)	A = B – Low A = B – Low
Latham, 1992 ^	Fertilisation and Light regimes	Sand/Peat/Vermiculite (1/3;1/3;1/3)	Tol (<i>Fagus grandifolia</i> , <i>Nyssa sylvatica</i>) Mid (<i>Castanea dentata</i> , <i>Quercus rubra</i>) Int (<i>Carya tomentosa</i> , <i>Liriodendron tulifera</i>)	A = B – Low A = B – Medium A = B – Medium
Dillenburg et al., 1993	Trenching and Above-ground space partitioning in open area	Temperate open forest (Maryland, USA)	Int (<i>Liquidambar styraciflua</i>) versus vines (<i>Lonicera japonica</i> , <i>Parthenocissus quinquefolia</i>)	A < B – Medium
Horn, 1984	Trenching and Gaps	Temperate hardwood forest (North Carolina, USA)	Tol (<i>Acer rubrum</i>) Mid (<i>Cornus florida</i>)	A > B – Low A < B – Medium
Dalling and Tanner, 1995	Fertilisation in poor-open site	Tropical mountain landslide (Jamaica)	Int (<i>Alchornea latifolia</i> , <i>Clethra occidentalis</i> , <i>Vaccinium meridionale</i>)	A < B – Medium
Christy, 1986	Trenching and Gaps	Temperate mixed forest (Oregon, USA)	Tol (<i>Tsuga heterophylla</i>)	A < B – Low
Coomes and Grubb, 1998	Trenching and Gaps	Tropical nutrient starved forest (Venezuela)	Gradient of tolerance (14 sp.)	A < B – Low to Medium
Bauhus et al., 2000	Contrasting proportion of planted trees in open area	Dry mixed forest (Australia)	Int (<i>Eucalyptus globulus</i> , <i>Acacia mearnsii</i>)	A < B – Medium
Jäderlund et al., 1997	Above- and below-ground space partitioning	Northern boreal forest (Sweden)	Tol (<i>Picea abies</i>)	A < B – High
Wilson, 1993	Plantation in open grassland	Grassland snowy mountain (Australia)	Int (<i>Eucalyptus pauciflora</i>)	A < B – High
Putz and Canham, 1992	Trenching and Gaps	Temperate abandoned nutrient poor area (New York, USA)	Tol (<i>Acer rubrum</i>)	B; no A – Low
Kadmon, 1995 †	Watering in a natural gradient of soil moistures	Sandy Mediterranean area (Israel)	Unkown tol (<i>Stipa capensis</i>)	B; no A – High
Pantastico-Caldas and Venable, 1993 †	Natural gradient of soil moistures along a hill	Dry desert (Arizona, USA)	Unkown tol (<i>Plantago patagonica</i>) Unkown tol (<i>Pectocarya recurvata</i>)	B; no A – Medium B; no A – Medium

Tol = Shade tolerant species; Mid = Intermediate tolerant species; Int = Shade intolerant species. A = Above-ground competition; B = Below-ground competition. ^: Studies carried out in controlled conditions. †: Studies performed on herbaceous species. *: Soil categories are indicated according to authors description in their material and methods. #: Results were standardised and represent first Above- and Below-ground competition rank and second the impact of competition(s) on species performance.

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en BIOLOGIE FORESTIERE

VU, APPROUVÉ ET PERMIS D'IMPRIMER N°940

Nancy, le 7 juin 2004

Le Président de l'Université



**INFLUENCE DE LA DISPONIBILITÉ EN LUMIÈRE ET DE LA TAILLE
SUR LES ATTRIBUTS FONCTIONNELS ET LE BILAN EN CARBONE DE L'ARBRE**

Résumé:

À l'échelle de l'individu, la tolérance à l'ombre des arbres est définie par la somme de nombreux paramètres qui déterminent leur bilan carboné. Dans cette étude, différentes échelles de processus (physiologie foliaire, morphologie de cime, répartition de biomasse) ainsi que le fonctionnement intégré à l'échelle de l'individu (efficacité interception de lumière et échanges gazeux des parties aériennes et souterraines) ont donc été étudiés chez l'érable à sucre (*Acer saccharum* Marsh., tolérant à l'ombre) et le bouleau jaune (*Betula allghaniensis* Britt., semi tolérant à l'ombre). L'ensemble des résultats démontre qu'en plus de la disponibilité en lumière, la taille des individus représente un facteur important de variation de la performance des semis. De ce fait, la performance d'un individu dans un environnement lumineux donné pourrait ne pas être constante au cours de son développement et être très dépendante de la taille atteinte sous cet environnement.

Mots clés:

Azote foliaire, Bouleau jaune, Echanges gazeux, Erable à sucre, Interception de lumière, Morphologie de cime, Répartition de biomasse, Tolérance à l'ombre.

**INFLUENCE OF LIGHT AVAILABILITY AND INDIVIDUAL SIZE ON TREE
TRAITS
AND TREE CARBON BALANCE**

Abstract:

At the individual tree scale, species shade tolerance abilities are governed by the sum of numerous traits, which, in turn, define tree carbon balance. In this study, contrasting scales of processes (leaf physiology, crown morphology and biomass partitioning) as well as the individual integrated functioning (light interception efficiency, above- and below-ground gas exchanges) were studied on sugar maple (*Acer saccharum* Marsh., a shade tolerant species) and yellow birch (*Betula allghaniensis* Britt., a mid shade tolerant species). Results showed the additional importance of individual size, alone or in interaction with light availability, in the variation of seedling performance. Thus, species shade tolerance may not be constant during whole tree life span and may be highly dependent on the size reached by an individual under any given light environment.

Key words:

Biomass partitioning, Crown morphology, Gas exchanges, Leaf nitrogen, Light interception efficiency, Shade tolerance, Sugar maple, Yellow birch.
