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LISTE DES ABRÉVIATIONS

Symbole	Définition	Unité
A_c , et A_j	Limitation de l'assimilation nette par la Rubisco et par le flux d'électrons	$\mu\text{mol m}^{-2} \text{s}^{-1}$
AGB	Biomasse aérienne	masse anhydre
A_{max}	Photosynthèse maximal à saturation lumineuse	$\mu\text{mol m}^{-2} \text{s}^{-1}$
A_n	Photosynthèse nette foliaire	$\mu\text{mol m}^{-2} \text{s}^{-1}$
A_{qe}	Rendement quantique apparent	$\text{g } \mu\text{mol}^{-1}$
C_a	Pression partielle atmosphérique en CO_2	$\mu\text{mol mol}^{-1}$
C_b	complexe protéine-chlorophylle	mmol g^{-1}
C_i	Pression intercellulaire en CO_2	$\mu\text{mol mol}^{-1}$
CV	Volume de l'houpier	m^3
D	Diamètre basal de l'arbre à 10 cm du sol	cm
dbh	Diamètre à hauteur de poitrine	cm
DM	Masse anhydre	
FRD	Densité de racines fines	g cm^{-3}
Gs	Conductance stomatique	$\text{mmol m}^{-2} \text{s}^{-1}$
LAI	Indice de la surface foliaire	
Lcp	Point de compensation de la lumière	$\mu\text{mol PAR m}^{-2} \text{s}^{-1}$
LCR	Ratio d'houpier vivant	
I_n	Rayonnement reçu par un plan horizontal à un niveau n à l'intérieur de la canopée	
J	Vitesse de transport des électrons	$\mu\text{mol electron m}^{-2} \text{s}^{-1}$
J_{max}	Vitesse maximale de transport d'électron	$\mu\text{mol electron m}^{-2} \text{s}^{-1}$
J_{mc}	Flux potentiel d'électrons par unité de cytochrome f	$\frac{\text{mol}}{\text{s}}(\text{cytochrome f})^{-1}$
K_a	Coefficient d'extinction du rayonnement	
K_c	Constante de Michaelis-Menten pour la carboxylation	$\mu\text{mol mol}^{-1}$
K_o	Constante de Michaelis-Menten pour l'oxygénation	$\mu\text{mol mol}^{-1}$
M_a	Masse surfacique foliaire	g m^{-2}
N_{area}	Azote foliaire par unité de surface foliaire	g m^{-2}
N_{mass}	Concentration massique de l'azote foliaire	mg g^{-1}

SI	Indice d'élancement	
Θ_1	Angles d'insertion des branches	degré
Θ_2	Angle de terminaison des branches	degré
PAR	Rayonnement photosynthétiquement actif	$\mu\text{mol m}^{-2}\text{s}^{-1}$
P_{et}	Proportion d'azote allouée au transport d'électron	
P_i	Proportion d'azote alloué à l'interception de lumière	
PNUE	Efficacité d'utilisation photosynthétique de l'azote	$\mu\text{mol CO}_2 \text{ g}^{-1} \text{ N s}^{-1}$
P_r	Proportion d'azote allouée à la carboxylation	
[O]	Pression partielle d'Oxygène dans les espaces sous stomatiques	Pa
R	Constante des gaz parfait	$\text{J mol}^{-1}\text{K}^{-1}$
Rd	Respiration à l'obscurité	$\mu\text{mol m}^{-2} \text{ s}^{-1}$
REML	Maximum de vraisemblance restreint	
RH	Humidité relative de l'air	%
$S_{\text{c/o}}$	Coefficient de spécificité de la Rubisco pour le CO_2 par O_2	
SLA	Surface foliaire spécifique	$\text{cm}^2 \text{ g}^{-1}$
T_K	Température foliaire	k
V_{cmax}	Vitesse maximale de carboxylation	$\mu\text{mol m}^{-2} \text{ s}^{-1}$
V_{cr}	Activité spécifique de la Rubisco	$\mu\text{mol g}^{-1} \text{ s}^{-1}$
VPD	Déficit de pression de vapeur de l'air	mba
ΔH_a	Énergie d'activation	J mol^{-1}
ΔH_d	Énergie de désactivation	J mol^{-1}
ΔS	terme d'entropie	
Γ^*	Point de compensation pour le CO_2	Pa

RÉSUMÉ DE LA THÈSE

Cette thèse avait pour objectifs i) d'étudier la réponse morphologique et physiologique du peuplier hybride aux variations de l'intensité de la compétition intraclonale, ii) de comparer la productivité des plantations pures vs mixtes de peuplier hybride avec celles de l'épinette blanche ou de Norvège et iii) de développer un modèle éco-physiologique de la photosynthèse à l'échelle de la canopée.

Trois parcelles expérimentales ont été installées en 2003 en Abitibi- Témiscamingue, Québec, Canada. Deux clones de peuplier hybride (*P. balsamifera* x *trichocarpa* (BT747) et *P. maximowiczii* x *balsamifera* (MB915)), une famille génétiquement améliorée d'épinette blanche (*Picea glauca* (WS)) et une famille génétiquement améliorée d'épinette de Norvège (*Picea abies* (NS)) ont été utilisés. Le dispositif expérimental comprend trois différents espacements (1×1 m, 3×3 m et 5×5 m) et trois types de plantations : pure épinette, pure peuplier hybride et mélange peuplier hybride-épinette (1:1).

Après six saisons de croissance, La réponse en termes de croissance des deux clones de peuplier hybride aux changements de l'espacement entre les arbres a été différente. L'accroissement de la compétition intraclonale avec la réduction de l'espacement entre les arbres s'est traduit par une réduction de la croissance en hauteur et en diamètre à hauteur de poitrine (dhp) chez le clone MB915. Chez le clone BT747, la croissance en hauteur a été favorisée par l'intensification de la compétition alors que la croissance en dhp a été insensible aux variations de la compétition.

La réponse morphologique des deux peupliers hybrides à l'intensification de la compétition entre les arbres a été caractérisée par une réduction du volume du houppier, l'augmentation de la courbature des branches, la réduction de la croissance et de la biomasse allouée aux branches. La réduction de la biomasse allouée au feuillage a été observée seulement chez le clone MB915. Ces changements structuraux ont contribué à la migration de la surface foliaire vers la strate supérieure du houppier. La profondeur des racines, l'allocation de la biomasse aux racines et le degré de syllepsie n'ont pas été affectés par l'intensité de la compétition intraclonale.

L'accroissement de la compétition, avec la réduction de l'espacement s'est traduit au niveau physiologique et à l'échelle du houppier par : (1) une réduction de la teneur en azote foliaire par unité de surface foliaire (N_{area}), (2) une augmentation de la surface foliaire spécifique (SLA), (3) une augmentation de l'utilisation photosynthétique de l'azote (PNUE), (4) une réduction de la respiration à l'obscurité et (5) une réduction du point de compensation lumineuse (L_{cp}). La pente de la relation entre la photosynthèse à saturation lumineuse (A_{max}) et N_{area} était la plus forte lorsque l'espacement était le plus faible et elle était plus grande pour le clone MB915 par rapport au clone BT747.

La mixture entre le peuplier hybride et l'épinette a été bénéfique pour la croissance des deux clones de peuplier hybride en espacement 1×1 m et 3×3 m. Cependant, la croissance des épinettes était, à ce stade de la plantation, généralement insensible au déploiement et à l'espacement. Due aux grandes différences de croissance entre le peuplier hybride et l'épinette, la biomasse produite après six années de croissance en parcelles mixtes a été inférieure à celle produite dans les parcelles monoclonales de peuplier hybride à l'exception de la mixture entre le clone MB915 et l'épinette blanche. La distribution verticale des racines fines a cependant été similaire entre les différents déploiements. L'interaction positive entre le peuplier hybride et l'épinette est attribuée à la stratification de la canopée qui a par conséquent réduit la compétition pour la lumière dans la parcelle.

Le modèle développé dans cette thèse se veut plus réaliste dans la représentation de l'hétérogénéité physiologique au sein de la canopée par rapport aux modèles existants. Ainsi, les paramètres de la photosynthèse ont été modélisés en fonction des propriétés stœchiométriques et morphologiques des feuilles. La conductance stomatique a été modélisée par l'approche empirique de Ball (Ball et al., 1987). Le passage de l'échelle foliaire à l'échelle de la canopée a été réalisé par la subdivision de la canopée en quatre couches verticales proportionnellement à la hauteur de la canopée. Les résultats montrent une très bonne adéquation du modèle pour la prédiction des échanges gazeux foliaires (photosynthèse et conductance stomatique). Les simulations à l'échelle de la canopée ont montré une nette corrélation entre la photosynthèse à l'échelle de la canopée et l'indice de surface foliaire (LAI).

Nous concluons que l'acclimatation des arbres aux changements de l'intensité de la compétition intraclonale est un processus contrôlé à la fois par la morphologie et la physiologie de l'arbre (whole plant process). Principalement, l'acclimatation se traduit d'une part par la modulation de l'orientation et l'allocation de la biomasse aux branches pour une meilleure distribution de la surface foliaire totale de l'arbre et d'autre part par la modulation de surface foliaire spécifique (SLA) pour une meilleure utilisation photosynthétique de l'azote à l'échelle de la feuille, une réduction de la respiration foliaire, une optimisation de la distribution de l'azote à l'intérieur du houppier. Nous pensons aussi que les plantations mixtes de peuplier hybride-épinette pourraient être plus productives ou du moins similaires aux parcelles monoclonales à mesure que la compétition s'accroît dans les parcelles pures de peuplier.

Mots-clés : Peuplier hybride; foresterie à courte rotation; compétition; photosynthèse; azote foliaire SLA, plantation mixte; modélisation mécanistique.

1. INTRODUCTION GÉNÉRALE

1.1 Mise en contexte

La foresterie à courte rotation (FCR) est un concept de la sylviculture apparu dans les années 60 pour répondre à la demande accrue de bois à l'échelle planétaire (FAO 2001). Elle a bénéficié du progrès technologique de l'amélioration génétique, ce qui a permis l'émergence de nouvelles espèces issues de croisements interspécifiques de différentes espèces de peuplier. Le peuplier hybride est la principale espèce utilisée en FCR dans les régions nordiques (Weih 2004). Les clones de peuplier hybride utilisés au Canada résultent des croisements interspécifiques entre trois espèces de la section Tacamahaca (*Populus balsamifera*, *P. maximowiczii*, et *P. trichocarpa*) et deux espèces de la section Aigeiros (*P. deltoides*, et *P. nigra*). Le peuplier hybride est caractérisé par une croissance juvénile rapide et une grande production de biomasse par rapport aux espèces naturelles (DeBell and Harrington 1997; Dickmann et al. 2001). Il a été rapporté que le rendement annuel en biomasse chez le peuplier hybride est de l'ordre de 10 Mg de matière sèche par hectare et par année en régions boréales (Christersson 2010), et jusqu'à 35 Mg en régions tempérées (DeBell et al. 1996; Dowell et al. 2009; Rae et al. 2004). Le peuplier hybride peut être utilisé pour diverses applications telles que le bois de déroulage, le sciage, les panneaux et les pâtes à papier. Au Québec, le Ministère des Ressources Naturelles et de la Faune (MRNF), direction de la recherche forestière, a produit une quarantaine de clones issus de divers croisements pour répondre aux spécificités de chaque région.

L'intérêt grandissant envers le peuplier hybride s'inscrit dans une thématique d'aménagement forestier durable visant le maintien des services écologiques de la forêt naturelle sans compromettre la demande croissante en bois dans le monde (FAO 2001). En région boréale canadienne, le peuplier hybride est une espèce prometteuse pour la restauration des friches agricoles abandonnées et la création d'une nouvelle et durable source de bois, permettant par le fait même de diminuer la pression de récolte en forêt naturelle. La quantité et la qualité de la biomasse produite en FCR est le résultat de nombreuses et complexes interactions éco-physiologiques. En effet, l'environnement de l'arbre peut être

modifié de plusieurs façons, notamment par le choix du matériel génétique, de l'espacement entre les arbres et du type de déploiement. La compréhension des mécanismes-clés de la croissance de l'arbre en relation avec son environnement est essentielle afin d'optimiser la productivité. De plus, la capacité de prévoir les conséquences à long terme des changements des variables climatiques sur l'écophysiologie des arbres est utile pour garantir la durabilité de la FCR.

1.2 Espacement, compétition et productivité

L'espacement entre les arbres est un facteur important dans l'évaluation de la productivité chez le peuplier hybride, car il détermine l'intensité et le début de la compétition pour les ressources du milieu (lumière, éléments nutritifs, eau) entre les individus. Par conséquent, l'espacement entre les arbres influence directement la dynamique du peuplement et la mortalité induite par la compétition. L'espacement entre les arbres a également une influence sur plusieurs pratiques sylvicoles culturales, telles que la fertilisation, le type de déploiement (monoclinal, polyclonal ou mixte) et la gestion des mauvaises herbes. De nombreuses études ont rapporté des variations dans la réponse des clones de peuplier hybride aux variations de l'espacement entre les arbres. Ces études se sont concentrées la plupart du temps sur la réponse des arbres aux variations de l'espacement en terme de croissance comme la hauteur, le diamètre à hauteur de poitrine (dhp), le volume des tiges et la biomasse aérienne (Cannell 1980; DeBell et al. 1996; Fang et al. 1999). Cependant, il y a encore peu d'information concernant l'effet des variations de l'espacement entre les arbres sur les processus morpho-physiologiques qui permettent d'optimiser l'occupation du site et d'utiliser de la façon la plus efficiente les ressources du milieu afin de maximiser la productivité. En particulier, on en sait peu sur les effets de l'espacement initial sur les processus clés de la production de biomasse (les composantes ou les déterminants de la productivité): la répartition de la biomasse entre les différentes parties de l'arbre, l'architecture du houppier, l'aspect physiologique (échanges gazeux) et l'architecture racinaire.

1.2.1 Acclimatation

L'acclimatation est la réponse phénotypique des arbres aux différents changements environnementaux biotiques et abiotiques (Tomé and Verwijst 1996). Il s'agit du processus par lequel l'aspect morpho-physiologique des plantes est modulé en fonction des paramètres environnementaux. Par conséquent, l'acclimatation est le processus par lequel les modifications physiologiques et/ou morphologiques permettent d'augmenter la capacité de gain de carbone par la plante dans un nouvel environnement (Givnish 1988). Le processus d'acclimatation permet aux plantes de compenser la diminution des ressources par l'amélioration de l'absorption et/ou l'efficacité d'utilisation de ces ressources (Anderson et al. 1995; Evans and Poorter 2001; Grams and Andersen 2007). La compréhension de l'acclimatation des plantes en réponse à un stress environnemental est essentielle pour accroître la production de biomasse (Givnish 1988; Niinemets and Valladares 2004). En effet, la compréhension du mécanisme de l'acclimatation à l'échelle de l'individu va permettre (i) d'améliorer la fiabilité des modèles physiologiques à simuler la croissance sous diverses conditions du milieu (ii) d'adapter la sélection du matériel génétique et des pratiques sylvicoles aux conditions du site. En conditions de forte densité de peuplement, la lumière devient un facteur limitant pour la croissance des arbres. Dans ces conditions, les arbres optent pour des changements structurels et physiologiques, tels que la modification de l'allocation de carbone aux différents compartiments de l'arbre (Weiner et Fishman 1994; Walter et Reich 1999; Delagrangé *et al.* 2004), les changements dans l'architecture des cimes et la morphologie et la physiologie du feuillage (Tomé et Verwustt 1996; Gardiner et Hodges 1998; Canham *et al.* 1999). La capacité d'acclimatation des plantes aux conditions du milieu varie considérablement entre les espèces.

1.2.2 Compétition et allocation de biomasse

La croissance de l'arbre est un processus dynamique qui résulte de l'interaction permanente entre la morphologie aérienne et racinaire, les processus physiologiques et l'allocation de biomasse (Lambers et al. 2008). La modulation de l'allocation de la biomasse aux différentes parties de l'arbre est un processus central dans l'acclimatation des arbres à la compétition pour les ressources du site (Casper et al. 1998; Lambers et al. 2008; McCarthy

and Enquist 2007). Selon la théorie d'optimalité, les arbres répondent aux conditions suboptimales par la réduction du taux de croissance relative et la modulation de l'allocation de la biomasse afin de réduire l'effet négatif du facteur limitant sur la croissance (Lacointe 2000; Lambers et al. 2008). Ceci permet d'optimiser la croissance en rapport avec les ressources du milieu. En condition de forte compétition pour la lumière (les peuplements denses), les arbres d'espèces intolérantes à l'ombre adoptent une stratégie de croissance préférentielle pour la hauteur comparativement au diamètre (Grams and Andersen 2007; Lanner 1985). Ceci nécessite la réduction du ratio de biomasse alloué au méristème secondaire (croissance en diamètre) comparativement au méristème apical (croissance en hauteur) mais aussi par la réduction du ratio de biomasse alloué aux branches au profit de la tige (Grams and Andersen 2007; Ilomäki et al. 2003). En plus de la compétition pour la lumière en condition de forte densité de peuplement, les arbres sont en compétition pour les éléments nutritifs du sol et l'eau du sol. La théorie d'optimalité veut que la biomasse soit allouée en ordre de priorité pour l'assimilation de la ressource la plus limitante (Bloom et al. 1985; Chapin et al. 1987; Lambers et al. 2008; McCarthy and Enquist 2007). Ceci a pour but de converger vers un état d'équilibre où la croissance est co-limitée par toutes les ressources du milieu. Cette approche trouve son fondement dans le modèle biochimique de l'assimilation du carbone (Farquhar et al. 1980) où la photosynthèse est limitée soit par la vitesse de carboxylation ou le flux d'électrons, autrement dit soit par la concentration d'azote foliaire ou la lumière. Des données concernant les plantes herbacées supportent ce modèle d'allocation, avec une allocation préférentielle de la biomasse pour le système racinaire en cas de compétition pour les ressources du sol (Casper et al. 1998; McCarthy and Enquist 2007). Les arbres ne suivent pas toujours cette analogie (Casper et al. 1998). En effet, les arbres se différencient des plantes herbacées par l'influence de l'aspect structurel et phénologique sur leur physiologie (Grams and Andersen 2007). De plus, le degré d'acclimatation du système racinaire et du houppier à la compétition pour les ressources du milieu varie largement entre les espèces (Cahill 2003; Lepik et al. 2004; Shipley and Meziane 2002). La théorie de l'équilibre structure-fonction comme approche alternative suggère que le patron de l'allocation de la biomasse vise le maintien de (1) l'équilibre structurel entre le système racinaire et la structure aérienne et (2) l'équilibre structure-fonction (Müller et al.

2000; Thornley 1991). Conséquemment, le patron d'allocation de la biomasse varie selon le stade phénologique et la taille de l'arbre.

1.2.3 Compétition, morphologie aérienne et racinaire

La structure du houppier joue un rôle considérable dans la productivité en FCR (Ceulemans et al. 1990; Hall 1994; Wu and Stettler 1998). Plusieurs études ont montré que la croissance en diamètre était linéairement liée aux dimensions de la cime de l'arbre (Foli et al. 2003; Hemery et al. 2005). Cette importance de la cime s'est matérialisée par l'intérêt grandissant des programmes d'amélioration génétique pour la sélection des traits fonctionnels qui permettent d'obtenir une architecture idio-type de la cime (Ceulemans et al. 1990; Dickmann et al. 2001; Wu and Stettler 1998). La distribution spatiale du feuillage, la dimension des branches, leur nombre et leur orientation sont les principaux éléments qui définissent l'architecture de la cime et qui influencent l'efficacité d'occupation de l'espace et l'efficacité d'interception de la lumière (Burk et al. 1983; Ceulemans et al. 1990) et par le fait même le degré d'acclimatation des arbres à la compétition pour la lumière (Burk et al. 1983; Ceulemans et al. 1990; Hall 1994). Chez le peuplier hybride on note la présence de deux types de branches (i) sylleptiques dont la formation et l'élongation du méristème latéral (bourgeon) se produisent sans repos préalable; (ii) proleptiques, dont le méristème latéral subit une phase de dormance avant de donner naissance à une branche (Mitchell et al. 1992). Plusieurs auteurs ont mis en évidence l'influence de la syllepsie (pourcentage des branches sylleptiques) sur la productivité (Wu and Stettler 1994, 1998). Cependant, l'influence de la syllepsie sur l'acclimatation à la compétition reste inconnue.

Bien que la partie racinaire soit un élément important dans la définition de la productivité en FCR, la majorité des études effectuées ont focalisé sur la croissance et le développement de la partie aérienne en raison de la facilité d'étude de cette partie des arbres et son importance en tant que produit final récolté. Les connaissances sur la partie souterraine (racines) restent insuffisantes à l'heure actuelle. En particulier, on ignore l'impact de la compétition sur le développement et la distribution spatiale de la biomasse racinaire chez le peuplier hybride.

1.2.4 Compétition et physiologie

Les processus physiologiques, particulièrement la photosynthèse, permettent aux plantes d'utiliser l'énergie solaire pour l'acquisition de CO₂ atmosphérique et la synthèse des hydrates de carbone qui sont par la suite incorporés dans la biomasse végétale. La photosynthèse comme processus central dans la croissance de l'arbre est fortement et positivement liée à la disponibilité de la lumière et de l'azote, mais aussi à la teneur en eau du sol ainsi qu'aux conditions climatiques (la température, le déficit de pression de vapeur d'eau de l'atmosphère (VPD), l'humidité relative de l'air (RH), la vitesse du vent).

L'acclimatation physiologique (essentiellement la photosynthèse) à la compétition permet d'augmenter l'efficacité de capture de la lumière et l'utilisation de l'azote. L'acclimatation de la photosynthèse à l'augmentation de la compétition pour la lumière à l'intérieur de la canopée se fait par l'augmentation de la surface foliaire spécifique (SLA, ratio surface foliaire: masse sèche) et la modification de l'allocation de l'azote foliaire aux différentes composantes de la photosynthèse (capture de lumière, transfert d'électrons et carboxylation) (Evans et Poorter 2001). La modulation de la SLA en réponse aux changements de la lumière permet aux plantes d'optimiser l'investissement de l'azote dans le feuillage (Hirose et al. 1988). Par conséquent, on s'attend à une forte corrélation entre le gradient lumineux et la distribution de l'azote foliaire à l'intérieur de la canopée. La modulation de la SLA est aussi au centre du mécanisme d'acclimatation des feuillages aux multiples facteurs environnementaux (lumière, fertilité et teneur en eau du sol). En effet, il a été rapporté que la surface foliaire spécifique était positivement corrélée au taux de précipitation annuel (Gouveia and Freitas 2008) et négativement corrélée à la fertilité du sol (Chapin et al. 1987; Rosati et al. 1999). La surface foliaire spécifique augmente avec la diminution de l'épaisseur de la feuille ce qui contribue à : (i) augmenter la transmittance de la lumière au niveau de la feuille et de ce fait augmenter l'interception de la lumière à l'intérieur de la canopée; (ii) diminuer le point de compensation lumineuse, ce qui permet d'augmenter le taux d'assimilation de carbone à faible luminosité; et (iii) diminuer les coûts liés à la construction du feuillage. L'augmentation de la surface foliaire spécifique se traduit par une réduction de l'allocation de l'azote au processus responsable de capture de la lumière ce qui

permet d'augmenter la proportion d'azote allouée à la carboxylation et ainsi de maximiser l'efficacité photosynthétique d'utilisation de l'azote foliaire (Chapin et al. 1987; Hikosaka and Terashima 1995; Hirose and Werger 1987; Poorter and Evans 1998).

1.3 Déploiement mixte vs monoclonal

Les plantations forestières polyclonales (plusieurs clones de la même espèce) ou mixtes (plusieurs espèces) par opposé aux plantations monoclonales font depuis quelque temps l'objet d'un intérêt croissant de la part des forestiers. Cet intérêt se manifeste essentiellement par les problèmes ou craintes phytosanitaires liés aux cultures monoclonales (ex : *Melampsora sp.*). L'idée générale est que les peuplements mixtes constituent un bon moyen pour la lutte contre les pathogènes et pourraient mieux correspondre à des objectifs de diversification écologique (DeBell et Harrington 1993). Les individus de différentes espèces en plantation mixte peuvent interagir négativement ou positivement. L'interaction négative ou l'exclusion a lieu quand le degré de compétition interspécifique est supérieur à celui de la compétition intraspécifique. Le phénomène d'exclusion se produit quand les espèces en question utilisent les ressources du milieu de la même manière, autrement dit quand les espèces ont la même niche écologique. L'interaction positive entre les individus de différentes espèces mises ensemble a lieu quand ces espèces utilisent les ressources du milieu différemment, ce qui se traduit par une faible compétition interspécifique comparativement à la compétition intraspécifique. L'interaction positive entre espèces permet d'augmenter la productivité des peuplements mixtes comparativement aux peuplements monospécifiques. Théoriquement, l'interaction positive entre espèces peut être subdivisée en trois catégories : la facilitation, la complémentarité et l'effet de sélection.

1.3.1 La complémentarité ou 'évitement de l'exclusion compétitive'

Le mécanisme de la complémentarité entre espèces suppose l'évitement de l'exclusion compétitive grâce à la séparation des niches écologiques des espèces en mélange. Ce mécanisme permet d'accroître l'efficacité de l'utilisation des ressources du milieu. La stratification de la canopée est l'un des modèles de complémentarité le plus étudiée dans la littérature scientifique. Cela se produit lorsque la combinaison d'espèces dans le mélange diffère dans le taux de croissance en hauteur, leur tolérance à l'ombre et leur phénologie. La

stratification du système racinaire et la différence dans la durée de l'activité photosynthétique peuvent aussi engendrer une complémentarité entre espèces. Plusieurs résultats ont montré l'effet positif de la stratification de la canopée (Menalled et al. 1998) et de la distribution différentielle des racines (Ewel et Mazzarino 2008) sur la productivité.

1.3.2 La facilitation

La facilitation se produit quand une espèce est avantagée par la présence d'une autre espèce. L'exemple le plus commun et bien étudié qui appuie ce principe écologique est le mélange d'espèces d'*Eucalyptus* avec les espèces fixatrices d'azote d'*Acacia*. Le mélange des deux espèces fournit un niveau élevé de productivité comparativement aux plantations mono-spécifiques d'eucalyptus (Bauhus et al 2000; Binkley et al 2003; Forrester et al 2004). La facilitation peut également avoir lieu lorsque la décomposition de la litière d'une espèce est accélérée par la présence de la litière d'autres espèces (Forrester et al. 2006; Gartner et Cardon 2004). Ceci est principalement dû au fait que les feuilles de mélange d'espèces affectent les facteurs biologiques et les aspects physico-chimiques de la litière mélangée (Gartner et Cardon 2004).

1.3.3 L'effet de sélection

L'effet de sélection repose sur la probabilité de l'existence, parmi les espèces en mixture, d'une espèce ayant des traits fonctionnels particuliers (espèce dominante et compétitive) et qui aurait un effet majeur sur l'augmentation de la productivité en mixture (Hooper et al 2005; Loreau et Hector 2001). La séparation entre la complémentarité et l'effet de sélection (l'effet d'échantillonnage) n'a pas été toujours évident. En effet, ces deux mécanismes ne sont pas forcément exclusifs et peuvent opérer simultanément. Il se pourrait également qu'il s'agisse de deux extrêmes d'un même processus. En effet, les deux mécanismes découlent du même processus naturel de sélection qui aboutit à l'habilité de coexistence entre espèces.

1.4 Modélisation de l'assimilation de carbone et de la productivité

Les modèles de croissance des arbres peuvent être classés en deux catégories: les modèles empiriques 'statistiques' et les modèles physiologiques plus spécifiquement nommés

modèles basés sur les processus ou également modèles mécanistiques. Les modèles empiriques sont généralement basés sur l'établissement de relations empiriques statistiques entre les paramètres de la croissance et les conditions spécifiques du site sans aucune référence aux processus physiologiques et biophysiques qui régissent la croissance. Les modèles empiriques sont inadéquats pour refléter des changements dans les conditions de croissance. Les modèles basés sur les processus sont conçus en se basant sur notre compréhension biophysique et biochimique des phénomènes biologiques qui contrôlent la croissance des arbres. Les modèles basés sur les processus reçoivent une attention de plus en plus importante due principalement au rôle qu'ils peuvent jouer dans l'amélioration de notre compréhension des mécanismes biologiques de la croissance, dans la prédiction de l'impact des changements climatiques sur la productivité forestière et dans l'aide à la prise de décision dans l'aménagement forestier.

Les modèles basés sur les processus sont généralement subdivisés en trois grands compartiments: l'assimilation du carbone et la respiration, l'allocation du carbone, et l'assimilation de l'azote. Dans cette étude, nous nous limitons à la première partie qui est l'assimilation du carbone.

Le taux d'assimilation du carbone à l'échelle de la feuille est généralement modélisé par le modèle biochimique de Farquhar et von Caemmerer (1981), qui peut se résumer à deux principales réactions: la première, dite photodépendante, a lieu dans les membranes thylakoïdales et fait intervenir les deux photosystèmes et la chaîne des transporteurs membranaires des électrons. La seconde réaction dite photo-indépendante a lieu dans le stroma et fait intervenir la ribulose biphosphate carboxylase/oxygénase (Rubisco). Le modèle de Farquhar et von Caemmerer (1981) suppose trois limitations de la photosynthèse, soit par l'activité de la Rubisco, la régénération du RubP ou la vitesse d'utilisation des trioses-phosphate.

Si la modélisation de l'assimilation du carbone à l'échelle de la feuille est passablement maîtrisée, le passage à l'échelle de la canopée (scaling-up) demeure insatisfaisant pour reproduire la complexité morpho-physiologique de l'arbre. À ce sujet trois approches existent: la première approche dite «Big-leaf» fait une analogie avec la situation des plantes herbacées en considérant la canopée comme une grosse feuille dont les processus physiologiques, notamment les paramètres de la photosynthèse (V_{cmax} et J_{max}) sont

linéairement liés à la lumière à l'intérieur de la canopée (Running et Coughlan 1988). La deuxième approche consiste à subdiviser la canopée en deux types de feuilles, soit des feuilles de lumière et des feuilles d'ombre (sunlit et shaded leaves). Plusieurs observations écophysiologicals ont montré l'existence de changements physiologiques des feuilles à différents niveaux dans la canopée, ce qui met en cause la capacité des modèles simplistes (grosse feuille ou deux feuilles) à simuler le taux de photosynthèse à l'échelle de la canopée (Sellers *et al.* 1992; Raulier *et al.* 1999). La troisième approche consiste à subdiviser la canopée en plusieurs couches. Ces derniers modèles semblent être plus robustes que les deux premiers types pour expliquer l'hétérogénéité, la complexité et la non-linéarité des processus écophysiologicals au sein de la canopée (Raulier *et al.* 1999; Larocque 2002).

1.5 Objectifs de la thèse

La quantité et la qualité de la biomasse produite en FCR est le résultat de nombreuses et complexes interactions éco-physiologicals. En effet, l'environnement de l'arbre peut être modifié de plusieurs façons, notamment par le choix de l'espacement entre les arbres et du type de déploiement. La compréhension des mécanismes-clés de la croissance de l'arbre en relation avec son environnement est essentielle afin d'optimiser la productivité. De plus, la capacité de prévoir les conséquences à long terme des changements des variables climatiques sur l'écophysiological des arbres est utile pour garantir la durabilité de la FCR.

Le deuxième chapitre de cette thèse a consisté à étudier l'effet de la compétition intracolonale sur la morphologie aérienne et racinaire ainsi que le patron d'allocation de biomasse des arbres chez deux clones de peuplier hybride (MB915; *P. maximowiczii* × *P. balsamifera* et BT747; *P. balsamifera* × *P. trichocarpa*). Un dispositif expérimental en parcelles divisées (split-plot) a été mis en place dans la région de l'Abitibi-Témiscamingue en mai 2003. Le design comprend trois espacements initiaux : 1×1 m (10,000 tiges/ha), 3×3m (1,111 tiges/ha) et 5×5m (400 tiges/ha) en parcelle principale et les deux clones de peuplier hybride en tiroir (parcelle élémentaire). Les hypothèses posées étaient qu'une meilleure acclimatation des arbres à l'augmentation de l'intensité de la compétition intracolonale se traduirait par une augmentation de l'efficacité d'utilisation de l'espace via, i) la réduction de la longueur, le diamètre, l'angle d'origine et l'angle de terminaison des branches, ii) l'augmentation du degré de syllepsie des branches, iii) l'augmentation de l'allocation de

biomasse pour la partie racinaire, et iv) l'augmentation de la profondeur d'enracinement. Les mesures effectuées portaient sur les paramètres de la croissance, les caractéristiques du houppier (hauteur, diamètre et projection horizontale et le degré de syllepsie) les caractéristiques des branches (longueur, diamètre, angle à l'origine et à la terminaison par rapport à la tige principale), la distribution spatiale du feuillage, la proportion de biomasse dans chaque partie de l'arbre (tige, branches, feuilles et racines), la profondeur, le diamètre et la longueur des racines.

Le troisième chapitre s'est focalisé sur l'aspect physiologique de la compétition et avait pour but de déterminer les attributs fonctionnels impliqués dans l'acclimatation de la photosynthèse aux variations des ressources du milieu chez les deux clones de peuplier hybride. Nous avons supposé que l'augmentation de la compétition pour les ressources du milieu se traduirait par l'augmentation de la surface foliaire spécifique et de l'efficacité de l'utilisation photosynthétique de l'azote. Pour répondre à ces questions, le houppier des arbres échantillonnés a été subdivisé verticalement en quatre strates. Des feuilles de 3 points radiaux sur les 3 premières strates ainsi qu'une feuille de la pousse terminale ont été échantillonnées et pour lesquelles on a mesuré les échanges gazeux foliaires, la surface foliaire spécifique, l'azote foliaire, et l'efficacité de l'utilisation photosynthétique de l'azote et ce pour trois saisons de croissance successives.

Le quatrième chapitre avait pour but d'évaluer la croissance en déploiement pur et mixte à différentes densités de plantation des deux clones de peuplier hybride et de deux familles d'épinette améliorées génétiquement. Nous avons émis les hypothèses suivantes: i) la croissance des espèces étudiées serait supérieure en mixture (épinette-peuplier hybride) comparativement à leurs croissances en déploiement monoclonal grâce aux différenciations spatiales des structures racinaires et aériennes des deux espèces en mixture, ii) la disponibilité en éléments nutritifs pour chaque arbre diminuerait en peuplement pur par rapport au peuplement mixte et avec une augmentation de la densité de plantation iii) la compétition intra ou interspécifique influencerait le patron de distribution verticale des racines fines chez les espèces étudiées.

Le cinquième chapitre avait pour objectif de mettre en œuvre un outil de prédiction de la productivité primaire à l'échelle de la canopée chez le peuplier hybride. Le modèle repose

sur notre compréhension des liens entre les facteurs environnementaux (température, humidité relative, lumière) et les processus physiologiques (photosynthèse, respiration, conductance stomatique, teneur en azote foliaire) de l'assimilation du carbone. Le passage de l'échelle foliaire à l'échelle de la canopée a été réalisé par la subdivision de la canopée en quatre couches verticales proportionnellement à la hauteur de la canopée, afin d'avoir une meilleure représentation de l'hétérogénéité physiologique au sein de la canopée qui découle principalement des variations de la lumière et de la distribution spatiale de l'azote foliaire. Le modèle prédira la photosynthèse à l'échelle de la canopée avec un pas de temps horaire durant la période de croissance (juin-septembre). Le contenu foliaire en chlorophylle, protéines solubles et insolubles et azote qui ont été dosés sur un échantillon de 180 feuilles ont servi à la dérivation des paramètres de la photosynthèse. Aussi, une station météorologique avait été installée dans chaque site pour enregistrer les données climatiques (PAR, vitesse du vent, température et humidité relative de l'air).

2. Chapitre II

THE EFFECTS OF SPACING ON GROWTH, MORPHOLOGY AND BIOMASS PRODUCTION AND ALLOCATION IN TWO HYBRID POPLAR CLONES GROWING IN THE BOREAL REGION OF CANADA

Benomar, L., DesRochers, A. et Larocque, G. R (2012) *Trees - Structure and Function*, 26(3):939-949

2.1 Abstract

Intra-clonal competition was studied in young hybrid poplar plantations in order to assess the effects of spacing on growth, biomass production and allocation, and morphological characteristics of above- and below-ground tree parts. Three spacings were used as whole-plots (1×1 m, 3×3 m and 5×5 m), with two hybrid poplar clones as subplots (BT747, *Populus balsamifera* L. × *P. trichocarpa* Torr. & Gray; MB915, *P. maximowiczii* A. Henry × *P. balsamifera* L.) in a split-plot design. After six growing seasons, diameter at breast height (dbh) increased by about 120% from the 1×1 m to the 5×5 m spacing for clone MB915, while there was no significant change in dbh for the other clone. The effect of spacing on height growth was opposite for the clones; it increased by about 175% from the narrowest to the widest spacing for clone MB915, while it decreased by about 27% for clone BT747. Estimates of above-ground biomass production after six growing seasons were significantly reduced with increasing spacing, with 29.6, 4.9 and 3.2 MgDM ha⁻¹ on average from the narrowest to the widest spacing. Reduced spacing between trees was characterized by smaller and acute branches and high proportion of leaf area in upper crown section. While, live crown ratio (LCR) and percentage of syllepsis did not change. Spacing also affected proportions of biomass allocated to stem, leaves, and branches, but allocation to roots did not change.

2.2 Introduction

In boreal forest regions across Canada, short-rotation forestry (SRF) using hybrid poplar (*Populus* spp.) plantations has a great potential for i) restoring abandoned agricultural lands and degraded forests, ii) reducing harvesting pressure on natural forests, and iii) becoming sustainable sources of wood supplies. However, a better understanding of the factors that influence biomass production is required to maximize the productivity of plantations. Among the site factors that govern productivity, stand density is critical, as it affects establishment costs, site occupancy, average piece size, and wood quality. Studies of tree response to initial spacing have previously focused on growth traits such as height, diameter at breast height (dbh), stem volume, and above-ground biomass (Cannell 1980; DeBell et al. 1996; Fang et al. 1999; Ferm et al. 1989; Larocque 1999; Strong and Hansen 1993; Willebrand et al. 1993). Even though estimates of productivity exist, little is known on the effects of spacing on biomass allocation, crown architecture, and root distribution in hybrid poplar plantations.

Crown architecture plays an important role in SRF productivity (Ceulemans et al. 1990; Wu and Stettler 1994). For example, a strong relationship was found between crown diameter and dbh for several species (Foli et al. 2003; Hemery et al. 2005). This relationship may offer substantial information that is required to optimize spacing between trees (Hall 1994; Hemery et al. 2005). Crown architecture varies widely among poplar species and their hybrids (Burk et al. 1983; Ceulemans et al. 1990; Dunlap et al. 1995; Gielen et al. 2002), and since it determines the spatial distribution of foliage and, consequently, solar radiation interception efficiency (Mitchell et al. 1992), such differences may explain the variation in growth responses to intra-clonal competition (Cannell 1980; Hall 1994; Harper 2008; Nelson et al. 1981). Branch characteristics (number, size, and orientation) have a decisive role in controlling crown architecture (Ceulemans et al. 1990). Hybrid poplar trees produce two types of branches: i) sylleptic branches, in which bud formation and branch elongation occur in the same year, and ii) proleptic branches, which are formed when the bud undergoes dormancy and the branch develops only a year later (Mitchell et al. 1992). Sylleptic branches, in contrast to proleptic branches, are known to translocate (export) a larger proportion of their photosynthates to the main stem (Scarascia-Mugnozza et al. 1999). Increasing syllepsis

(percentage of sylleptic branches) can also increase leaf area of the tree, resulting in a higher growth rate (Ceulemans et al. 1990; Wu et al. 2000). Hence, syllepsis has become an important criterion in selective breeding of hybrid poplar clones with respect to productivity (Ceulemans et al. 1990; Wu and Stettler 1994, 1998), and geographic variation and phenotypic plasticity (Dillen et al. 2007). The involvement of syllepsis in tree responses to intra-clonal competition remains unknown. The increase in syllepsis in response to decreased spacing between trees could be a plastic response that optimizes crown architecture in narrow spacings through i) efficient filling of available space within the crown, ii) increased allocation of biomass to the stem, or iii) an increase in crown leaf area.

The pattern of biomass allocation also varies greatly among hybrid poplar clones (Wu and Stettler 1998; Wullschleger et al. 2005; Zsuffa 1995) and constitutes an important information because of its influence on harvestable biomass (Alcorn et al. 2007; Fang et al. 1999; Pinkard and Neilsen 2003). When spacing between trees is reduced, biomass that is allocated to branches and foliage usually decreases to the benefit of the stem (Fang et al. 1999; Pinkard and Neilsen 2003). However, the influence of initial spacing on below-ground biomass remains unknown. Plasticity of rooting patterns in response to competition likely plays a role in nutrient uptake when resources are limited. For example, maximum rooting depth is expected to increase under high competitive stress, to enhance access to soil nitrogen (Casper and Jackson 1997).

The main objective of this study was to determine the effects of intra-specific competition on growth, crown architecture, biomass allocation, and coarse root system distribution in two young hybrid poplar clones (MB915; *P. maximowiczii* × *P. balsamifera* and BT747; *P. balsamifera* × *P. trichocarpa*) growing at three spacings in the boreal region of Quebec, Canada. We hypothesized that a decrease in spacing between trees would: i) increase allocated biomass to below-ground parts of trees; ii) increase rooting depth; iii) decrease the length, diameter and angle of origin and termination of branches; and iv) increase branch syllepsis.

2.3 Materials and methods

2.3.1 Study area and experimental design

The study area was located in the boreal region of Abitibi-Témiscamingue, Quebec, Canada. Three sites were selected for this study: Amos (48°36'N, 78°04'W), Rivière Héva (48°11'N, 78°16'W), and Nédelec (47°45'N, 79°22'W). The Amos site was an abandoned farmland with heavy clay soil, which was dominated by grasses and sparse patches of speckled alder (*Alnus incana* (L.) Moench ssp. *rugosa* (Du Roi) R.T. Clausen), willow (*Salix* spp.) and trembling aspen (*Populus tremuloides* Michaux). Rivière Héva was also an abandoned farmland site with heavy clay soil, which was dominated by shrubs, again including alder, willow and trembling aspen. Nédelec was previously dominated by a trembling aspen forest type which was commercially harvested in 2000. The main species that were present included, in addition to trembling aspen, white or paper birch (*Betula papyrifera* Marsh.) and pin cherry (*Prunus pensylvanica* L.) growing on a sandy-loam soil. Based on the 30-year running average, Amos and Rivière Héva experience 1387 degree-days above 5°C annually, while the annual total for Nédelec is 1480 degree-days (Environment Canada 2008). Additional details on site preparation prior to planting and weed management can be found in Benomar et al. (2011).

The experiment was designed as a split-plot layout with initial square spacing as the whole plot factor and each site as a replicate. Each spacing was sub-divided into two clones (sub-plot factor). Three square spacings were tested: 1×1 m, 3×3 m, and 5×5 m, which are equivalent to about 10,000, 1111, and 400 stems ha⁻¹, respectively. The size of the experimental unit was related to initial spacing, and consisted of 36 trees (6×6 rows of trees), of which the 16 interior trees were considered for the study, leaving a 1-row buffer on each plot edge. The two hybrid poplar clones were BT747 (*Populus balsamifera* L. × *P. trichocarpa* Torr. & Gray) and MB915 (*P. maximowiczii* A. Henry × *P. balsamifera* L.). Selection of these clones was based on their availability at the local tree nursery. They constitute two of the eight clones that are recommended for the region by the Quebec Ministry of Natural Resources and Wildlife (Périnet et al. 2006).

2.3.2 Growth

Immediately following planting and after the first six growing seasons, total height, stem basal diameter (D, m: 10 cm above the soil surface), and survival at the end of each growing season (mid-October) were measured. Diameter at breast height (dbh, m) was only measured for the last five growing seasons because stem dieback damage was observed for most trees during the first season (most trees were under 1.3 m height). Measurements were made on the 16 central trees in each plot. Trees that died in 2003 and 2004 were replaced in 2005 to maintain competition levels representative of the spacing; the replacement trees were not included in our calculations. A slenderness index (SI), which is a good indicator of competitive status, was calculated as: $SI = \text{height (m)}/\text{dbh (m)}$.

2.3.3 Crown traits

During the fourth growing season (2006), morphological characteristics were examined on four randomly selected trees in the centre of each spacing \times clone \times site combination, for a total of 72 trees. Crown morphology was assessed by measuring crown diameter (CD, m), live crown length (L, m), total number of branches, and number of current year sylleptic and proleptic branches. Because of their continuous development from a terminal meristem, sylleptic branches can be identified by their lack of basal bud scales and the first pair of leaves having similar size and shape as adult leaves, while proleptic branches have one or more basal bud scales due to their discontinuous growth (Mitchell et al. 1992). These measures allowed us to derive the following variables:

(i) crown volume = $0.3927 CD^2L$ (assuming a parabolic form of the crown); (ii) live crown ratio (LCR) = live crown length/stem height; and (iii) syllepsis = number of current year sylleptic branches/number of current year total branches.

2.3.4 Branch characteristics

Only first-order branches from each of the 72 trees were measured and divided into three groups according to their ages: i) bottom crown section branches (branches of the first and second growing seasons), ii) middle crown section branches (branches of the third growing season), and iii) upper crown section branches (branches of the current growing

season). The upper group was subdivided into two subgroups according to their origin, i.e., proleptic *versus* sylleptic. The following variables were measured for each branch: length, diameter, and angles of origin and termination.

2.3.5 Spatial distribution of leaf area

Following the measurement of crown and branch characteristics for each tree (end of July), its crown was subdivided into three equal vertical sections (33% of crown length for each section: bottom, middle, and upper). The total amount of foliage in each section was manually harvested. Total leaf area for each section was measured using a leaf area meter (LI-3100C, LI-COR Biosciences, Lincoln, NE). Dry mass was measured after drying to constant mass at 72°C.

2.3.6 Biomass allocation and coarse root morphology

On 15 July 2007, one tree per treatment (3 sites \times 2 clones \times 3 spacings = 18 total trees) was selected for biomass allocation sampling. The tree that was sampled in each plot was selected based on its dbh that best represented a treatment mean. Total height (H), dbh, and basal diameter were measured in the field. Following the removal of foliage from each tree, the branches were separated from the stem. Coarse roots $>$ 5 mm in diameter were excavated manually using picks and shovels and root number and depth were recorded. Root depth was measured at the end of the root, where it had reached less than 5 mm in diameter. Total leaf area was measured using a leaf area meter (LI-3100C, LI-COR Biosciences, Lincoln, NE). All tree parts were oven-dried (at 72°C for 8 d), after which dry mass was recorded. Percentages of biomass for leaves, stem, branches and roots were obtained by dividing the biomass of each component by the total tree biomass (i.e., leaves + stem + branches + roots).

The above-ground biomass of an additional 17 trees was harvested by the end of summer of 2008 to relate growth traits (D, dbh, and height) to leafless above-ground biomass per tree. These additional trees were taken from the plot buffer strips to cover a maximum range of dbh. Based on our data, the relationship between dbh and above-ground biomass

(AGB) was nonlinear. Data were fitted iteratively, using procedure NLIN (SAS Inc., 2000), to the following power function model:

$$W = a dbh^b \quad \text{Eq 1}$$

where W is above-ground biomass (AGB, kg dry mass), dbh is the diameter at breast height (cm), and a and b are estimated parameters of the model. Above-ground biomass production per hectare was calculated in absolute terms from the derived equations.

2.3.7 Statistical Analyses

All data were analyzed using the Mixed Procedure in SAS (version 9.2, SAS Institute, Cary, NC, USA). Response variables such as survival, proportions (%) of biomass allocated to roots, stem, branches and leaves and crown characteristics were analyzed separately using the following general linear mixed model with spacing and clone as a fixed effects, and site as a random effect:

$$Y_{SSC} = \mu + E_{Site} + \beta_S + E_{Site*S} + \beta_C + \beta_{S*C} + E_{Site*S*C} + E_R \quad \text{Eq 2}$$

where Y is the dependent variable, μ is the grand mean, β_S is the fixed effect of spacing, β_C is the fixed effect of clone, β_{S*C} is the spacing by clone interaction, E_{Site} , E_{Site*S} , $E_{Site*S*C}$ are the random effect for site, whole plot and subplot respectively. E_R is the residual error. Biomass allocation data were arcsine transformed to satisfy model assumptions (homoscedasticity and normality of residuals).

Aboveground biomass and growth in terms of D, dbh, and height were subjected to repeated-measures analysis using the following mixed model:

$$Y_{SSCT} = \mu + E_{Site} + \beta_S + E_{Site*S} + \beta_C + \beta_{S*C} + E_{Site*S*C} + \beta_T + E_{Site*T} + \beta_{S*T} + E_{Site*S*T} + \beta_{C*T} + \beta_{S*C*T} + E_{Site*S*C*T} + E_R \quad \text{Eq3}$$

where Y_{SSCT} is the dependent variable, μ is the grand mean, β_T is the fixed effect of time, β_{S*T} is the spacing by time interaction, β_{C*T} is the clone by time interaction, β_{S*C*T} the spacing by clone by time interaction, E_{Site*T} , $E_{Site*T*S}$, $E_{Site*T*S*C}$, are the random time specific for site, whole plot and subplot respectively and the remaining parameters are defined as in (Eq 2).

The variance component was estimated by restricted maximum likelihood (REML). An autoregressive covariance structure was chosen because of between-subject correlation (Richard et al. 1987). The growth data were log-transformed to satisfy model assumptions (homoscedasticity and normality of residuals).

Proportion of leaf area by crown section, and frequency of roots by depth, were analysed after arcsine transformation using the model in Eq3 and substituting the time factor by section or depth as a fixed effect factor. Means comparisons were performed using Tukey tests. All differences were considered significant at $P \leq 0.05$.

2.4 Results

2.4.1 Growth

Tree basal diameter increased by about 44 % and 131 % for clones BT747 and MB915, respectively, as spacing increased from 1x1 m to 5x5 m. Trees had reached a mean dbh of 3.48 cm and 5.61 cm and a mean height of 3.55 m and 5.77 m, respectively for clones BT747 and MB915, after six growing seasons (Table 2-1). There was a significant interaction between spacing and clone for height and basal diameter growth (Table 2-2), with the two clones showing opposite reactions to changes in spacing; Height decreased by about 20% for clone BT747, while it increased by 32% for clone MB915, when spacing rose from 1 x 1 m to 5 x 5 m (Table 2-1). Growth in term of dbh depended on spacing×clone×time interaction, and increased by 120 % with spacing from 1×1 m to 5×5 m for clone MB915, while dbh of clone BT747 was unaffected by the change in spacing. For the later, basal diameter did increase with an increase in spacing but the gains were modest compared to those of clone MB915 (Table 2-1).

Tableau 2-1: Characteristics of two hybrid poplar clones (BT747 and MB915) at three spacings (1×1 m, 3×3 m and 5×5 m), after six growing seasons.

Clone	Spacing	Survival (%)	dbh (cm)	Basal diameter (cm)	Height (m)
BT747	1×1m	94	3.32 ^a	5.20 ^a	4.11 ^b
	3×3m	95	3.28 ^a	6.21 ^b	3.28 ^a
	5×5m	75	3.84 ^a	7.47 ^c	3.27 ^a
Mean		88	3.48	6.29	3.55
MB915	1×1m	78	3.61 ^a	5.45 ^a	5.03 ^c
	3×3m	81	5.27 ^b	8.00 ^d	5.63 ^c
	5×5m	60	7.94 ^c	12.57 ^e	6.64 ^d
Mean		73	5.61	8.67	5.77

Dbh: diameter at breast height. Within a column, means followed by the same letter do not significantly differ at $\alpha \leq 0.05$.

Spacing effect on growth was time dependent (Table 2-2) as indicated by two different growth phases; The first phase was characterized by the absence of a spacing effect, which lasted two years for clone MB915 and four years for clone BT747 (Fig. 2-1). The second phase was characterized by an increase in dbh at the greatest spacing, particularly for clone MB915 (Fig. 2-1). After six growing seasons, mean tree survival ranged from 60 to 94%. Survival was greater in the 1×1 m and 3×3 m spacings compared to that of the 5×5 m spacing, and greater for clone BT747 than for MB915 (Table 2-1).

Tableau 2-2: Repeated-measures ANOVA giving sources of variation, degrees of freedom (DF), F-values, and associated probabilities for height, basal diameter, and dbh.

source	DF	Height		Basal diameter		dbh	
		F	P-value	F	P-value	F	P-value
Spacing	2	3.91	0.049	14.38	0.0001	3.39	0.068
Clone	1	186.26	<0.0001	69.96	0.0004	11.42	0.006
S*C	2	11.43	0.0005	7.1	0.0047	2.14	0.161
Time	5 (4)	2912.01	<0.0001	5190.35	<0.0001	450.35	<0.0001
S*T	10 (8)	1.65	0.103	40.39	<0.0001	10.32	<0.0001
C*T	5 (4)	129.02	<0.0001	38.68	<0.0001	42.12	<0.0001
S*C*T	10 (8)	4.47	<0.0001	2.75	0.005	3.74	0.0054

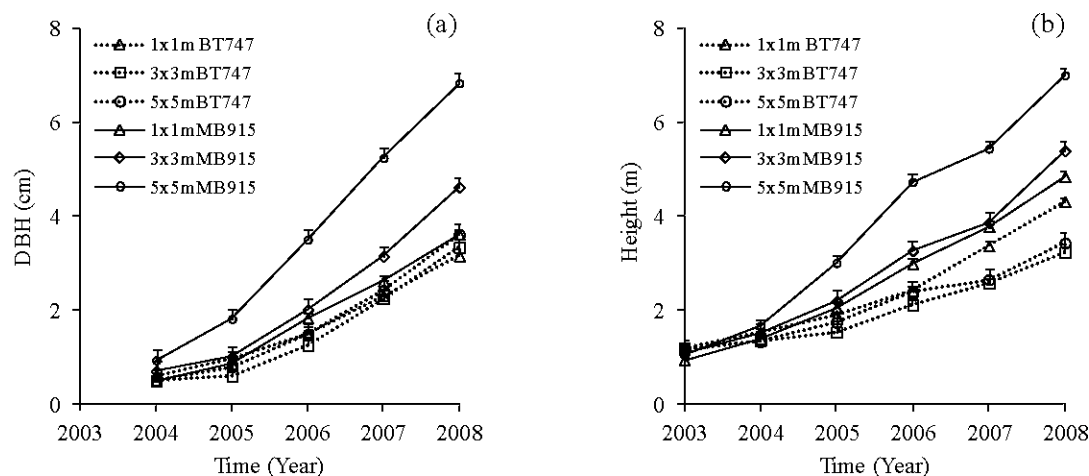


Figure 2-1 : Diameter at breast height (dbh) (a) and height (b) growth during six growing seasons for two hybrid poplar clones, BT747 and MB915, growing at three initial square spacings (1x1 m, 3x3 m and 5x5 m).

2.4.2 Biomass predictions

There was a very significant relationship between above-ground biomass (AGB; leafless) as a function of stem dbh (Table 2-3). The models for the two clones were highly significant ($P = 0.001$), with 96 to 99 % of the variation in above-ground biomass explained by the model for clones BT747 and MB915, respectively.

Tableau 2-3 : Parameters of the power function model ($Y = a X^b$) relating dbh of individual trees to above-ground (leafless) biomass (kg).

Clone	Model parameters		N	R ²
	a	b		
BT747	0.32 (0.07)	1.92 (0.16)	17	0.96
MB915	0.28 (0.05)	1.79 (0.08)	18	0.99

N = Number of observations. Y = biomass (kg dry mass tree⁻¹). X = diameter at breast height (cm).

2.4.3 Biomass production and allocation

Increased spacing between trees significantly increased above-ground biomass (AGB) at the individual tree level (kg tree⁻¹), but decreased it at the plot level (Mg DM ha⁻¹) after the first six growing seasons (Table 2-4). Estimated biomass production after 6 years on

a per hectare basis was 8 to 20 times greater in the 1x1 m spacing compared to the 3x3 m and 5x5 m spacings, respectively for clone BT747, while clone MB915 produced 3.5 to 5.5 more AGB in the 1x1 m spacing compared to the 3x3 m and 5x5 m spacings, respectively. Similarly, mean annual production of above-ground biomass on a per hectare basis was also greater in the 1x1 m spacing (Table 2-4). In all spacing treatments, clone MB915 produced greater biomass than clone BT747. However, clonal differences were less pronounced in the 1x1 m spacing compared to the two other spacings.

Tableau 2-4 : Above-ground biomass (leafless) and mean biomass productivity following six growing seasons of two hybrid poplar clones (BT747 and MB915) at three initial spacings (1x1 m, 3x3 m, and 5x5 m).

Clone	Spacing	AGB (Mg ha ⁻¹)	AGB (kg Tree ⁻¹)	Yield (Mg ha ⁻¹ y ⁻¹)
BT747	1x1m	27.00 ^b	1.10 ^e	5.15 ^b
	3x3m	2.89 ^e	1.66 ^d	0.55 ^e
	5x5m	1.32 ^f	2.98 ^c	0.26 ^f
MB915	1x1m	32.19 ^a	1.68 ^d	6.15 ^a
	3x3m	6.98 ^c	6.79 ^b	1.37 ^c
	5x5m	5.00 ^d	10.63 ^a	1.25 ^d

AGB = above ground biomass. Within a column, means followed by the same letter do not significantly differ at $\alpha \leq 0.05$.

Biomass allocation to branches and leaves was significantly influenced by both spacing and clone, while biomass allocated to the stem depended only on spacing (Table 2-5). Biomass allocated to roots, however, was not significantly affected by spacing (Table 2-5), although BT747 allocated 3% more biomass to roots than did MB915. When spacing increased from 1x1 m to 3x3 m, biomass that was allocated to the stem decreased significantly, to the benefit of branches, a trend not observed when spacing increased from 3x3 m to 5x5 m (Table 2-6). The effect of spacing on biomass that was allocated to leaves was clone-dependent; leaf biomass for BT747 was unaffected by spacing but greater for MB915 in the 3x3 m and 5x5 m spacings, compared to trees growing in the 1x1 m spacing (Table 2-6).

Tableau 2-5: Analysis of variance giving sources of variation, F values, and associated probabilities for biomass allocation and crown characteristics.

Response variable	Spacing		Clone		Spacing*clone	
	F	Pr > F	F	Pr > F	F	Pr > F
% of biomass in branches	46.27	0.001	23.48	0.002	3.24	0.111
% of biomass in stem	20.86	0.007	1.74	0.235	1.55	0.286
% of biomass in foliage	4.47	0.040	4.06	0.071	3.3	0.324
% of biomass in roots	2.08	0.240	11.1	0.0158	0.64	0.5598
Crown volume	40.91	<0.0001	83.86	<0.0001	24.54	<0.0001
LCR	0.25	0.781	9.52	0.007	5.02	0.019
Syllepsis	2.04	0.32	72.71	<0.0001	1.10	0.345
SI	56.28	0.001	0	0.961	0.96	0.434

LCR = Live Crown ratio. SI = Slenderness index (H/dbh)*100.

Tableau 2-6: Proportion (%) of biomass allocated to roots, stem, branches and leaves of individual trees for two hybrid poplar clones (BT747 and MB915) growing under three spacings (1×1 m, 3×3 m and 5×5 m).

Clone	Spacing	Roots	Branches	Stem	Leaves
BT747	1×1m	27.2 ^b	19.9 ^a	35.9 ^a	16.8 ^b
	3×3m	28.1 ^b	25.1 ^b	27.2 ^b	19.7 ^b
	5×5m	30.4 ^b	30.1 ^c	23.4 ^b	16.1 ^b
MB915	1×1m	25.6 ^a	22.6 ^a	41.5 ^a	10.1 ^a
	3×3m	24.6 ^a	31.3 ^c	25.9 ^b	18.1 ^b
	5×5m	26.3 ^a	32.6 ^c	25.4 ^b	15.5 ^b

Data were collected after five growing seasons (2007). Values are the averages of three harvested trees for each treatment. Within a column, means followed by the same letter do not differ significantly at $\alpha \leq 0.05$

2.4.4 Crown structure and foliage distribution

Crown volume dramatically increased with spacing from 1×1 m to 5×5 m (812% for clone MB915 and 276% for clone BT747; Table 2-7). The interaction between spacing and clone was significant (Table 2-5) and reflected the much greater increase for clone MB915. Live crown ratios increased only slightly with spacing for clone MB915 (Tables 2-5 and 2-7). The slenderness index (SI) decreased markedly with spacing (Table 2-7) for both clones (Table 2-5). Spacing had no significant effect on the level of syllepsis for both clones. However it was greater for clone MB915 (58%) compared to BT747 (42%) (Tables 2-5 and 2-7).

Tableau 2-7: Crown characteristics after four growing seasons of two hybrid poplar clones (BT747 and MB915) growing at three initial spacings (1×1 m, 3×3 m and 5×5 m).

Clone	Spacing	Crown Volume (m ³)	LCR	SI (m m ⁻¹)	Syllepsis (%)
BT747	1×1m	1.46 ^a	0.92 ^a	140.4 ^a	43.6 ^a
	3×3m	2.12 ^a	0.89 ^a	111.6 ^b	43.5 ^a
	5×5m	5.50 ^b	0.92 ^a	94.5 ^c	40.7 ^a
MB915	1×1m	2.42 ^a	0.92 ^a	140.5 ^a	62.4 ^b
	3×3m	10.5 ^c	0.95 ^b	117.7 ^b	56.2 ^b
	5×5m	22.1 ^d	0.94 ^b	87.7 ^c	57.7 ^b

LCR = Live Crown ratio. SI = Slenderness index (H/dbh)*100. Within a column, means followed by the same letter do not significantly differ at $\alpha \leq 0.05$.

Spacing effect on leaf area distribution in the crown depended significantly on both clone and crown section (three-way interaction, $P < .0001$); There was a sharp decrease in foliage allocated to the bottom section in the 1×1 m spacing for clone MB915 while it slightly increased in the two largest spacings. In contrast, clone BT747 had similar leaf area distribution in the upper and middle crown sections among the spacings, and less foliage in the bottom crown section for all spacings (Fig. 2-2).

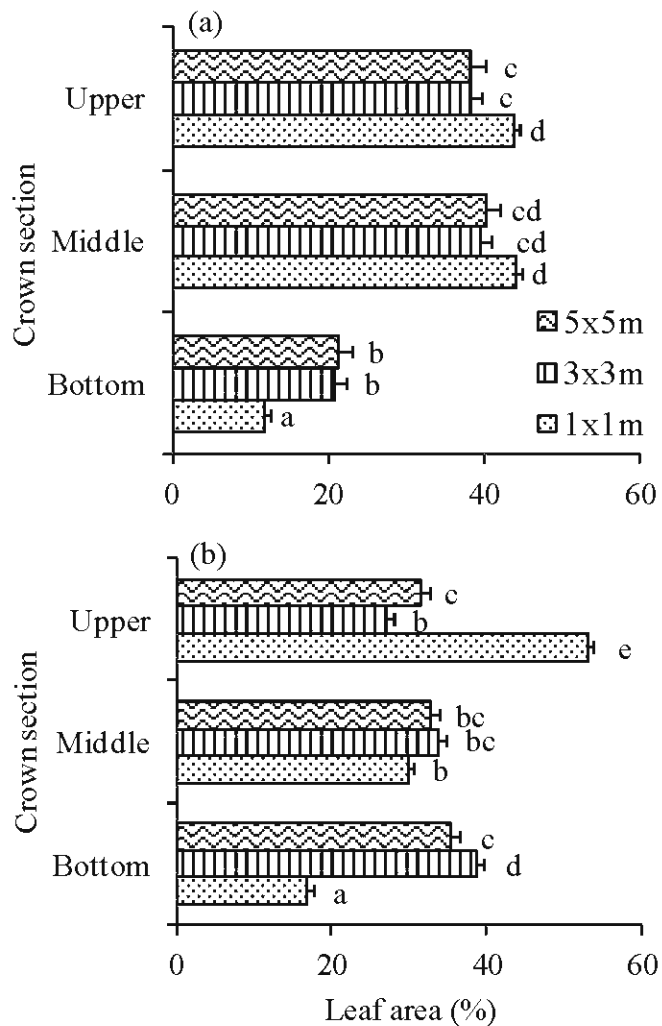


Figure 2-2: Leaf area distribution within the crown of two hybrid poplar clones (a) BT747 and (b) MB915, growing at three initial spacings (1×1m, 3×3m and 5×5m). For each clone section, columns followed by the same letters are not significantly different.

2.4.5 Branch characteristics

Spacing and crown section had strong effects on branch dimension and orientation (Table 2-8). First, an increase in spacing increased branch diameter and length (Table 2-9) similarly between all crown sections and clones (Table 2-8). Mean branch diameter and length increased from the upper to bottom crown sections (Table 2-9). The interaction between clone and crown section for branch size revealed that mean branch length of clone MB915 was greater than that of BT747 only for the bottom and middle crown sections (Table 2-9). Mean angle of origin was unaffected by spacing in the bottom and middle sections of the crown, whereas it increased significantly with an increase in spacing in the upper crown section (Tables 2-8 and 2-9). Except for the upper crown section, clone MB915 had a greater mean angle of origin than clone BT747 (Table 2-9). Branches of clone MB915 generally had a greater mean angle of termination than clone BT747 and it increased with an increase in spacing only in the bottom and upper crown sections for clone MB915, and only in the upper crown section for clone BT747 (Tables 2-8 and 2-9).

Tableau 2-8: Analysis of variance giving sources of variation, F values, and associated probabilities for mean angle of origin, angle of termination, diameter and length of branch.

Source	DF	Diameter		Length		Θ_1		Θ_2	
		F	Pr > F	F	Pr > F	F	Pr > F	F	Pr > F
Spacing	2	226.08	<.0001	105.69	<.0001	7.78	0.001	6.25	0.002
Clone	1	0.08	0.7711	62.92	<.0001	43.35	<.0001	4.21	0.040
S*C	2	0.22	0.8056	0.75	0.471	7.06	0.001	7.93	0.001
Section	2	336.12	<.0001	370.51	<.0001	11.16	<.0001	14.25	<.0001
S*Section	4	1.92	0.094	2.07	0.082	12.56	<.0001	3.31	0.011
C*Section	2	3.53	0.0294	4.07	0.017	6.32	0.002	0.52	0.594
S*C*Section	4	0.28	0.890	0.08	0.989	0.94	0.440	1.20	0.310

Θ_1 = angle of origin of branches. Θ_2 = angle of termination of branches.

Tableau 2-9: Mean angle of origin, angle of termination, diameter and length of branch of two hybrid poplar clones (BT747 and MB915) growing at three initial spacings (1×1 m, 3×3 m and 5×5 m) after four growing seasons.

Crown section	Clone	Spacing	Θ_1 (degree)	Θ_2 (degree)	Diameter (mm)	Length (cm)
Upper	BT747	1×1m	54 ^{ab}	46 ^{ab}	6.14 ^a	44.35 ^a
		3×3m	57 ^b	50 ^b	7.67 ^b	55.64 ^b
		5×5m	65 ^c	50 ^b	8.58 ^c	58.64 ^b
	MB915	1×1m	50 ^a	43 ^a	5.64 ^a	48.48 ^a
		3×3m	58 ^{bc}	57 ^c	7.64 ^b	65.52 ^{bc}
		5×5m	62 ^{bc}	58 ^c	8.91 ^c	80.10 ^d
Middle	BT747	1×1m	60 ^b	42 ^a	7.91 ^a	67.39 ^a
		3×3m	58 ^b	41 ^a	11.39 ^b	86.51 ^c
		5×5m	59 ^b	42 ^a	14.29 ^c	111.82 ^d
	MB915	1×1m	50 ^a	44 ^a	7.64 ^a	78.50 ^b
		3×3m	51 ^a	39 ^a	11.34 ^b	106.31 ^d
		5×5m	53 ^a	49 ^a	14.13 ^c	144.85 ^c
Bottom	BT747	1×1m	64 ^b	43 ^{ab}	9.39 ^a	83.55 ^a
		3×3m	60 ^b	45 ^{ab}	13.28 ^b	102.24 ^b
		5×5m	66 ^b	42 ^{ab}	16.11 ^c	124.65 ^c
	MB915	1×1m	54 ^a	35 ^a	10.13 ^a	109.74 ^b
		3×3m	53 ^a	47 ^b	14.50 ^b	141.41 ^d
		5×5m	55 ^a	52 ^c	17.65 ^c	171.19 ^c

Θ_1 = angle of origin of branches. Θ_2 = angle of termination of branches. For each crown section, means within column followed by the same letter do not differ significantly at $\alpha \leq 0.05$.

2.4.6 Root characteristics

Root numbers per tree were similar among spacings for clone MB915, while they were significantly greater in the 3×3 m and 5×5 m than in the 1×1 m spacing for clone BT747 (data not shown). Maximum rooting depth observed in this study was about one meter with mean rooting depth at 25 cm. The pattern of root distribution was unaffected by both spacing and clone (Table 2-10). Over 80% of roots were located between 0 and 40 cm.

Tableau 2-10: analysis of variance giving sources of variation, F values, and associated probabilities for the frequency distribution of roots.

Effet	DF	F	Pr > F
Spacing	2	0.02	0.9773
Clone	1	0.07	0.799
Spacing*Clone	2	0.32	0.7457
Depth	3	12.05	0.0002
Spacing*Depth	6	0.54	0.7733
Clone*Depth	3	1.78	0.1911
Spacing*Clone*Depth	6	0.43	0.8482

2.5 Discussion

2.5.1 Spacing effects on stem size

Basal diameter increased predictably as spacing between trees increased (Table 2-3), as has been observed elsewhere (Alcorn et al. 2007; DeBell et al. 1996). An increase in dbh with spacing was only observed for clone MB915, which is likely the result of smaller changes in crown dimensions with increasing available space for BT747 (Table 2-7), showing the greater growth plasticity of clone MB915 to rapidly take advantage of the available space.

Interestingly, the height growth response to increase in spacing was opposite for the two clones (Table 2-1). While height growth is commonly assumed to be insensitive to changes in spacing between trees (Lanner 1985; Woodruff et al. 2002), this may be only true in softwood species. In fast-growing hardwoods, tree height may increase, decrease, or

remain unchanged with increasing spacing between trees (Alcorn et al. 2007; DeBell et al. 1996; Fang et al. 1999; Kerr 2003; Pinkard and Nielsen 2003). Variations in height growth with changes in available growing space could be attributed to ontogeny, to the range of tested spacing treatments, or to species. Height growth plays an important role in morphological acclimation to light competition (Lanner 1985), with plants tending to allocate more photosynthates to height than diameter growth, which results in increasing stem slenderness (Table 2-7). This response could explain why height growth was greater in the 1×1 m spacing for clone BT747, while faster growth and the associated trade-off between mechanical stability of the stem and height growth may explain why the trend was reversed for clone MB915.

2.5.2 Spacing effects on biomass production

Cumulative above-ground biomass (leafless) per ha after six growing seasons increased as spacing between trees decreased, probably due to an increase in LAI (Fang et al. 1999; Gower 2003). By the end of the sixth growing season, the estimated yield at the greatest spacing was very low ($<1.5 \text{ Mg ha}^{-1} \text{ y}^{-1}$) compared with published data under the same spacing conditions (Fang et al. 1999). Average yield attained under the 1×1 m spacing was about $6.15 \text{ Mg ha}^{-1} \text{ y}^{-1}$ and $5.15 \text{ Mg ha}^{-1} \text{ y}^{-1}$ for clones MB915 and BT747, respectively (Table 2-4). Reported aboveground yields in dense plantations of different hybrid poplar clones in central Europe, the USA, and Canada are greater, and range between 10 and 30 $\text{MgDM ha}^{-1} \text{ y}^{-1}$ (Cannell and Jeffery 2004; DeBell et al. 1996; Dowell et al. 2009; Labrecque and Teodorescu 2003). Our results mirror yields under boreal (cold temperate) conditions; In Sweden, Christersson (2010) reported that average yields ranging from 3 to 10 $\text{MgDM ha}^{-1} \text{ y}^{-1}$ in five-year-old plantations, while Willebrand et al. (1993) reported average yields that varied between 8 and 14 $\text{MgDM ha}^{-1} \text{ y}^{-1}$ in six-year-old plantations. In spite of the short duration of the growing season and low soil nitrogen in boreal Canada, a 10 $\text{MgDM ha}^{-1} \text{ y}^{-1}$ yield should easily be achieved by adding fertilizer and selecting appropriate clones and spacings (Weih 2004). However, several elements suggest that above-ground yields will change with respect to spacing in the future, as canopy closure occurs in the greater spacings: i) the absence of significant differences in LCR between spacings (Table 2-7) indicates that competition was not yet severe enough to cause density-dependent mortality in the close

spacing, ii) full occupancy of space in the large spacings had not yet occurred at the end of the six growing seasons to successfully counter-balance yields for the low stand densities. We thus anticipate an increase in above-ground yield in the 3×3 m and 5×5 m spacings after canopy closure and a decrease in biomass production in the 1×1 m spacing due to intensification of intra-clonal competition.

2.5.3 Spacing effects on biomass allocation

Biomass allocation is involved in growth efficiency and plastic responses of trees to their environment (Casper et al. 1998; McCarthy and Enquist 2007; Reich et al. 1998). In this study, biomass allocation was substantially affected by changes in spacing between trees. In large spacings, biomass that was allocated to branches exceeded biomass that was allocated to the stem (Table 2-6), which is not desirable for lumber production. Light availability likely stimulated growth and production of branches (Benomar et al. 2011). However, light seemed to have little effect on biomass allocation to leaves (Hegazy et al. 2008; Poorter and Nagel 2000; Proe et al. 2002), while biomass allocation to leaves may decrease under low nitrogen conditions. Leaf area is the photosynthetic surface supporting any growth process. Under low nitrogen conditions, the increase in specific leaf area (SLA, the ratio of leaf area to leaf dry mass) may compensate for a decrease in biomass allocation to leaves. According to our previous results (Benomar et al 2011), SLA was significantly and negatively associated with spacing between trees. Biomass allocated to leaves did not change with spacing for clone BT747, probably due to low levels of below-ground competition and slower growth rate of this clone. According to advanced theoretical concepts in biomass partitioning (optimal partitioning theory; McCarthy and Enquist 2007), biomass is allocated in order of priority for the acquisition of limiting resources. Thus, the fraction of biomass that is allocated to roots is predicted to increase under conditions of nitrogen limitation and to decrease under competition for light. Under intraspecific competition (dense plantation), both nitrogen and light presumably decrease. Our results showed similar investments of biomass in roots among spacings (Table 2-6), and similar results were reported by Bernardo et al. (1998) and Casper et al. (1998). However, our sampling was limited to the structural roots (taproot and lateral roots) and did not include functional parts (fine roots). It is possible that trees responded to

the increase in competition by increasing fine root longevity or by increasing the rate of N uptake rather than increasing coarse root depth (Casper and Jackson 1997; Litton et al. 2003).

2.5.4 Spacing effects on branch size and orientation

Our results showed that reduced spacing between trees reduced the frequency and development of branches (Alcorn et al. 2007; DeBell et al. 1996; Henskens et al. 2001). Crown volume (space occupied by foliage) and spatial distribution of the foliage are important in carbon gain at the crown level. This is because of their direct effect on the availability and efficient use of light within the crown (Roeh and Maguire 1997; Wang and Jarvis 1990). Crown volume increased with an increase in spacing between trees, more so for clone MB915 than clone BT747 (Table 2-7). This occurred by increasing branch length and angles of origin and termination (Table 2-9). Indeed, in contrast to clone MB915, branches of clone BT747 had similar angles of termination in low and middle crown sections at the various spacings, explaining why leaf area distribution remained unchanged. In contrast, taller and less acute branches at the bottom of the crown in large spacings resulted in both a greater crown volume and proportion of leaf area in the bottom crown section for clone MB915. Longer branches for clone MB915 (Table 2-9) allowed this clone to display more leaf area per branch (Ceulemans et al. 1990) and, thus, experience faster growth rates. Plasticity in angles of origin and termination allows trees to display their foliage efficiently, thereby maximizing light capture (Burk et al. 1983; Ceulemans et al. 1990). In this study, the angle of origin was unaffected by spacing in the bottom and middle parts of crown, probably because these branches were developed before crown closure occurred in this part of the crown, during the first years following establishment. Live crown ratio was also insensitive to changes in spacing due to the absence of branch mortality at the time of measurement, since canopy closure had only started to occur in the plots.

Our results show that branch traits are important in clonal selection for spacing trials. Clone BT747 had acute short branches even at the greatest spacing, which decreased its utility for efficient biomass production under various conditions. In contrast, clone MB915 had less acute and longer branches, making its selection more appropriate for growth at large spacings. In addition, this clone showed plasticity in branch traits and other crown traits in

response to spacing. Retention of this plasticity is very useful if dense plantations are followed by thinning. Our results do not support the involvement of syllepsis in morphological plasticity in response to competition. Increased syllepsis has been found to be positively related to radial growth (Wu and Stettler 1998), and this response could explain the superior growth of clone MB915. Further, it suggests that syllepsis is an attribute of fast growth but not necessary an attribute of morphological plasticity.

2.6 Conclusion

Results of our study showed that as spacing increased, basal diameter growth increased and dbh increased or remained unchanged, depending on the clone. At the same time, height growth increased or decreased, again depending on the clone. Above-ground biomass per ha was maximized at the 1×1 m spacing, mostly likely due to the young age of the plantation, since canopy closure had not yet been attained at greater spacings. Crown structure of the two hybrid poplar clones was under considerable control exerted by the level of competition between trees (spacing), through changes in branches development and orientation, which led to changes in the spatial distribution of leaf area. Syllepsis apparently had no effect on morphological acclimation to intra-clonal competition. Trees responded to the increase in competition by decreasing their investment in branches. Decreases in biomass allocation to leaves in response to the increase of competition depended on clone. Both rooting depth and biomass allocation to roots were insensitive to changes in spacing between trees.

2.7 Acknowledgements

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3. Chapitre III

CHANGES IN SPECIFIC LEAF AREA AND PHOTOSYNTHETIC
NITROGEN-USE EFFICIENCY ASSOCIATED WITH PHYSIOLOGICAL
ACCLIMATION OF TWO HYBRID POPLAR CLONES TO INTRA-CLONAL
COMPETITION.

Benomar, L., DesRochers, A. et Larocque, G.R (2011) Canadian Journal of
Forest Research, 41(7):1465-1476.

3.1 Abstract

Photosynthesis is the most important process driving productivity, and its acclimation to intra-clonal competition is not well understood in hybrid poplars. The aim of this study was to examine the physiological response of the crown of two hybrid poplar clones (BT747215, *Populus balsamifera* L. × *P. trichocarpa* Torr. & Gray; MB915319, *P. maximowiczii* A. Henry × *P. balsamifera* L.) to intra-clonal competition. We measured light-saturated photosynthesis (A_{\max}), leaf nitrogen content on an area basis (N_{area}), specific leaf area (SLA), and photosynthetic nitrogen-use efficiency (PNUE) for three successive growing seasons on trees planted at three spacings (1×1m, 3×3m and 5×5m). Crowns were sampled at 10 locations corresponding to vertical and horizontal subdivisions. Significant changes took place at the crown level in the closest spacing (1×1m) compared to the wider spacings (3×3m, 5×5m): i) 30% decrease in N_{area} , ii) 20% increase in SLA, and iii) 40% increase in PNUE. The slope of the A_{\max} - N_{area} curve was greatest in the closest spacing, indicating a greater change in A_{\max} per unit change in N_{area} . The two hybrid poplar clones had a similar morpho-physiological response to changes of spacing. Both clones showed physiological acclimation of their foliage in response to intra-clonal competition through modulation of SLA and PNUE.

3.2 Introduction

In light of predicted shortages of wood from natural forests, there is a renewed interest in short-rotation forestry (SRF) in many parts of the world (Dickmann et al. 2001). Hybrid poplars (*Populus* spp.) are particularly well-suited to SRF, since they can reach very high productivity within relatively short periods of time for efficient fiber or energy production, CO₂ sequestration, or phyto-remediation of polluted lands (Dickmann et al. 2001).

Biomass production in SRF is a result of various factors and their interactions, including spacing, site quality, weed management, fertilization, and genetic background (Makeschin 1999). Spacing determines the intensity of competition between trees, which is known to affect resource availability, stand dynamics, and productivity (DeBell et al. 1996). In hybrid poplar improvement programs, most selected traits, such as sylleptic branchiness, productivity, net photosynthesis, and stomatal characteristics, have been examined under conditions of low competition (large spacings) (Green et al. 2001). Previous studies have shown great variability in growth responses to inter- or intra-clonal competition (DeBell et al. 1996; Fang et al. 1999). Hence, a better understanding of hybrid poplar trait plasticity under different competitive regimes is essential for selecting appropriate planting densities and genetic materials (Green et al. 2001). For instance, hybrid poplar clones that perform well under high levels of intra- and inter-clonal competition have been characterized by high light-use efficiency (Green et al. 2001) and high water- and nutrient-use efficiency (Bungart and Hüttl 2004; Yin et al. 2005). However, knowledge is lacking regarding the physiological response and foliage acclimation of hybrid poplars to different levels of intra-clonal competition.

Nitrogen (N) and light are common resources driving photosynthesis and plant carbon gain (Chapin et al. 1987). Accordingly, photosynthesis at light saturation (A_{\max}) is strongly positively related with light and leaf N content on an area basis (N_{area}). In forest plantations, competition for light and N is strongly governed by spacing between trees (Szendrödi 1996). As a consequence, competition for these resources increases in parallel to the reduction of their growing space. Plants respond to competition for site resources partially through physiological acclimation of their foliage (Grams and Andersen 2007). The acclimation process allows plants to compensate for reduced resources by improving uptake and

utilization efficiency of site resources. Yet, acclimation capacity can vary considerably among species (Grams and Andersen 2007), and a better understanding of this phenomenon is essential for determining the competitive potential of different hybrid poplars in specific environments.

Photosynthetic acclimation to conditions of reduced photosynthetically active radiation (PAR) occurs through changes in specific leaf area (SLA, leaf area: dry mass ratio) and N allocation to carboxylation, electron transfer, and light-harvesting processes (Evans and Poorter 2001). The modulation of SLA in response to changes in PAR allows plants to optimize N investment in foliage (Hirose et al. 1988). Thus, patterns of leaf N distribution are intimately linked to PAR gradients in the canopy (Anten et al. 1998; Hirose and Werger 1987). Plants may also respond to multiple environmental factors (N, light, or water availability) by modulating SLA (Chapin et al. 1987; Grams and Andersen 2007). Specific leaf area has been reported to be correlated positively with rainfall (Gouveia and Freitas 2009) and negatively with N availability (Chapin et al. 1987; Rosati et al. 1999). These observations suggest that a plant's capacity to modulate SLA can play a key role in photosynthetic acclimation to intraspecific competition.

Specific leaf area increases as leaf thickness decreases (Aranda et al. 2004; Onoda et al. 2004) or leaf area/mass increases, which may contribute to i) increasing canopy light interception and transmittance (Vile et al. 2005) and ii) a lower light compensation point in leaves (Niinemets and Sack 2006). The fraction of leaf N allocated to light harvesting may decrease, leaving more N for carboxylation and electron-transfer processes (Evans and Poorter 2001). Increases in SLA are also associated with a decrease in leaf construction costs (Feng et al. 2008) and decrease in the fraction of leaf N allocated to cell walls, leaving more N for the photosynthetic machinery (Onoda et al. 2004). Improvement of N partitioning between- and within-leaves through the modulation of SLA under competition may increase photosynthetic nitrogen-use efficiency (PNUE) at all levels of the crown, thereby altering the steepness of the photosynthesis–N curve. Indeed, a strong relationship has been found between SLA and PNUE (Poorter and Evans 1998). Hence, the increase of SLA is very important in maximizing PNUE and carbon gains within the canopy at high intensities of competition (Schieving and Poorter 1999). However, there is a lack of knowledge with

respect to the physiological acclimation of hybrid poplars to competition, in particular regarding the role of SLA and PNUE in photosynthetic acclimation to changing PAR and N under different levels of competition.

In this study, we examined the physiological responses of the crown in two hybrid poplar clones, BT747215 (*Populus balsamifera* L. × *P. trichocarpa* Torr. & Gray) and MB915319 (*P. maximowiczii* A. Henry × *P. balsamifera* L.), to increasing intensities of intra-clonal competition and the effect of competition on leaf traits such as SLA, gas exchanges, leaf N, and PNUE. There is little knowledge on hybrid poplar ecophysiology in boreal conditions under various intensities of intra-clonal competition. We hypothesized that increasing intra-clonal competition would be associated with increases in SLA and PNUE. This study would contribute not only to the evaluation of the critical role of changing SLA and PNUE in the physiological acclimation to intra-clonal competition and clonal selection in hybrid poplar, but also to the examination of the influence that these two leaf traits exert on the A_{\max} - N_{area} relationship, which is fundamental to ecophysiological modelling of leaf photosynthesis.

3.3 Materials and methods

3.3.1 Study area

The study was located in the boreal region of Abitibi-Témiscamingue, western Quebec, Canada. Three sites were randomly selected for this study: Amos (48°36'N, 78°04'W), Rivière Héva (48°11'N, 78°16'W), and Nédelec (47°45'N, 79°22'W). The Amos site was an abandoned farmland with heavy clay soils, which were dominated by grasses and a few patches of speckled alder (*Alnus incana* (L.) Moench ssp. *rugosa* (Du Roi) R.T. Clausen), willow (*Salix* spp.), and trembling aspen (*Populus tremuloides* Michaux). Rivière Héva was also on abandoned farmland with heavy clay soils, which had been colonised by shrubs including patches of alder, willow, and trembling aspen. Nédelec had been previously forested, but was now dominated by scattered trembling aspen, white or paper birch (*Betula papyrifera* Marsh.), and pin cherry (*Prunus pensylvanica* L.). This last site was characterised by soils with a sandy-loam soil texture and had been commercially harvested in 2000. The mean numbers of growing degree-days (above 5°C; 30-year average) were 1,387 for Amos

and Rivière Héva, and 1,480 for Nédélec (Environment Canada 2008). Precipitation over the three growing seasons of our study averaged 420 mm, 352 mm, and 620 mm for 2006, 2007, and 2008, respectively (Ministère du Développement Durable de l'Environnement et des Parcs 2009).

Site preparation before planting was conducted in 2002. A bulldozer was used to remove tree stumps at Nédélec, while shrubby vegetation at Rivière Héva was removed using a brush shredder mounted on a farm tractor. At Amos, scattered tree stumps and shrub clumps were removed using chains and a farm tractor. Sites were then ploughed to a depth of about 30 cm, followed by disking in spring 2003 to level the soil surface and remove most woody debris. Large, dormant bareroot hybrid poplar stock, which averaged 1.36 m and 1.15 m in height for clones MB915319 and BT747215, respectively, was planted during the last week of May 2003 at Amos, the last week of June at Nédélec, and the second week of July at Rivière Héva. During the first five growing seasons, competing weedy vegetation was removed mechanically to a depth of about 5-10 cm using a farm tractor equipped with disks. Mechanical weed control was conducted twice each year from 2003 to 2007, after which disking was conducted only once in 2008, due to heavy precipitation that limited access to the sites.

3.3.2 Experimental design

The experiment was designed as a split-plot array, with initial square spacing as the whole plot factor (three levels) and each site as a replicate. Each level of spacing was then subdivided into two clones (the sub-plot factor). Three square spacings were tested: 1×1 m, 3×3 m, and 5×5 m; these were equivalent to about 10,000 stems ha⁻¹, 1,111 stems ha⁻¹, and 400 stems ha⁻¹, respectively. The size of the experimental units was related to spacing, and contained 36 trees (6×6 rows of trees), in which the 16 interior trees were sampled, leaving 2×2 rows of border trees as a buffer zone. The clones that were selected, viz., MB915319 (MB915; *P. maximowiczii* A. Henry × *P. balsamifera* L.) and BT747215 (BT747; *Populus balsamifera* L. × *P. trichocarpa* Torr. & Gray), are among those clones that have been recommended by the MRNFQ (Quebec Ministry of Natural Resources and Wildlife for the region).

3.3.3 Sampling

Physiological measurements began in 2006, when canopies began to overlap in the closest spacing (1×1 m). Two trees were randomly selected within each treatment for physiological measurements ($N = 36 = 3 \text{ spacings} \times 2 \text{ clones} \times 3 \text{ sites} \times 2 \text{ trees}$). The crown of each sampled tree was divided vertically into four layers from the bottom to the top of the crown (Fig. 3-1). The first layer consisted in the top 10% of the crown, the second layer corresponded to the middle 30% of the crown, the third layer was located between 30 and 60% of crown depth and the fourth layer consisted of the lowest 30% of crown depth. One leaf from three points corresponding to horizontal subdivisions (inner, middle and outer leaves) was sampled in the second, third and fourth layers, while one leaf from the terminal shoot was sampled from the top layer. During the third (2006), fourth (2007) and fifth (2008) growing seasons, leaf gas exchange and SLA were measured at the different crown levels, while leaf N was measured only in 2007 and 2008. All measurements were conducted between July 15 and August 15. This period corresponds to the seasonal peak in leaf area index (LAI), based on our LAI measurements (Plant Canopy Analyzer, LAI-2000, LI-COR, Lincoln, NE, USA) during the growing season of 2008 (unpublished data). Size and leaf area index (LAI) of the two clones after six growing seasons are given in Table 3-1.

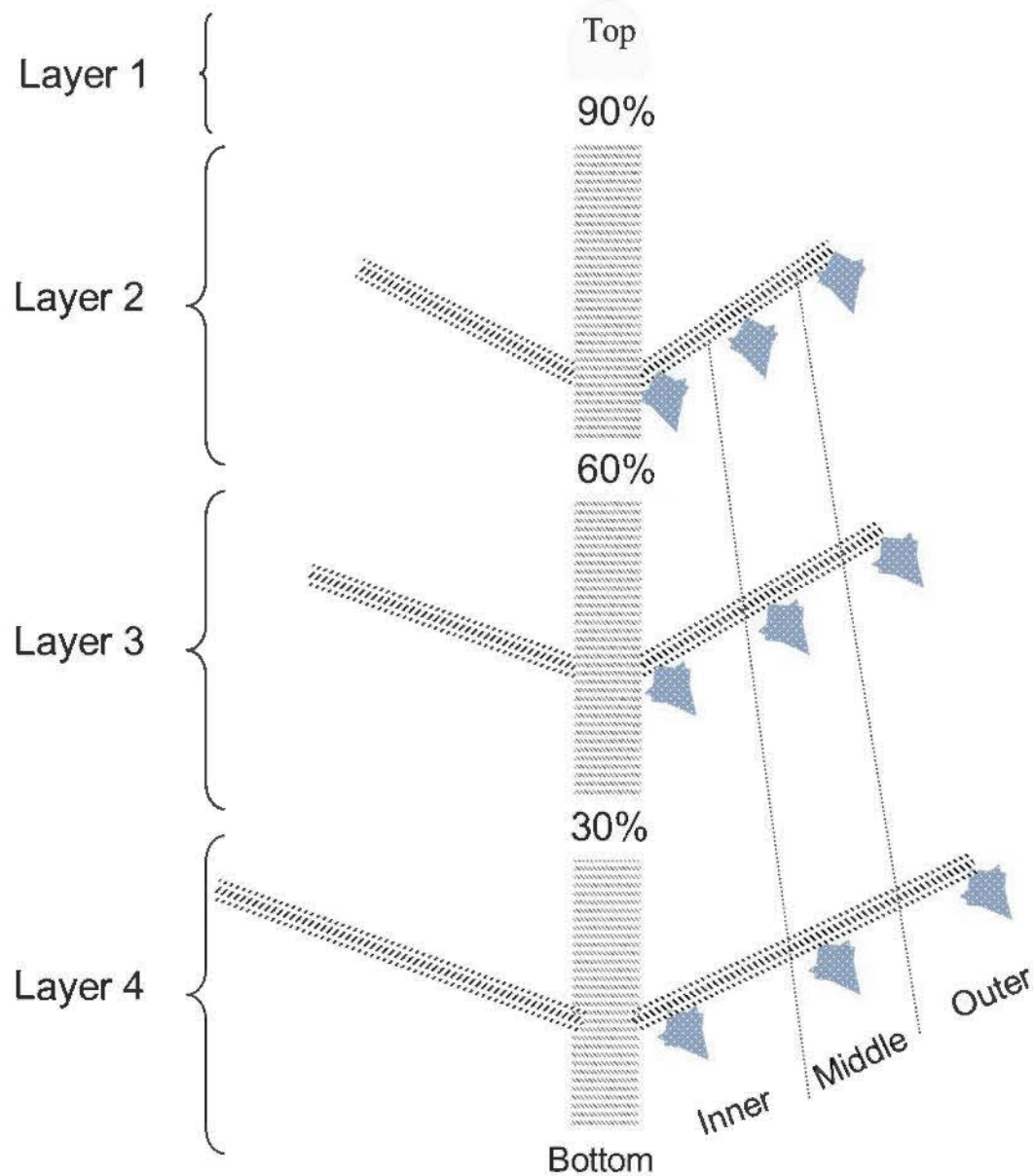


Figure 3-1: Scheme of sample positions within crowns for physiological measurements. Layer 1: top of the crown, layer2: between 60 and 90% of crown length, layer3: between 30 and 60% of crown length and layer4: lowest 30% section of crown length.

Tableau 3-1: Size and leaf area index (LAI) of the two hybrid poplar clones (BT747 and MB915) for each spacing (1×1 m, 3×3 m and 5×5 m), after six growing seasons.

Clone	Spacing	Dbh (cm)	Height (m)	LAI
BT747	1×1m	3.32 ^a	4.11 ^b	2.93 ^c
	3×3m	3.28 ^a	3.28 ^a	0.79 ^c
	5×5m	3.84 ^a	3.27 ^a	0.21 ^a
MB915	1×1m	3.61 ^a	5.03 ^c	2.84 ^c
	3×3m	5.27 ^b	5.63 ^c	1.17 ^d
	5×5m	7.94 ^e	6.64 ^d	0.59 ^b

Dbh: diameter at breast height; LAI: leaf area index. Within a column, means followed by the same letter do not significantly differ at $\alpha \leq 0.05$.

3.3.4 Gas exchange measurements

Measurements of light-saturated photosynthesis (A_{\max}) and stomatal conductance (G_s) were performed using a portable infra-red gas analyser (IRGA), operating in an open mode (CIRAS-2, PP-Systems, Amesbury, MA, USA). The IRGA was equipped with a broadleaf cuvette that was illuminated using a LED light unit (PLC6-broad, PP Systems). Photosynthetically active radiation (PAR), flow rate and CO_2 concentration in the leaf cuvette were maintained, respectively, at $1600 \mu\text{mol m}^{-2} \text{s}^{-1}$, 300 mL min^{-1} , and $360 \mu\text{mol mol}^{-1}$. Measurements were made at 50-75 % relative humidity (RH) and under a vapour pressure deficit (VPD) between 0.8 and 1.8 kPa. All measurements were taken between 09:00 and 12:00. Hourly variation in RH, VPD and temperature was minimized between treatments by randomizing the order of measurement of selected trees. Ambient temperature recorded inside the cuvette ranged between 16°C and 28°C during measurements.

Photosynthetic light response curves (A-Q curves) were constructed in August 2007 using leaves from the upper layer of the crown. Measurements were taken following a 10 min steady-state period of illumination at $1600 \mu\text{mol PAR m}^{-2} \text{s}^{-1}$. Thereafter, PAR was raised to $2000 \mu\text{mol m}^{-2} \text{s}^{-1}$ and subsequently stepped down to the following levels: 1600, 1000, 900, 800, 700, 600, 500, 400, 300, 100, 50, and $0 \mu\text{mol m}^{-2} \text{s}^{-1}$, based on Peek et al (2002). Within the leaf cuvette, air temperature was maintained at $25 \pm 0.5^\circ\text{C}$, while VPD and CO_2 concentration were fixed at 1 kPa and $360 \mu\text{mol mol}^{-1}$, respectively. Dark respiration (Rd)

corresponds to net CO₂ exchange at the end of each A-Q curve (i.e., 10 min after reducing PAR to 0 $\mu\text{mol m}^{-2} \text{s}^{-1}$).

3.3.5 SLA and leaf nitrogen content

Leaf samples were immediately harvested and packed in dry ice following gas-exchange measurements in the field. The area of each sampled leaf (including petioles) was measured with a leaf area meter (LI-3100C, LI-COR Biosciences, Lincoln, NE) before oven-drying (72 °C for 72 h) and weighing. SLA was calculated as the ratio of leaf area (cm²) to leaf dry mass (g). Samples from 2007 and 2008 were then ground using a Wiley mill (Model 3383-L10, Thomas Scientific, Swedesboro, NJ, USA), equipped with a 0.4-mm mesh sieve. Leaf N concentrations (mg/g) was determined by high-temperature combustion using a LECO elemental analyser (CNS2000, Leco Corp., St. Joseph, MI) at the Forest Resources and Soil Testing Laboratory, Lakehead University (Thunder Bay, ON, Canada). Nitrogen content per unit dry mass (N_{mass}) was then converted to an area basis using the SLA measurements for each sample. Photosynthetic nitrogen-use efficiency (PNUE) was defined as light-saturated photosynthesis (A_{max}), divided by N_{area} .

3.3.6 Light measurement

Available PAR at each sampled position in the crown was measured following gas exchange measurements in 2008. Measurements were conducted between 12h00 and 14h00 (zenith) using a CIRAS-2 PAR sensor (PP-Systems). Above-canopy light was measured using permanent micro-meteorological stations. These measurements indicated the maximum light that was intercepted at each sampled position within the crowns.

3.3.7 Statistical analyses

Data were analyzed using SAS (version 9.1, SAS Institute, Cary, NC, USA). Light-saturated photosynthesis (A_{max}), SLA, N_{area} , and PNUE were subjected to repeated measures analysis of variance (RM-ANOVA), with year as the repeated measure in the following model:

$$Y_{tsclh} = \mu + \beta_t + \beta_s + \beta_c + \beta_l + \beta_h + \beta_{int} + E_{site} + E_{tree} + E_{sitexspacing} + \varepsilon \quad (1)$$

where Y is the dependent variable, μ the grand mean, β_t the fixed effect of time (years), β_s the fixed effect of spacing, β_c the fixed effect of clone, β_l the fixed effect of layer, β_h the fixed effect of horizontal position, β_{int} the fixed effect of all interactions, E_{site} the random effect of site, E_{tree} the random effect of tree, $E_{site \times spacing}$ the random effect of the site \times spacing interaction, and ε the residual error. The mixed-model procedure (PROC MIXED) was used with maximum likelihood (ML) estimates of the variance components, except in the case of A_{max} where MIVQUE0 (i.e., minimum variance quadratic unbiased estimates) was used because ML estimates failed to converge on a solution (infinite likelihood). The Satterthwaite method was used to test the fixed effects, i.e., generate approximate F -tests, and to compute their associated denominator degrees-of-freedom (Littell et al. 2006). An autoregressive covariance matrix was selected to represent the structure of the repeated measures model rather than the usual assumption of compound symmetry, as the former had the lowest Akaike information criterion (AIC) among the candidate matrix structures (Littell et al. 2006). Nitrogen and SLA data were log-transformed to achieve homoscedascity, likelihood distance, and normality of residuals. Orthogonal contrasts were used to compare spacings, years, clones, and their interactions. To test the effect of spacing on response variables at each crown position (layer \times horizontal position) using Orthogonal contrasts, two adjustments have been made to the model in eq1, i) Layer and horizontal position variables were gathered to form a new variable called position in the crown ii) analysis was made by clone.

Individual light response curves were analyzed using the nonlinear Mitscherlich function (Peek et al. 2002):

$$A = A_{max} [1 - e^{-Aqe(Q-Lcp)}] \quad (2)$$

Where: Q is PAR, A_{max} the light-saturated photosynthetic rate, Aqe the apparent quantum yield (the slope of the linear phase of the response curve) and Lcp , the light compensation point. The model was fitted using non-linear least-squares regression (NLIN procedure SAS

version 9.1, SAS Institute, Cary, NC, USA). For the iterative procedure, the Gauss–Newton algorithm was used. Parameter estimates from the photosynthetic light response curve (A_{\max} , A_{qe} , L_{cp} and R_d) were subjected to analysis of variance (ANOVA), as dependent (response) variables using the following model:

$$Y_{sc} = \mu + \beta_s + \beta_c + \beta_{sxc} + E_{site} + E_{sitexspacing} + \varepsilon \quad (3)$$

where Y is the dependent variable (A_{\max} , A_{qe} , L_{cp} and R_d), β_{sxc} is the fixed effect of the spacing \times clone interaction, and the other terms are as in Eq. (1). Treatment means were compared using orthogonal contrasts.

Different functional relationships between leaf traits were analyzed using linear regression (GLM procedure in SAS): SLA vs N_{area} , $PNUE$, and L_{cp} , N_{area} vs A_{\max} , $PNUE$ and R_d and N_{area} vs relative irradiance. The slopes of the curves were compared among spacing treatments and clones (ANCOVA).

3.4 Results

3.4.1 Variation in crown light environments

Generally, the proportion of PAR that was intercepted by the foliage decreased with crown depth in each spacing treatment, with the pattern of PAR reduction being more pronounced as spacing decreased (Table 3-2). The fraction of available PAR declined rapidly from the top to the bottom of the crown for all horizontal positions in the closest spacing. The bottom of the crown in the 1×1 m spacing received only 12% of incident radiation, while in the 3×3 m spacing, light attenuation was comparatively moderate relative to the closest spacing, so that the bottom of the crown received about 32% of incident PAR for the outer and middle leaves (Table 3-2). In the 5×5 m spacing, the decrease in PAR as a function of crown depth occurred at all crown positions for clone BT747, but only in the inner and middle leaf positions for clone MB915 (Table 3-2).

Tableau 3-2: Average photosynthetically active radiation (PAR) fractions intercepted at each horizontal and vertical position within the crowns of the two hybrid poplar clones, which have been planted at three spacings (1×1 m, 3×3 m and 5×5 m).

Spacing	Vertical	BT747			MB915		
		Inner	Middle	Outer	Inner	Middle	Outer
1×1 m	layer 1			1 ^h			1 ^j
	layer 2	0.40 ^e	0.63 ^e	0.95 ^{gh}	0.64 ^f	0.50 ^e	0.90 ⁱ
	layer 3	0.14 ^a	0.27 ^b	0.37 ^e	0.08 ^a	0.25 ^b	0.27 ^b
	layer 4	0.09 ^a	0.10 ^a	0.14 ^a	0.10 ^a	0.14 ^a	0.12 ^a
3×3 m	layer 1			1 ^h			1 ^j
	layer 2	0.45 ^e	0.75 ^f	0.90 ^g	0.37 ^e	0.82 ^h	0.98 ⁱ
	layer 3	0.22 ^b	0.40 ^e	0.45 ^e	0.20 ^{ab}	0.60 ^f	0.62 ^f
	layer 4	0.11 ^a	0.26 ^b	0.30 ^b	0.12 ^a	0.33 ^e	0.34 ^e
5×5 m	layer 1			1 ^h			1 ^j
	layer 2	0.40 ^e	0.75 ^f	0.90 ^g	0.30 ^e	0.68 ^{fg}	0.98 ⁱ
	layer 3	0.15 ^a	0.54 ^d	0.55 ^d	0.40 ^d	0.40 ^d	0.96 ⁱ
	layer 4	0.12 ^a	0.27 ^b	0.50 ^{cd}	0.10 ^a	0.33 ^e	0.97 ⁱ

For each clone, means followed by the same letter do not significantly differ at $\alpha \leq 0.05$.

3.4.2 Light-saturated photosynthesis (A_{\max}) and stomatal conductance (Gs)

Mean light-saturated photosynthesis (A_{\max}) of trees growing in the closest spacing (1×1 m) was $12.13 \pm 0.2 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$, which was significantly lower than A_{\max} for trees growing in the 3×3 m and 5×5 m spacings (14.41 ± 0.19 and $14.96 \pm 0.2 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$, respectively; Table 3-3). Moreover, the pattern of change in A_{\max} with spacing was similar for both clones (Spacing × Clone interaction, $P = 0.13$; Table 3-3). Clone MB915 had a greater A_{\max} ($14.48 \pm 0.17 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) than BT747 ($13.18 \pm 0.16 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$). A_{\max} values in 2006 ($13.31 \pm 0.16 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) were similar to those of 2007 ($13.49 \pm 0.17 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) for both clones, and significantly greater in 2008 ($14.17 \pm 0.18 \mu\text{mol CO}_2$

Tableau 3-3: Repeated measures ANOVA giving sources of variation, F values and associated probabilities for light-saturated photosynthesis (A_{max}), stomatal conductance (Gs), specific leaf area (SLA), leaf nitrogen content per leaf area unit (N_{area}) and photosynthetic nitrogen-use efficiency (PNUE).

Source	A_{max}		Gs		SLA		N_{area}		PNUE	
	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Spacing (S)	15.1	<0.001	0.5	0.57	23.85	<0.001	17.4	<0.001	3.1	0.04
Contrast										
1×1m vs 3×3m + 5×5m	5.4	<0.001	-	-	6.8	<0.001	5.75	<0.001	2.1	0.03
3×3m vs 5×5m	0.6	0.49	-	-	1.1	0.32	1.4	0.17	1.4	0.17
Clone (C)	8.6	<0.001	2.6	0.10	17.86	<0.001	5.4	0.02	26.7	<0.001
S×C	2.1	0.13	0.1	0.94	0.4	0.61	0.2	0.80	0.8	0.46
Year (Y)	10.83	<0.001	57.78	<0.001	10.1	<0.001	6.9	0.009	11.5	0.001
Contrast										
2006 vs 2007 + 2008	4.2	<0.001	1.3	0.16	4.9	<0.001	-	-	-	-
2007 vs 2008	2.1	0.03	4.2	<0.001	5.1	<0.001	2.6	0.009	3.4	0.001
S × Y	0.9	0.42	0.5	0.69	2.3	0.05	0.1	0.92	0.4	0.68
C × Y	0.1	0.86	2.1	0.13	1.1	0.33	0.1	0.71	1.4	0.23
S × C × Y	1.3	0.26	0.1	0.97	0.4	0.81	0.5	0.61	0.3	0.77

$\text{m}^{-2} \text{s}^{-1}$) compared to the two previous years. The effect of spacing on A_{max} was independent of time (Spacing \times Time interaction, $P = 0.42$; Table 3-3). Stomatal conductance (Gs) was similar for the three spacings and the two clones ($305 \pm 17 \text{ mmol m}^{-2} \text{ s}^{-1}$; Table 3-3), but significantly greater ($436 \pm 30 \text{ mmol m}^{-2} \text{ s}^{-1}$) in 2008 compared to 2006 ($226 \pm 29 \text{ mmol m}^{-2} \text{ s}^{-1}$) and 2007 ($252 \pm 29 \text{ mmol m}^{-2} \text{ s}^{-1}$).

Tableau 3-4: Mean A_{max} ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) for each horizontal and vertical position within the crown, by spacing treatment ($1 \times 1 \text{ m}$, $3 \times 3 \text{ m}$ and $5 \times 5 \text{ m}$) and clone (BT747 and MB915).

Spacing	Vertical	BT747			MB915		
		Inner	Middle	Outer	Inner	Middle	Outer
$1 \times 1 \text{ m}$	layer 1			19.8 ^g			18.7 ^g
	layer 2	10.1 ^{ab}	13.3 ^c	16.7 ^c	9.9 ^b	14.8 ^d	18.6 ^g
	layer 3	9.8 ^a	12.2 ^b	13.7 ^c	8.2 ^a	12.2 ^c	14.4 ^d
	layer 4	8.2 ^a	8.9 ^a	8.4 ^a	6.6 ^a	9.1 ^b	10.8 ^b
$3 \times 3 \text{ m}$	layer 1			19.1 ^g			19.9 ^g
	layer 2	9.8 ^a	13.3 ^c	19.1 ^g	10.8 ^c	16.9 ^{de}	18.8 ^g
	layer 3	8.1 ^a	13.4 ^{bc}	16.7 ^c	11.1 ^c	14.8 ^d	18.0 ^f
	layer 4	9.1 ^a	12.1 ^b	14.7 ^d	9.4 ^b	13.2 ^d	17.1 ^e
$5 \times 5 \text{ m}$	layer 1			19.6 ^g			18.4 ^g
	layer 2	11.1 ^b	14.3 ^d	19.2 ^g	14.6 ^d	17.6 ^e	18.6 ^g
	layer 3	7.1 ^a	11.2 ^b	18.6 ^f	11.0 ^c	17.5 ^e	19.4 ^g
	layer 4	8.1 ^a	12.7 ^b	17.0 ^e	11.2 ^c	13.5 ^d	17.6 ^e

For each clone, means followed by the same letter do not significantly differ at $\alpha \leq 0.05$.

In general, A_{max} decreased vertically from the top to the bottom of the crown (Table 3-4). Mean A_{max} at the top of the crowns (layer 1) was $19 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$, which was similar among all spacings and between clones. A_{max} of layer 2 did not differ between spacings for the outer leaves of clone MB915, but was significantly lower for BT747 at the $1 \times 1 \text{ m}$ compared to the $3 \times 3 \text{ m}$ and $5 \times 5 \text{ m}$ spacings (Table 3-4). In the third and fourth layers, A_{max} in the closest spacing was significantly reduced compared to the wider spacings for all horizontal positions for MB915 and mostly for the outer leaves of BT747 (Table 3-4).

Mean A_{\max} in the 3×3 m spacing was significantly lower than in the 5×5 m spacing, but only for the fourth layer (Table 3-3). For each layer, A_{\max} significantly increased from inner to outer leaf positions, except for the fourth layer in the 1×1 m spacing of clone BT747, where there were no differences among leaf positions (Table 3-4).

Tableau 3-5: Mean specific leaf area ($\text{cm}^2 \text{g}^{-1}$) for each horizontal and vertical position within the crown, by spacing treatment (1×1 m, 3×3 m and 5×5 m) and clone (BT747 and MB915).

Spacing	Vertical	BT747			MB915		
		Inner	Middle	Outer	Inner	Middle	Outer
1×1 m	layer 1			80 ^g			99 ^{cd}
	layer 2	93 ^d	91 ^e	95 ^{de}	104 ^c	100 ^d	104 ^{cd}
	layer 3	105 ^e	96 ^d	94 ^d	115 ^b	121 ^b	103 ^{cd}
	layer 4	133 ^a	108 ^c	96 ^d	122 ^b	142 ^a	95 ^c
3×3 m	layer 1			73 ^h			87 ^f
	layer 2	91 ^e	85 ^e	77 ^h	115 ^{bc}	94 ^{cd}	78 ^g
	layer 3	101 ^e	89 ^f	78 ^g	122 ^b	118 ^b	88 ^e
	layer 4	103 ^e	93 ^d	102 ^d	129 ^b	110 ^b	95 ^c
5×5 m	layer 1			69 ⁱ			70 ^h
	layer 2	100 ^d	89 ^e	76 ^h	111 ^c	92 ^e	77 ^g
	layer 3	116 ^{bc}	109 ^e	85 ^f	115 ^b	102 ^e	71 ^h
	layer 4	111 ^c	108 ^e	84 ^f	131 ^b	110 ^b	86 ^f

For each clone, means followed by the same letter do not significantly differ at $\alpha \leq 0.05$.

3.4.3 Specific leaf area (SLA)

Reduced spacing significantly increased specific leaf area (SLA) for the two hybrid poplar clones (Table 3-3). Clone MB915 had greater SLA than BT747 at all spacings (Table

3-5), but both clones responded in a similar fashion to changes in spacing (Table 3-3). For both clones, mean SLA was significantly greater in 1×1m than in 3×3m and 5×5m. However SLA was similar in 3×3m and 5×5m spacings (Table 3-3). Mean values for MB915 were 119, 104, and 99 cm² g⁻¹ for 1×1m, 3×3m and 5×5m respectively, and for BT747: 109, 90 and 91 cm² g⁻¹ for 1×1m, 3×3m and 5×5m, respectively. The spacing effect was also time dependent with respect to SLA, which significantly increased from 2006 to 2008 (Table 3-3). Specific leaf area significantly increased vertically from the top to the bottom of the crown and horizontally from the crown edge to the inside of the crown near the stem (Table 3-5), at all spacings. Unlike A_{max} , SLA significantly increased at all levels of the crown, including the top layer, as spacing decreased (Table 3-5).

3.4.4 Leaf nitrogen content (N_{area}) and PNUE

The increase in spacing between trees significantly increased N_{area} (Table 3-3). Indeed, N_{area} of trees growing in the closest spacing (1.55 g m⁻²) was about 27-30% lower than that of trees growing in the 3×3 m (2.01 g m⁻²) and 5×5 m (2.14 g m⁻²) spacings, while there was no difference in N_{area} between the 3×3 m and 5×5 m spacings. Clone BT747 had greater mean N_{area} (1.99 g m⁻²) than clone MB915 (1.81 g m⁻²). Mean N_{area} was lower in 2008 (1.81 g m⁻²) compared to 2007 (1.98 g m⁻²). Like A_{max} , the effect of spacing on leaf N_{area} was also independent of time, as there was no interaction between spacing and year ($P = 0.92$; Table 3-3). Leaf N_{area} distribution within crowns showed patterns similar to A_{max} , increasing from bottom to top of the crown and from the inner to outer leaves (Table 3-6). Leaf N_{area} was significantly lower in the 1×1 m spacing compared to the wider spacings, at all crown positions (Table 3-6). Except for the fourth layer of clone BT747, there was no difference in N_{area} between the 3×3 m and 5×5 m spacings (Table 3-6).

Photosynthetic nitrogen-use efficiency (PNUE) was significantly higher in the closest spacing (7.96 $\mu\text{mol CO}_2 \text{ g}^{-1} \text{ N s}^{-1}$) compared to the 3×3 m (7.45 $\mu\text{mol CO}_2 \text{ g}^{-1} \text{ N s}^{-1}$) and 5×5 m spacings (7.06 $\mu\text{mol CO}_2 \text{ g}^{-1} \text{ N s}^{-1}$) (Table 3-3). Clone MB915 had greater PNUE mean values (8.3 $\mu\text{mol CO}_2 \text{ g}^{-1} \text{ N s}^{-1}$) than clone BT747 (6.7 $\mu\text{mol CO}_2 \text{ g}^{-1} \text{ N s}^{-1}$; Table 3). Photosynthetic nitrogen-use efficiency increased by 13% from 2007 (7.06 $\mu\text{mol CO}_2 \text{ g}^{-1} \text{ N s}^{-1}$) to 2008 (7.93 $\mu\text{mol CO}_2 \text{ g}^{-1} \text{ N s}^{-1}$) in all spacing treatments (Table 3-3).

Tableau 3-6: Mean leaf nitrogen concentration (g m^{-2}) for each horizontal and vertical position within the crown, by spacing treatment (1×1 m, 3×3 m and 5×5 m) and clone (BT747 and MB915).

Spacing	Vertical	BT747			MB915		
		Inner	Middle	Outer	Inner	Middle	Outer
1×1m	layer 1			2.65 ^f			1.87 ^d
	layer 2	1.50 ^e	1.84 ^d	1.99 ^d	1.32 ^{ab}	1.68 ^e	1.76 ^d
	layer 3	1.23 ^a	1.66 ^c	1.69 ^c	1.24 ^a	1.38 ^{ab}	1.60 ^{bc}
	layer 4	1.14 ^a	1.28 ^b	1.53 ^c	1.15 ^a	1.08 ^a	1.53 ^c
3×3m	layer 1			3.25 ^g			2.72 ^f
	layer 2	1.77 ^d	2.24 ^e	2.87 ^f	1.52 ^e	2.01 ^d	2.50 ^e
	layer 3	1.57 ^c	1.86 ^{cd}	2.63 ^f	1.41 ^a	1.67 ^{ac}	2.30 ^e
	layer 4	1.51 ^c	1.63 ^c	2.06 ^c	1.24 ^a	1.51 ^c	2.01 ^d
5×5m	layer 1			3.41 ^g			2.99 ^f
	layer 2	1.81 ^d	2.24 ^e	3.09 ^{fg}	1.75 ^d	2.04 ^d	2.69 ^e
	layer 3	1.62 ^c	1.71 ^{cd}	2.67 ^f	1.59 ^c	1.96 ^{cd}	2.73 ^e
	layer 4	1.32 ^b	1.70 ^d	2.53 ^f	1.29 ^a	1.68 ^c	2.28 ^d

For each clone, means followed by the same letter do not significantly differ at $\alpha \leq 0.05$.

3.4.5 Light response curves

In the upper crown, spacing affected neither A_{\max} nor apparent quantum yield (Aqe) ($P = 0.3$), and their values were statistically similar between the two clones ($P = 0.23$). Across all treatments (spacing and clone), A_{\max} and Aqe averaged $18.5 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ and $0.0017 \text{ g } \mu\text{mol}^{-1}$, respectively. Dark respiration (Rd) was significantly lower ($P = 0.02$) in the 1×1 m spacing ($2.3 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) than in 3×3 m and 5×5 m ($3.5 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$). Also, Lcp was significantly lower ($P = 0.03$) in the 1×1 m spacing ($83 \mu\text{mol PAR m}^{-2} \text{ s}^{-1}$) than in 3×3 m

and 5×5 m (110 $\mu\text{mol PAR m}^{-2} \text{ s}^{-1}$). Dark respiration and L_{cp} were similar between the two hybrid poplar clones.

3.4.1 Leaf trait relationships

Specific leaf area (SLA) and N_{area} were significantly and negatively associated with a log-linear relationship ($P = 0.001$; Fig. 3-2a, 3-2b). Photosynthetic nitrogen-use efficiency (PNUE) and SLA were positively and linearly associated ($P = 0.009$; Fig. 3-2c, 3-2d). The slope of this relationship was similar for the two clones. The light compensation point (L_{cp}) decreased with SLA (Fig. 3-2e, 3-2f). Light-saturated photosynthesis (A_{max}) increased with foliar N, when the latter was expressed on an area basis (N_{area}) (Fig. 3-3). For each value of A_{max} , MB915 had lower values of N_{area} compared to BT747, as determined by a greater slope for the A_{max} - N_{area} relationship for MB915 ($P = 0.001$). In other words, for a given investment in leaf nitrogen, clone MB915 had greater values of A_{max} than did clone BT747. Also, the slope of the A_{max} - N_{area} relationship was greatest in the closest spacing compared to the two wider spacings (Fig. 3-3). Slopes of A_{max} - N_{area} did not significantly differ between the 3×3 m and 5×5 m spacings. The A_{max} -SLA relationship was negative and significant ($P = 0.001$), although SLA explained only 30% of the variation in A_{max} . A linear relationship was found between PNUE and N_{area} (Fig. 3-4a, 3-4b), and the slope of this relationship was similar for the two clones ($P > 0.05$). A strong negative and linear relationship was found between dark respiration (R_d) and N_{area} (Fig. 3-4c, 3-4d), with similar slopes for the two clones ($P > 0.05$). Linear relationship was found between N_{area} and relative irradiance, slope of this relationship did not significantly differ between the three spacings for both clones (Fig. 3-5).

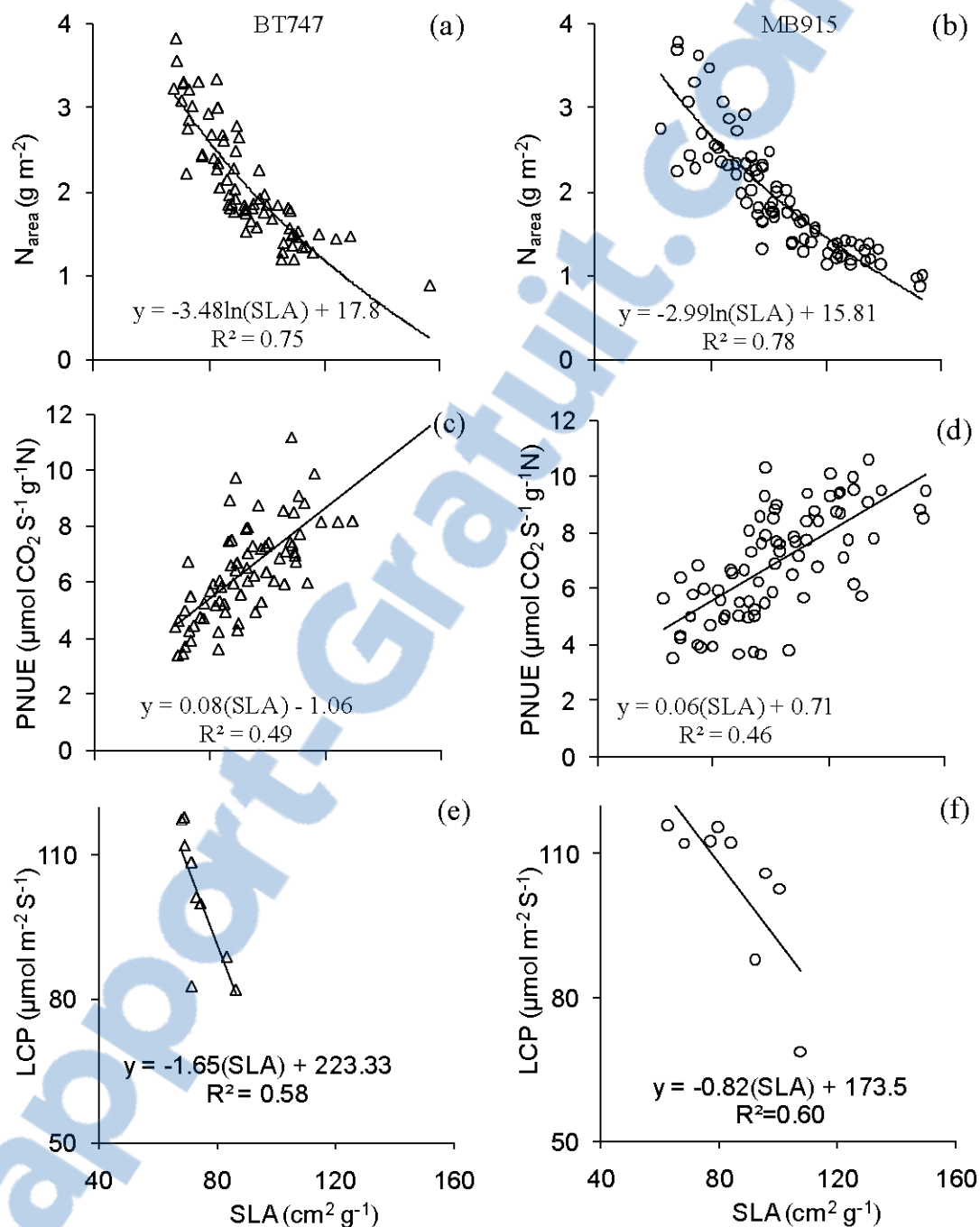


Figure 3-2: Relationships between (a, b) leaf nitrogen content (N_{area}), (c, d) photosynthetic nitrogen-use efficiency (PNUE), and (e, f) light compensation point (Lcp) versus specific leaf area (SLA) for the two hybrid poplar clones (BT747 and MB915).

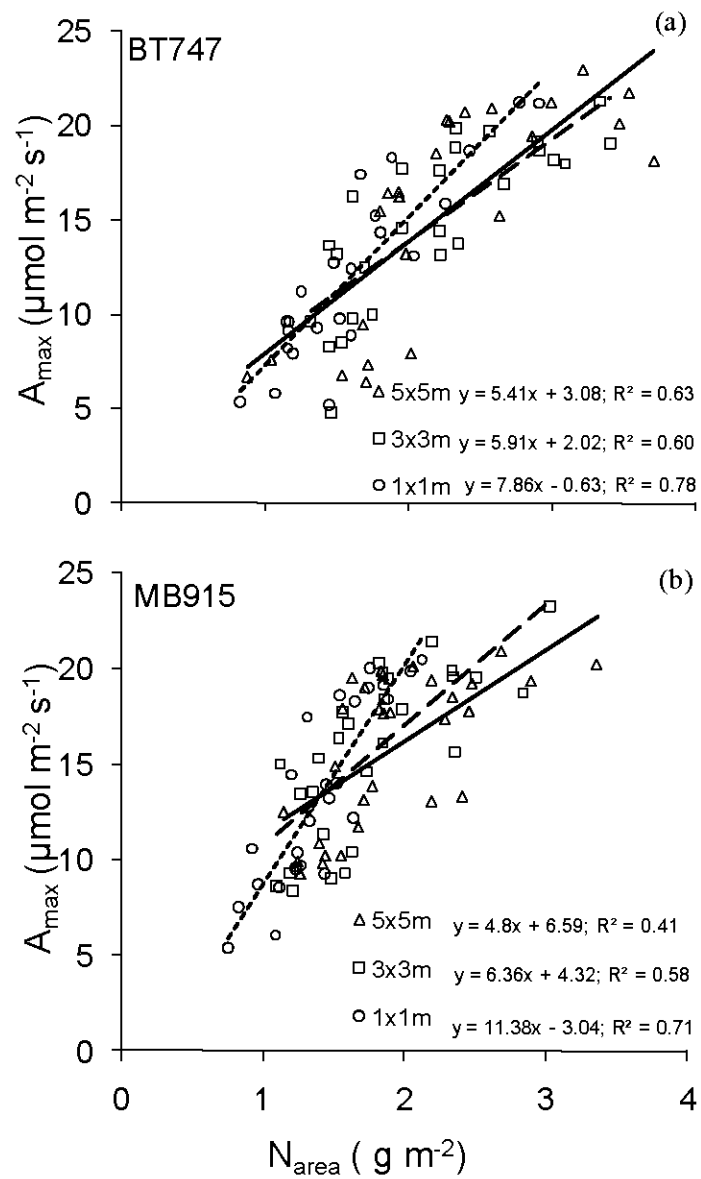


Figure 3-3: Relationships between light-saturated photosynthesis (A_{\max}) and leaf nitrogen on an area basis (N_{area}) for clones (a) BT747 and (b) MB915.

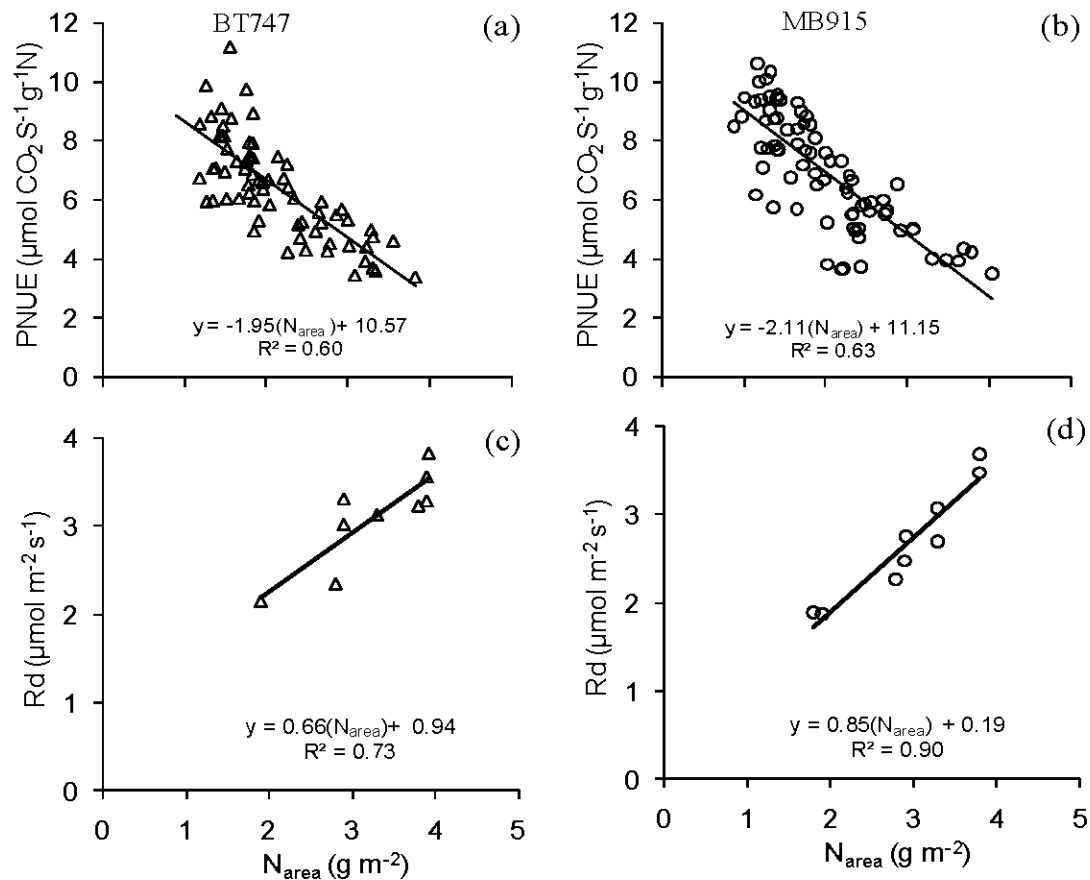


Figure 3-4: Relationships between (a, b) photosynthetic nitrogen-use efficiency (PNUE) and (c, d) dark respiration (R_d) and leaf nitrogen on area basis (N_{area}) for the two hybrid poplar clones (BT747 and MB915).

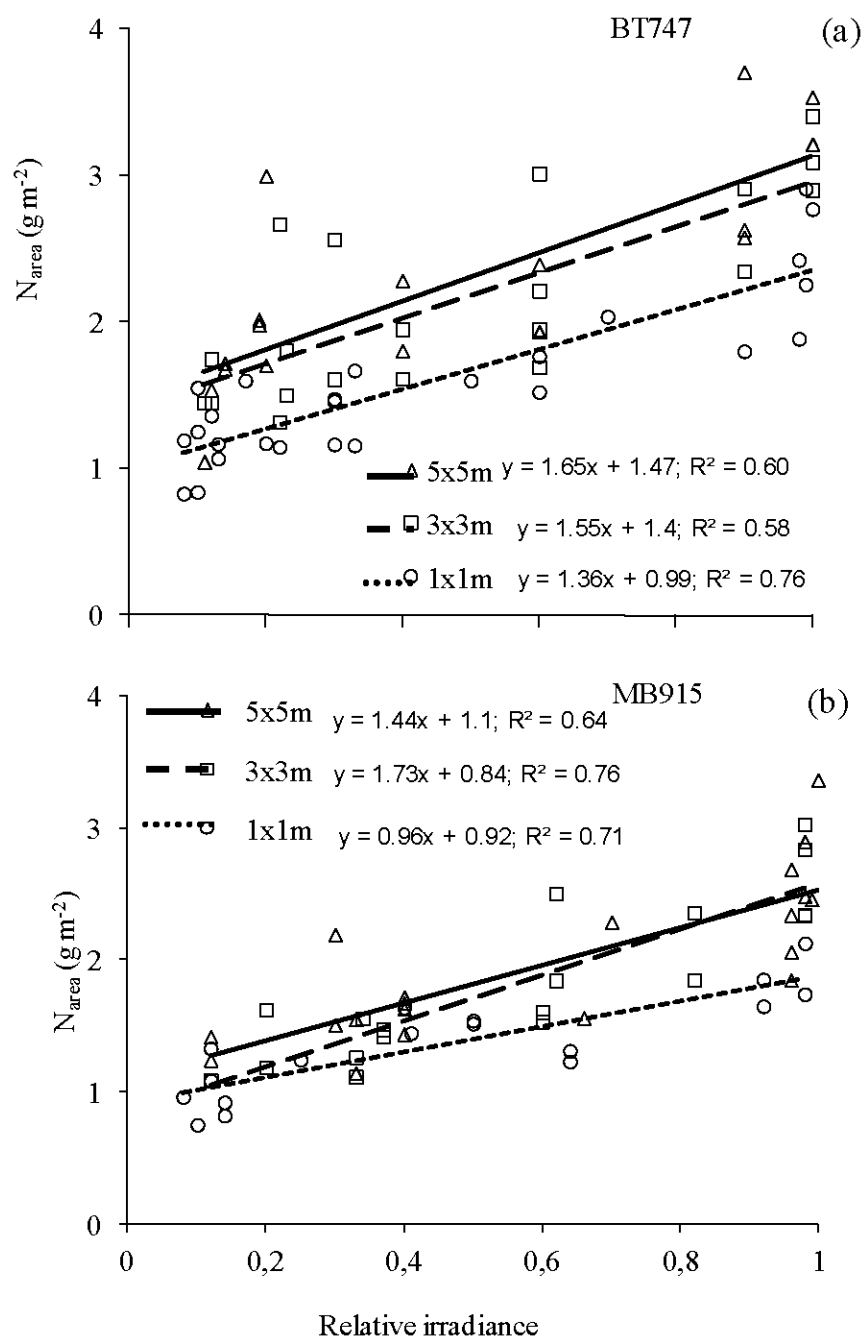


Figure 3-5: Relationships between leaf nitrogen on area basis (N_{area}) and relative irradiance for clones (a) BT747 and (b) MB915.

3.5 Discussion

Changes in SLA reflect leaf structure modulation, which can be described as the main mechanism for light acclimation within a canopy (Anten et al. 1998; Hikosaka et al. 1999), although SLA adjustments may also be related to nutrient availability (Meziane and Shipley 2001), water stress (Marron et al. 2002), and competitive ability (Burns and Winn 2006). This study showed how an increase in intraspecific competition increased SLA of trees in all vertical crown layers, except for inner leaves. Similar results were reported by Larocque (1999) for other hybrid poplar clones. Results of the present study suggest that, in addition to changes in PAR, nutrient availability affected SLA. Significant differences in SLA were also observed in the first section at the top of the crown, where leaves were growing under full sunlight. The increase in SLA with decreased spacing at the top of the crown was also correlated with decreases in the light compensation point and dark respiration. The consequence of increasing SLA under high intra-clonal competition was an increase in light capture per unit of leaf area and, therefore, optimization of carbon and N investment in the leaf (Niinemets and Sack 2006). Specific leaf area (SLA) also decreased from the inner to the outer crown and from the bottom to the top of the crown in all spacing treatments. This indicates foliage acclimation to irradiance, as indicated by previous studies (Iio et al. 2005; Medhurst and Beadle 2005). However, in our study, part of the horizontal variation in SLA was not explained by changes in the light environment. This is maybe due to the time-scale (min) of our light measurements, but leaf aging could also explain this variation (Field 1983). The effect of competition on SLA increased from 2006 to 2008, which suggested progressive acclimation of the leaf structure to competition. This progressive reaction of foliage to competition is probably a consequence of parallel changes in site resources and in other tree variables such as biomass allocation and tree morphology (Grams and Andersen 2007). Photosynthetic acclimation through progressive changes in leaf structure reflects the dynamic nature of photosynthetic acclimation (Walters 2005).

The increase in mean A_{\max} that we observed in the two widest spacings was the result of changes in A_{\max} of the foliage in the lower and middle zones of the crown due to decreased light availability, while the top half of the crowns was more or less unchanged by competition (Table 3-4). Similar results had been obtained for *Eucalyptus globulus*

(Henskens et al. 2001) and *E. nitens* (Medhurst and Beadle 2005) under increasing competition. In contrast, Kolb et al (1998) found a decrease in A_{\max} at the top of the crowns under increasing competition. In our study, trees in the 1×1 m spacing treatment had grown under a closed canopy environment since 2006, while crown closure in the 3×3 m and 5×5 m spacings did not occur until 2008. Light attenuation in the wider spacings was more pronounced in clone BT747 than clone MB915. This response was due to different crown structures between the two hybrid poplar clones: Clone BT747 was characterized by acute branching angles and greater leaf area density compared to clone MB915.

Leaf nitrogen (N_{area}) values for trees growing in the two widest spacings were comparable to published values for other hybrid poplar clones (Casella and Ceulemans 2002; Ripullone et al. 2003), but were greater than those reported by Coll et al (2007) and Curtis et al (2000). However, values of N_{area} in the closest spacing (1×1m), and particularly for clone MB915, were somewhat lower than these published values. The decrease in spacing from 5×5 m to 1×1 m was associated with a 30% decrease in N_{area} . These results are consistent with previous studies, which have argued that N_{area} is sensitive to tree growing space (Medhurst and Beadle 2005; Szendrödi 1996). A gradient in N_{area} was apparent in both vertical and horizontal planes. Variation in N_{area} within the crown was proportional to the light microenvironments experienced by the leaves (Fig. 3-5). As such, our results support the N allocation theory, in that N_{area} was distributed within the crown in a pattern paralleling the light environment (Field 1983). This optimal distribution of N_{area} may lead to an optimization of PNUE at the canopy level (canopy-PNUE). The theory of optimal N_{area} distribution within the crown has demonstrated that canopy-PNUE can be optimal through the allocation of more N_{area} for more strongly illuminated leaves and less N_{area} for more shaded leaves within the crown (Field 1983). Clone BT747 had greater N_{area} than clone MB915, which may have been due to differences in N uptake capacity in relation to root morphology (Al Afas et al. 2008), or to biomass investment in roots (Johnson and Biondini 2001).

Correlations between light-saturated photosynthesis and N_{area} were found in all treatments (Fig. 3-3). Our results are in agreement with other data showing a linear A_{\max} - N_{area} relationship in hybrid poplars (Curtis et al. 2000; Casella and Ceulemans 2002; Ripullone et

al. 2003). The variation of steepness of the A_{\max} - N_{area} curve is largely recognized as being species-dependent due to species-related variation in PNUE (Reich et al. 1995). In our study, the slope of the A_{\max} - N_{area} relationship was steeper in the 1×1 m spacing compared to the 3×3 m and 5×5 m spacings due to greater PNUE values in the 1×1 m spacing which were associated with lower N_{area} . This suggests that the decrease in N_{area} might have been associated with an increase in the proportion of N allocated to the photosynthetic apparatus and/or changes in the efficiency of N partitioning among photosynthetically derived compounds (Hikosaka and Terashima 1995). In the light of these results, a change in PNUE was induced by both light and N availability. Photosynthetic nitrogen-use efficiency was positively correlated with SLA in a manner consistent with other studies (Poorter and Evans 1998; Schieving and Poorter 1999), and which showed that SLA and PNUE modulation can be induced by the same processes; changes in leaf structure through SLA also could be the cause of variation in PNUE. The latter case could be explained by reduction in SLA through reduction in cell wall thickness (Onoda et al. 2004; Vile et al. 2005), and consequently, reduction in N allocation to processes other than photosynthesis. The decrease in light compensation point (L_{cp}) that paralleled the increase in SLA allows leaves to increase carbon assimilation at low PAR (Niinemets et al. 1998).

3.6 Conclusion

Intra-clonal competition affected N_{area} and light availability within the crown. Trees in the closest spacing were characterized by a pronounced gradient of light attenuation within the crown and by low leaf N content. Foliage response to intra-clonal competition was manifested by increases in SLA and PNUE. Leaves used N more efficiently when N and or light were limiting resources. The slope of the A_{\max} - N_{area} curve was increased under competitive conditions because of increases in PNUE. Hence, the A_{\max} - N_{area} relationship not only characterized the species, but also reflected photosynthetic acclimation of the species to growth conditions. As our study suggests, SLA and PNUE may be important traits in photosynthetic acclimation to intra-clonal competition in hybrid poplar. Comparative studies with other hybrid poplar clones under a wide range of intra-clonal competitive conditions would be necessary for determining the growth advantages provided by SLA and PNUE acclimation to competition. Finally, the influence of SLA and PNUE increases on other

ecophysiological traits, such as leaf photosynthetic capacity (i.e., maximal carboxylation rate, V_{cmax} ; maximal photosynthetic electron transport rate, J_{max}) should be essential in future studies.

3.7 Acknowledgements

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4. Chapitre IV

COMPARING GROWTH AND FINE ROOT DISTRIBUTION IN MONOCULTURES AND MIXED PLANTATIONS OF HYBRID POPLAR AND SPRUCE.

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4.1 Abstract

Disease prevention, biodiversity, productivity improvement and ecological considerations are all factors contributing to increase interest in mixed plantations. The objective of this study was to evaluate early growth and productivity of two hybrid poplar clones (PBT and PMB), one improved family of Norway spruce (PA) and one improved family of white spruce (PG) growing under different spacings in monocultures and mixed plots. The plantations were established in 2003 in Abitibi-Témiscamingue, Quebec, Canada, in a split plot design with spacing as the whole plot factor (1×1 m, 3×3 m and 5×5 m) and mixture treatments as subplot factor with (pure: PBT, PMB, PA and PG, and 1:1 mixture: PBT:PA, PBT:PG, PMB:PA and PMB:PG). Results showed a beneficial effect of the hybrid poplar-spruce mixture on diameter growth for hybrid poplar clones but not for the 5×5 m spacing because of the relatively young age of the plantations. Diameter growth of the spruces decreased in mixed plantings in the 1×1 m, while their height growth increased, resulting in similar aboveground biomass per tree across treatments. Because of the large size differences between spruces and poplars, aboveground biomass in the mixed plantings was generally less than for pure poplar plots. Vertical distribution of fine roots was insensitive to both mixture treatment and spacing.

4.2 Introduction

4.3 Materials and Methods

For the last two decades, short rotation forestry using fast-growing species has gained interest in response to worldwide increases in wood demand (FAO 2001). As a result, vast monoclonal plantations have been established in Europe and North America. Although monoculture plantations are easier to establish, tend and harvest, they are also associated with greater risks for diseases, such as those caused by fungal pathogens, e.g. *Melampsora* sp. (Burdon 2001; McCracken and Dawson 1997). In addition, environmental concerns of the public promote an unfavorable perception of monoclonal plantations, i.e. “Social social acceptability” (Hartley 2002; Howe et al. 2005). Scientists may also support the idea that monocultures have negative impacts on ecosystem functioning (Hooper et al. 2005; Kelty 2006; Knoke et al. 2008). Currently, polyclonal or mixed-species plantations are the most commonly proposed solutions to reduce risks associated with diseases (Roberds and Bishir 1997). Mixed plantations are attractive for several reasons, such as a potential increase in productivity (Kelty 2006; Nichols et al. 2006) diversification of final products (Nichols et al. 2006), habitat improvement for biodiversity (Felton et al. 2010), an increase of recreational values, ecological sustainability and ecosystem resilience (Hartley 2002; Knoke et al. 2008). Forest practitioners are however hesitant to establish mixed plantations, because of a lack of data on productivity of mixed-species plantations and conservative attitudes regarding management and harvesting of this type of plantation (Nichols et al. 2006).

In natural forest stands, the productive advantage of mixed comparatively to mono-specific stands remains controversial; In boreal mixedwood forests, several studies reported greater productivity of mixed stands compared to mono-specific stands of aspen and spruce (e.g. Chen et al. 2003; MacPherson et al. 2001; Man and Lieffers 1999), while no difference between mixed and mono-specific stands were detected in other studies (Cavard et al. 2010; Chen and Klinka 2003). Recently, however, there is growing number of studies reporting increased productivity with diversity of species (Paquet and Messier 2011; Zhang et al. 2012).

Theoretically, there are three types of interactions between species in mixed stands that can increase productivity: facilitation, complementarity and sampling effect (Aarssen 1983; Loreau et al. 2001). Facilitation occurs when one species benefits from the presence of another species. The most common and well-studied example supporting this ecological principle in forest plantations is the mixture of *Eucalyptus sp* with the nitrogen-fixing species of *Acacia*, where the mixture provided a high level of productivity comparatively to mono-specific plantations of *Eucalyptus sp* (Bauhus et al. 2000; Binkley et al. 2003). Facilitation can also take place when litter decomposition of one species is accelerated by the presence of the other species' litter (Forrester et al. 2006; Gartner and Cardon 2004). This is mainly due to the fact that mixing leaves from different species affects the biological, chemical and physical aspect of the litter (Gartner and Cardon 2004). The complementarity hypothesis, also called competitive reduction, refers to conditions of interspecific competition that are more favourable than intraspecific competition through niche separation and more efficient use of site resources in mixtures than in mono-specific cultures. This occurs when combinations of species in mixtures differ in shade tolerance, phenology, duration of photosynthetic activity and height growth rates, which may lead to canopy stratification contributing to an increased in light capture efficiency at the canopy level. Niche differentiation may also occur when species differ in their rooting depth leading to a more efficient use of soil resources. Several results in forest plantations have shown a positive effect of canopy stratification (Kelty 2006; Menalled et al. 1998) and differential distribution of roots (Ewel and Mazzarino 2008; Jose et al. 2006) on productivity. Lastly, the sampling effect theory suggests that species mixtures may have a chance of containing one or more over-yielding species which in turn would be largely responsible for an overall productivity increase of the mixture (Hooper et al. 2005; Loreau et al. 2001).

The main goal of this study was to compare productivity of pure and mixed plantations of hybrid poplar and white and Norway spruce (mixture spruce-hybrid poplar: 1:1). We hypothesized an increase in productivity in mixed plantations compared to monocultures of the poplars/spruces through spatial niche differentiation. Our hypothesis was based on two assumptions: The first assumption was that slow growth and shade tolerance of spruce and fast growth and shade intolerance of hybrid poplar would lead to the formation of two layers in the canopy, reducing competition for light within the canopy. The second assumption was

that there would be a vertical differentiation (spatial compartmentalization) of fine roots between spruce and hybrid poplar in mixed plantations, allowing species to use soil resources differentially and more efficiently which may improve the nutritional status of trees.

4.3.1 Study area

The study area was located in the boreal region of Abitibi-Témiscamingue, Quebec, Canada. Three sites were randomly selected for this study: Amos (48°36'N, 78°04'W), Rivière Héva (48°11'N, 78°16'W), and Nédelec (47°45'N, 79°22'W). The Amos site was an abandoned farmland with heavy clay soils dominated by grasses and a few patches of alder (*Alnus incana* ssp. *rugosa*), willow (*Salix* spp.) and trembling aspen (*Populus tremuloides* Michx.). Rivière Héva was also an abandoned farmland with heavy clay soils, dominated by shrubs and a few patches of alder, willow and trembling aspen. Nédelec was previously dominated by a trembling aspen forest that had been commercially harvested in 2000. The main species that were present included, in addition to trembling aspen, white birch (*Betula papyrifera* Marsh.) and pin cherry (*Prunus pensylvanica* L.) growing on a sandy-loam textured soil.

The plantations were established in 2003, and more details on plantation establishment and maintenance can be found in Benomar et al. (2011). Two hybrid poplar clones (*P. balsamifera* x *trichocarpa* (PBT) and *P. maximowiczii* x *balsamifera* (PMB)), one improved white spruce family (*Picea glauca* (PG)) and one improved Norway spruce family (*Picea abies* (PA)) were used. Each hybrid poplar clone and spruce family was planted in both monoculture and mixed plantations under 3 spacings: 1×1 m, 3×3 m and 5×5 m. The experiment was designed as a split-plot layout with spacing as the whole plot factor and each site as a replicate. Each spacing was sub-divided into 8 mixture treatments (*sub-plots*): monoculture of PBT, PMB, PA and PG, and mixed (ratio 1:1) PBT:PA, PBT:PG, PMB:PA, and PMB:PG (Fig. 1). Size of the experimental units (plots) was related to spacing (25 m², 225 m² and 625 m²), and contained 36 trees (6×6 rows of trees). Plots were distanced a minimum of 3 m to allow machinery travel between plots.

4.3.2 Growth

Total height, stem basal diameter (D: 10 cm above soil), diameter at breast height (DBH) and survival were measured at the end of the sixth growing season (mid-October 2008). Trees that died in 2003 and 2004 were replaced in 2005 to maintain competition levels representative of the spacing; the replacement trees were not included in the analyses. Cumulative biomass production after six growing seasons was estimated using biomass equations from Benomar et al. (2012) for hybrid poplar clones and Ter-Mikaelian and Parker (2000) for the spruces. Above-ground biomass production at plot scale ($\text{Mg dry mass ha}^{-1}$) was estimated without consideration of the mortality, i.e. by multiplying tree mean above-ground biomass with tree density at planting in a plot. Since competition-induced mortality did not yet occur in the plantations. Mean survival was similar across the different treatments and greater in 1×1 m and 3×3 m spacings (90%) than in 5×5 m spacing (67%). The higher mortality in 5×5 m spacing was seemingly due to animal browsing (moose and voles), machinery damage or perhaps higher wind velocity.

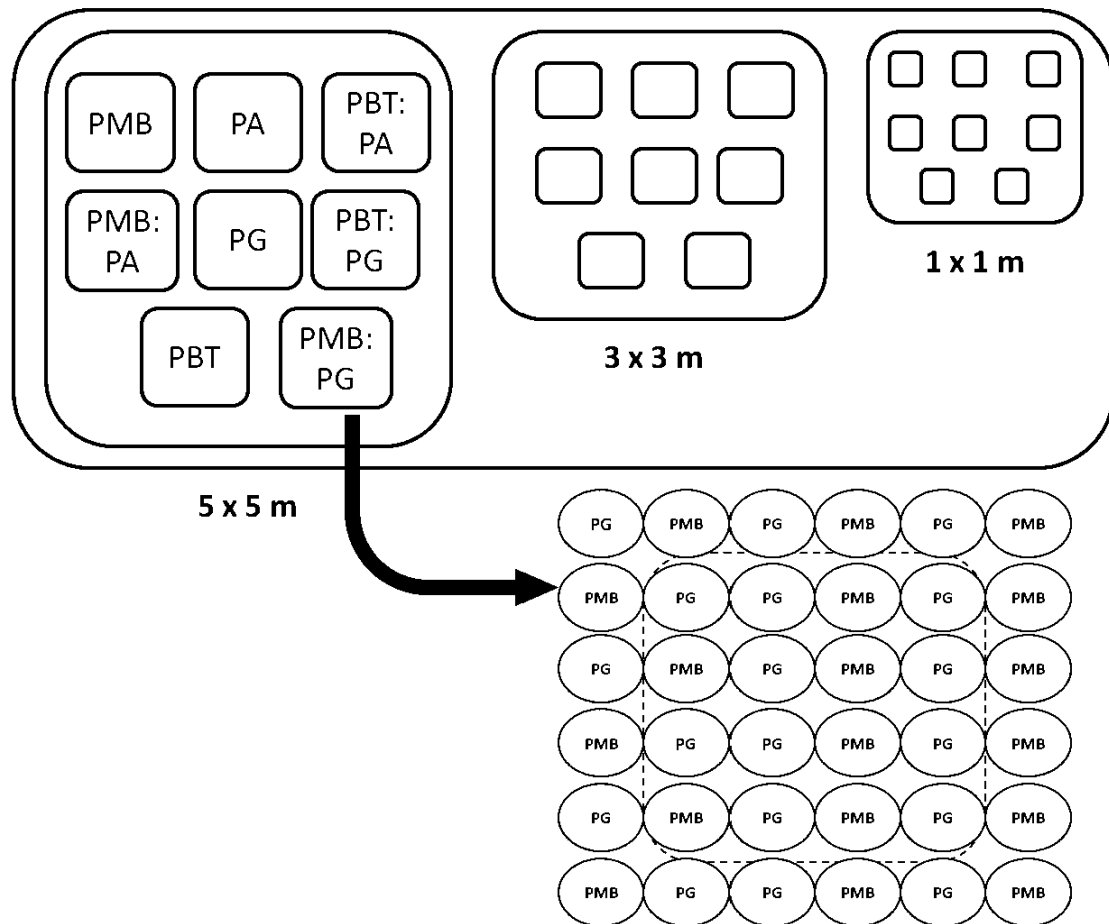


Figure 4-1: Schematic representation of the experimental design with spacing as whole plot and mixture treatment as subplot units and the trees arrangement within mixed plots. Only the inner 16 trees were used for measurements (dotted line).

4.3.3 Foliage nitrogen

During the first week of August 2008, two to three leaves per poplar tree and needles from two to three terminal shoots per spruce were sampled in the upper section of the crown of one representative tree within each treatment. After oven-drying (72 °C for 72 h), samples were ground using a Wiley mill (Model 3383-L10, Thomas Scientific, Swedesboro, NJ, USA), equipped with a 0.4-mm mesh sieve. Leaf nitrogen was determined by high-temperature combustion using a LECO elemental analyser (CNS2000, Leco Corp., St. Joseph, MI) at the Forest Resources and Soil Testing Laboratory, Lakehead University (Thunder Bay, ON, Canada).

4.3.4 Fine roots distribution

Root sampling was conducted on June 10, July 15, and September 15, 2008. These dates corresponded approximately to the beginning, middle and end of the growing season, respectively. One tree was randomly selected within each pure sub-plot and one tree from each species within each mixed sub-plot. For logistical reasons, roots were not sampled in the PA, PBT:PA and PMB:PA plots. For each selected tree, soil coring was performed in two directions (D1 and D2) (Fig. 2). For each direction, a soil core was taken at three distances from the trunk for the 1×1 m spacing (10 cm, 30 cm and 50 cm) and at four distances from the trunk for the 3×3 m and 5×5 m spacings (10 cm, 30 cm, 50 cm and 150 cm). Depth at which the cores were taken was first fixed to 60 cm, but since very little roots were found below 30 cm, we limited the coring depth to 40 cm after the first sampling at Amos (June). A total of 920 soil cores were collected. Each soil core was divided into two depth classes: 0-20 cm and 20-40 cm. Samples were placed in plastic bags and stored at -4°C until analysis (maximum of 1 week): Fine roots (< 2 mm) were separated from soil by washing the cores delicately. Live roots were distinguished from dead roots by colour and flexibility, before oven-drying for 3 days for biomass determination. Spruce, poplar and grass roots were easily distinguished from each by color and morphology.

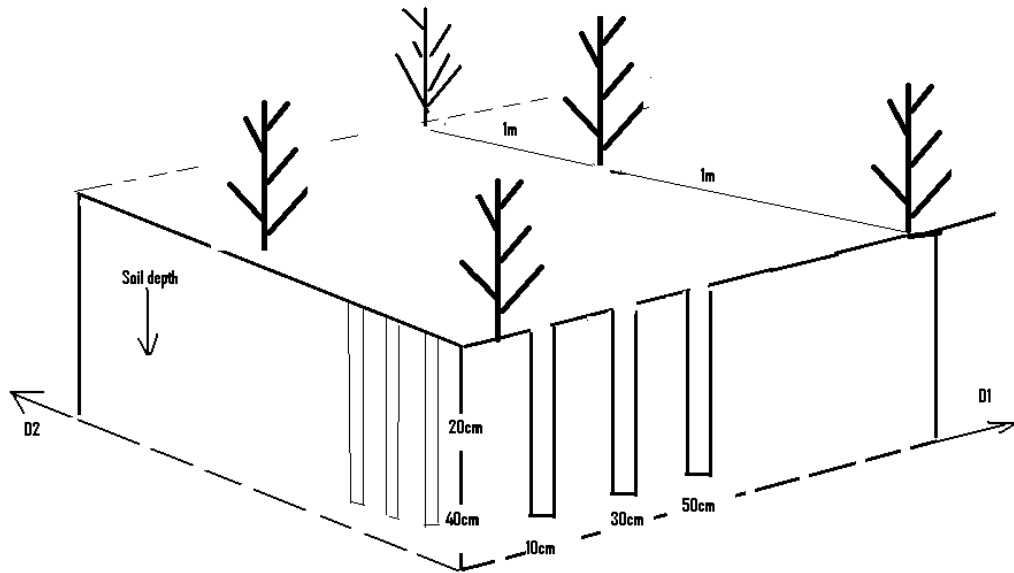


Figure 4-2: Layout of the soil coring positions and its directions in a 1×1 m plot.

4.3.5 Statistical analyses

Data were analyzed using the Statistical Analysis System (SAS Inc., 2000). Response variables such as diameter, height, cumulative aboveground biomass, and leaf nitrogen concentration were analyzed using the following general linear mixed effects model:

$$y = \mu + \beta_s + \beta_m + \beta_{s*m} + E_{site} + E_{site*spacing} + E_{site*spacing*mixture} + \varepsilon \quad \text{Eq1}$$

where y is the response variable, μ the grand mean: β_s the fixed effect of spacing (1×1m, 3×3m and 5×5m), β_m the fixed effect of mixture treatment (PBT, PMB, PA, PG, PBT:PA, PBT:PG, PMB:PA and PMB:PG), β_{s*T} the fixed effect of the interaction between spacing and mixture, E_{site} , $E_{site*spacing}$ and $E_{site*spacing*mixture}$ are the random effects for site, whole plot and subplot respectively. E_R is the residual error. Because of the infinite likelihood, non-iterative method such as Mivque (minimum variance quadratic unbiased estimation) was used to estimate the variance components. Data were log-transformed to achieve the assumptions of

normality and homoscedacity of residuals. Fine root density was analyzed using the following general linear mixed effects model:

$$Y = \mu + \beta_s + \beta_m + \beta_{s*m} + \beta_d + \beta_{s*d} + \beta_{m*d} + \beta_{s*m*d} + \beta_{time} + \beta_{s*time} + \beta_{m*time} + \beta_{d*time} + \beta_{s*m*time} + \beta_{s*d*time} + \beta_{m*d*time} + E_{site} + E_{site*s} + E_{site*s*m} + E_{ori} + \varepsilon \text{ Eq2}$$

Where Y is the fine root density, μ the grand mean, β_{time} the fixed effect of time of soil coring (June, July and September), β_d the fixed effect of soil depth (0-20cm and 20-40cm), β_{s*d} the fixed effect of interactions between spacing and depth, β_{m*d} the fixed effect of interactions between mixture and depth, β_{s*m*d} the fixed effect of interactions between spacing, mixture and depth, β_{s*time} the fixed effect of interactions between spacing and time, β_{m*time} the fixed effect of interactions between mixture and time, β_{d*time} the fixed effect of interactions between depth and time, $\beta_{s*m*time}$ the fixed effect of interactions between spacing, mixture and time, $\beta_{s*d*time}$ the fixed effect of interactions between spacing, depth and time, $\beta_{m*d*time}$ the fixed effect of interactions between mixture, depth and time, E_{ori} the random effect of direction (D1 and D2) and others symbols are as in Eq1. Root square transformation of the data was necessary to achieve model's assumptions. The proportion of area at each horizontal position was used as a weighting factor. The weighting factors for the 1×1 m spacing were 0.2, 0.4 and 0.4 for 10, 30 and 50 cm, respectively. The factors for the 3×3 m spacing were 0.066, 0.133, 0.133, 0.667 for 10, 30, 50 and 150 cm, respectively. For the 5 × 5 m spacing, the weighting factors were 0.04, 0.08, 0.08 and 0.8 for 10, 30, 50 and 150 cm, respectively. Means were compared by Tukey's multiple range tests for all possible comparisons and differences were considered significant at $P \leq 0.05$.

4.4 Results

4.4.1 Growth

Cumulative aboveground biomass estimated at stand level after six growing seasons ($\text{Mg dry mass ha}^{-1}$) was strongly affected by both spacing ($P < 0.001$) and mixture treatment ($P < 0.001$). The increase of spacing between trees strongly decreased stand aboveground biomass in all plots (Table 4-1). Hybrid poplar-spruce mixtures generally produced less aboveground biomass per hectare than pure hybrid poplar plots, except the mixture of

PMB:PG in the 1×1 m spacing. The two spruce species produced similar amounts of biomass which was very low compared to the hybrid poplar clones and contributed very little to the total plot biomass on a per hectare basis in mixtures with poplars.

Spacing and mixture treatment did not affect biomass accumulation on a per tree basis for clone PBT, except in the PBT:PA mixture at the 5×5 m spacing where trees produced a little more biomass (Fig. 4-3a). On the other hand, mixture treatment greatly affected aboveground biomass per tree for clone PMB, where it was greater in the PMB:PG mixture in the 1×1 and 3×3 m spacings (Fig. 4-3b). Aboveground biomass accumulated in the two spruce species was very small after 6 years compared to the poplars, and was unaffected by changes in spacing and mixture (Figs. 4-3c, d).

The two hybrid poplar clones responded similarly to spacing and mixture treatment in terms of basal diameter after 6 years; It increased significantly with the increase in spacing and was greater in mixtures compared to pure plot in the 1×1 and 3×3 m spacings (Figs. 4-4a, b). Unlike diameter growth, the two clones responded differently to spacing and mixture in height growth: Trees of clone PBT were taller in the 1×1 m spacing compared to the 3×3 and 5×5 m spacings, with no significant effect of mixture treatment (Fig. 4-4e). In contrast, trees of clone PMB were generally taller in the two larger spacings compared to the 1×1 m spacing (Fig. 4-4f). For Norway spruce (PA), basal diameter was slightly reduced when mixed with hybrid poplar in the 1×1 m spacing, while basal diameter was similar among mixtures in the 3×3 and 5×5 m spacings. However, PA trees in mixed plantings were taller in the 1×1 spacing (Fig. 4-4g). White spruce (PG) showed less variability than PA in basal diameter among spacings and mixtures (Fig. 4-4d), but also had a greater height in mixed plots in the 1×1m spacing compared to the rest of the treatments (Fig. 4-4h).

Tableau 4-1: Above ground biomass production after six growing seasons of two hybrid poplar clones (PBT and PMB) and two spruce families (PA and PG) growing in monocultures and mixed plots at three spacings (1×1 m, 3×3 m and 5×5 m).

		Aboveground biomass (Mg dry mass ha ⁻¹)				
		PBT	PMB	PA	PG	Total
Spacings	mixtures					
1x1m	PBT	26.6 (3.21)a	-	-	-	26.5 (3.21)a
	PBT:PA	12.6 (2.62)b	-	1.50 (0.12)b	-	14.1 (1.04)b
	PBT:PG	12.8 (4.65)b	-	-	1.56 (0.31)b	14.3 (4.65)b
	PMB	-	29.8 (4.87)a	-	-	29.8 (4.87)a
	PMB:PA	-	17.7 (2.71)b	1.46 (0.12)b	-	19.1 (2.51)b
	PMB:PG	-	25.9 (5.13)ab	-	1.48 (0.13)b	27.6 (5.03)a
	PA	-	-	4.39 (0.49)a	-	4.4 (0.49)c
	PG	-	-	-	3.95 (0.72)a	4.0 (0.72)c
3x3m	PBT	3.10 (0.30)a	-	-	-	3.1 (0.30)c
	PBT:PA	1.49 (0.41)b	-	0.44 (0.02)b	-	1.9 (0.47)d
	PBT:PG	1.62 (0.45)b	-	-	0.27 (0.07)b	1.9 (0.25)d
	PMB	-	6.87 (2.12)a	-	-	6.9 (2.12)a
	PMB:PA	-	4.01 (2.47)b	0.21(0.07)c	-	4.2 (2.31)bc
	PMB:PG	-	4.85 (3.12)b	-	0.29 (0.03)b	5.1 (3.05)ab
	PA	-	-	0.63 (0.15)a	-	0.6 (0.15)e
	PG	-	-	-	0.62 (0.04)a	0.6 (0.04)e
5x5m	PBT	1.21 (0.33)a	-	-	-	1.2 (0.33)c
	PBT:PA	0.76 (0.36)a	-	0.09 (0.01)b	-	0.9 (0.01)c
	PBT:PG	0.35 (0.12)b	-	-	0.14 (0.04)b	0.5 (0.11)d
	PMB	-	4.53 (1.40)a	-	-	4.5 (1.40)a
	PMB:PA	-	2.03 (0.24)b	0.13 (0.04)a	-	2.5 (0.00)b
	PMB:PG	-	1.81 (0.87)b	-	0.10 (0.04)b	1.9 (0.80)bc
	PA	-	-	0.17 (0.01)a	-	0.2 (0.01)d
	PG	-	-	-	0.21 (0.07)a	0.2 (0.07)d

Within spacing and column, means sharing the same letters are not significantly different at $P \leq 0.05$. Numbers in parentheses are standard errors of the mean.

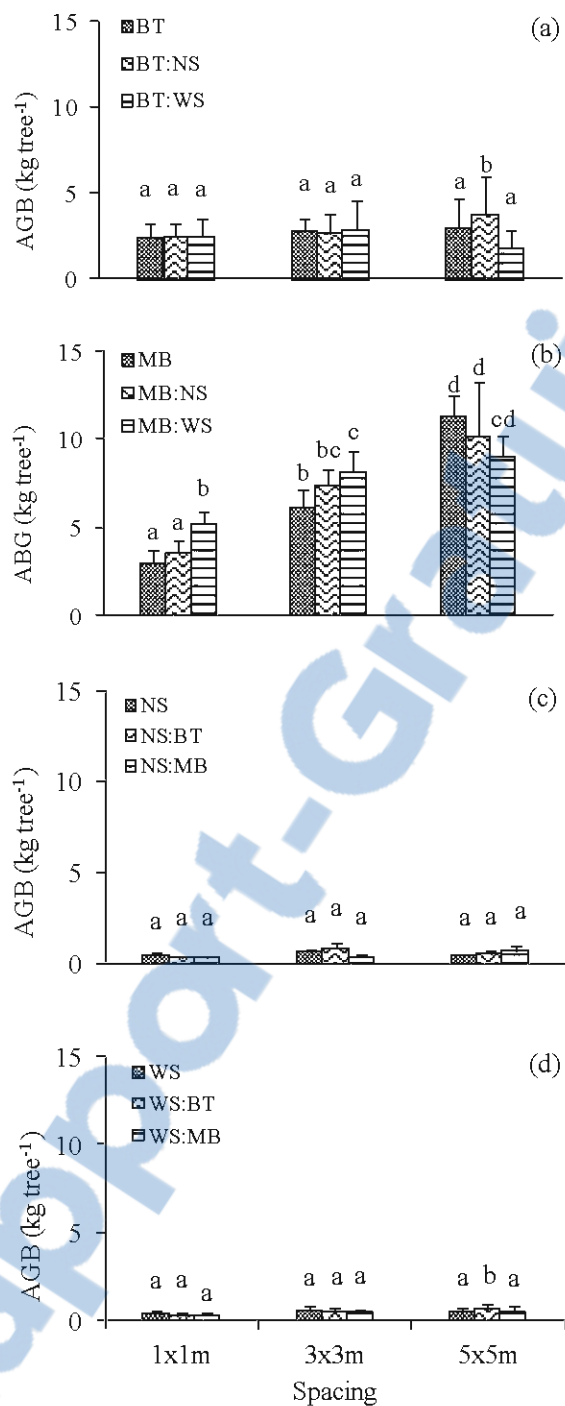


Figure 4-3: Aboveground biomass (AGB) after six growing seasons of two hybrid poplar clones (PBT and PMB) and two spruce families (PA and PG) growing in monocultures and mixed plots at three spacings. Means sharing the same letters are not significantly different at $P \leq 0.05$. Bars represent standard errors of the mean

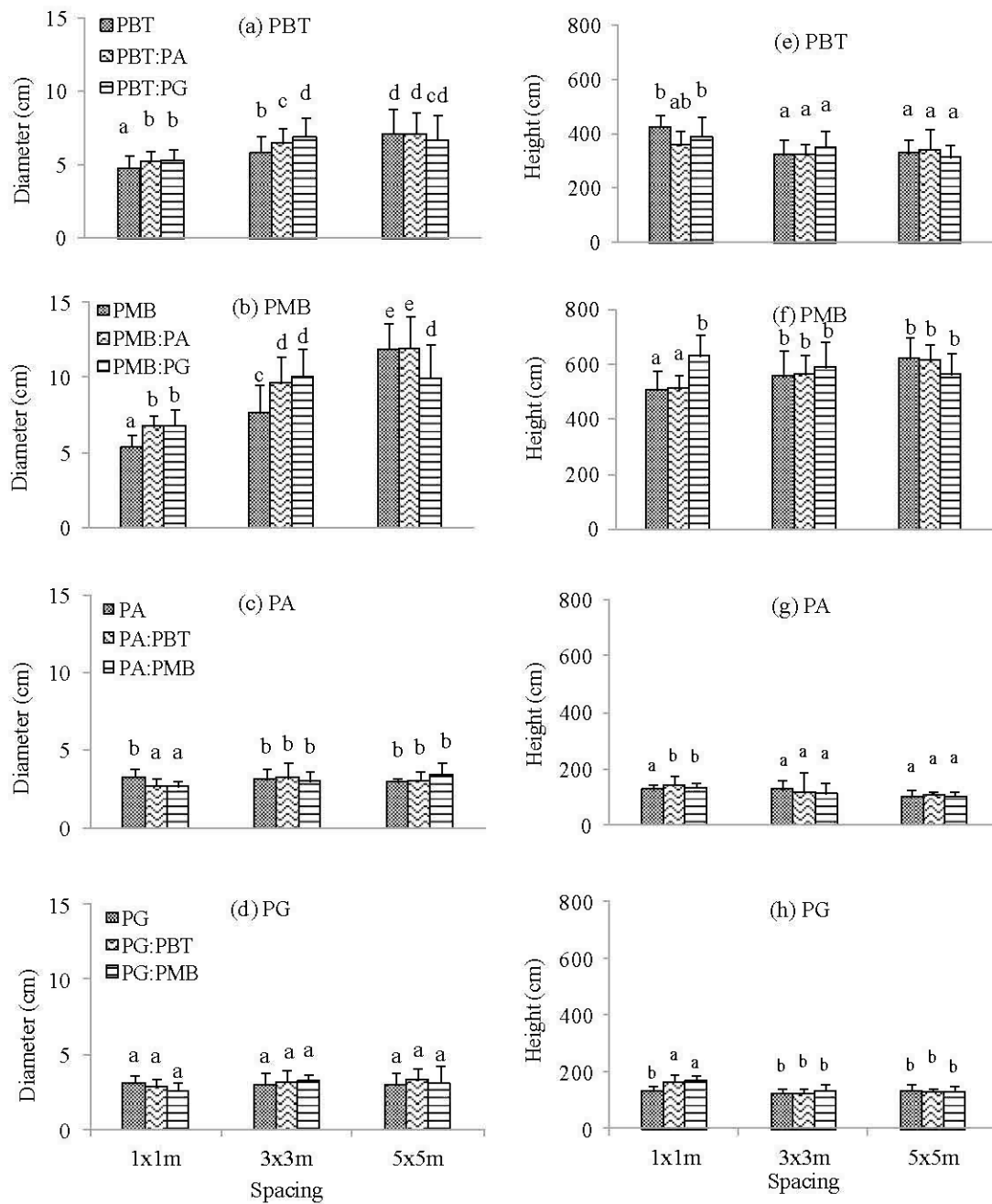


Figure 4-4: Basal diameter and height after six growing seasons growing at three spacings in monocultures and mixed plots. Means sharing the same letters are not significantly different at $P \leq 0.05$. Bars represent standard errors of the mean.

4.4.2 Leaf nitrogen

The response to both spacing and mixture treatments in terms of leaf nitrogen concentration (mg g^{-1}) was different among spruce species and hybrid poplar clones. Clone PBT had similar leaf N across spacings and mixtures (Fig. 4-5a), while clone PMB had greater leaf N concentrations when planted in mixed compared to pure plot (Fig. 4- 5b). Leaf N concentrations also increased significantly from the 1×1 to 5×5 m spacing in pure plots and from the 1×1 to 3×3 m spacing in mixed plots for this clone (Fig. 5b). Leaf N concentrations of clone PMB were similar whether the spruce was PG or PA in the 1×1 m and 3×3 m spacings, however in the larger spacing, leaf N of the PMB poplar was greater when mixed with PA than with PG. Leaf N concentrations were similar for PA and PG and across spacings and mixture treatments, except in pure plots at the 1×1 m spacing where leaf N concentrations were the lowest (Fig. 4-5c, d).

4.4.3 Fine roots distribution

Fine root density was much greater in the 1×1 m spacing comparatively to the other larger spacings, while there was no difference in fine root density between the 3×3 m and 5×5 m spacings (Table 4-2). The time of sampling had no effect on fine root density ($P > 0.05$). Mixture treatment had a significant effect on fine root density only in the 1×1 m spacing, where the two hybrid poplar clones had greater fine root density in pure compared to mixed plot (Table 4- 2). White spruce, in contrast, had similar fine root densities in mixed and pure plots across the spacings (Table 4-2). Fine root density was the greatest for PMB followed by PBT and PG. The vertical distribution of fine root density was similar across spacings and mixture treatments, and decreased from 0-20 cm to 20-40 cm depth by 50, 60 and 80% for PBT, PMB and PG respectively in 1×1 m spacing and by 65, 60 65% for PBT, PMB and PG respectively in 3×3 m and 5×5 m spacings.

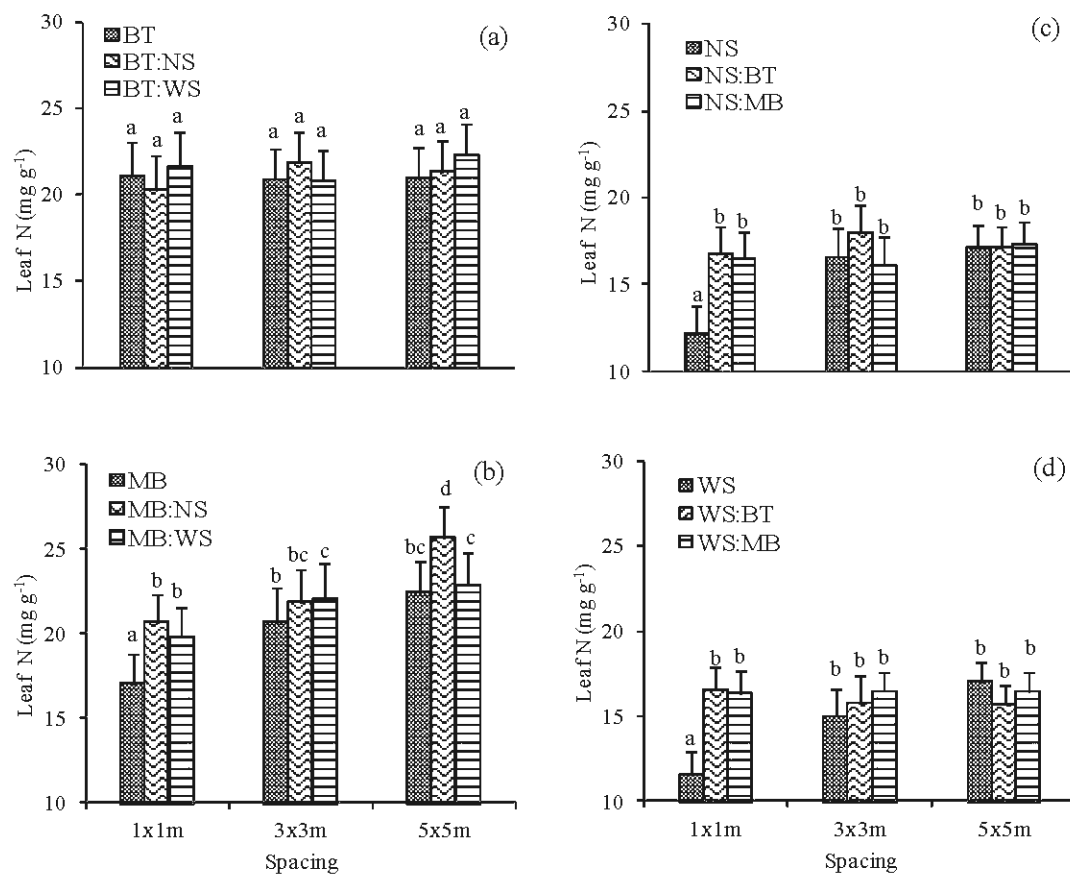


Figure 4-5: Mean leaf nitrogen concentration (mg g⁻¹) for each spacing and deployment at age 5. Means sharing the same letters are not significantly different at $\alpha \leq 0.05$. Bars represent standard errors of the mean.

Tableau 4-2: Vertical distribution of fine root density (g cm^{-3}) for hybrid poplar clones (PBT and PMB) and for white spruce (PG) growing at three spacings (1×1 m, 3×3 m and 5×5 m) in monocultures and mixed plantations after six growing seasons.

	1×1m		3×3m		5×5m	
	mixed	monoculture	mixed	monoculture	mixed	monoculture
0-20cm						
PBT	0.18b	0.24a	0.03c	0.04c	0.02c	0.04c
PMB	0.33b	0.41a	0.07c	0.07c	0.05c	0.10c
PG	0.13a	0.14a	0.03b	0.03b	0.01b	0.02b
20-40cm						
PBT	0.08b	0.13a	0.01c	0.02c	0.01d	0.02c
PMB	0.13b	0.16a	0.04c	0.03cd	0.02d	0.03cd
PG	0.03a	0.03a	0.01b	0.01b	0.01b	0.01b

Means sharing the same letters are not significantly different at $P < 0.05$.

4.5 Discussion

4.5.1 Growth and stand productivity: mixtures vs monocultures

Diameter of the poplars were slightly greater when mixed with spruces compared to pure plantings, which resulted in a slight increase in aboveground biomass on a per tree basis for clone PMB. The increase in basal diameter of hybrid poplars in mixed plantings in the smaller spacings probably arises from a reduction in competition, for light especially, through canopy stratification with the spruces. Although it may seem that the competitive reduction hypothesis or “complementarity” (Aarssen 1983) applies here, at this stage of stand development it most likely only reflects a decrease of intra-specific competition since there was only half the number of poplars in mixed plantings and also since the spruces were so small, exerting little interspecific competition. This could also be seen as an early example of the «sampling effect» (Hooper et al. 2005; Loreau et al. 2001), where one species, the hybrid poplars, takes advantage of the mixture and is largely responsible for an increase in overall

productivity of the plots. The productive advantage of mixed stands showing a stratification of the canopy in natural forest is still controversial; Mixtures of shade tolerant and shade intolerant species in boreal regions, for example, can have equivalent (Cavard et al. 2010; Chen and Klinka 2003), or greater (Chen et al. 2003; Légaré et al. 2004; Man and Lieffers 1999) productivity. This controversy is due to variations in site quality, stand density, stand developmental stage and proportion of each species within mixtures that affect the evolutionary interspecific interactions between species (Amoroso and Turnblom 2006; Chen et al. 2003; Man and Lieffers 1999). In our study, the mixtures of PBT:PG, PBT:PA et PMB:PA were less productive than pure plots of hybrid poplar clones across spacings, simply due to the relative much smaller size of the spruces compared to the poplars. The PMB:PG mixture had similar aboveground biomass than the pure PMB plots, due to a greater increase in aboveground biomass in a per tree basis for trees of clone PMB in this mixture, while clone PBT was inefficient in taking advantage of the greater canopy space available in the mixed plantings. Our data does not allow us to pose a plausible hypothesis on why PMB was more productive in the mixed plantings with PG but not with PA. Since the spruces find themselves quickly overtopped by poplars in mixed plantings, it was not surprising to find an effect of the mixture treatment on diameter and height growth. In the 1×1 m spacing where the canopy was closed, trees compensated by growing taller while their diameter growth slightly decreased, which translated into no significant difference in aboveground biomass per tree across mixture treatments for the spruces. However because the plantations are relatively young (i.e. canopies were not fully closed in the 3×3 and 5×5 m spacings), competitive relationships will likely become more significant in the future. Nevertheless, one can observe early the benefits of mixed plantings on spruce wood quality in the 1×1 m spacing, due to their reduced taper, and later perhaps a reduced branching and ratio of juvenile to mature wood (Jozsa and Middleton 1997).

4.5.2 Height growth and canopy stratification

Shade intolerant species usually exhibit greater initial height growth comparatively to shade tolerant species. Shade tolerant species also usually have a good ability to survive under low light conditions (Kelty 2006). Differences in early height growth thus generally lead to canopy stratification in mixture of these two types of species under natural conditions

(Kabzems et al. 2007). In this study, the hybrid poplar trees were very tall (3.5 to 7 m) compared to either spruce species (< 2 m), which indeed lead to canopy stratification in the mixed plantings.

Height growth is expected to remain insensitive to species mixtures (Amoroso and Turnbull 2006) and to changes in spacing between trees, except perhaps at very narrow or wide spacings (Lanner 1985). The increase in height we observed in the closest spacing for the spruces in mixed plantings and for clone PBT is a result of greater allocation of carbon to height rather than diameter in response to an increase in competition for light (Grams and Andersen 2007). Conversely, more carbon is allocated to diameter than height at very wide spacings (Sumida et al. 1997). This was not observed for clone PMB, which could be explained by a greater importance of below ground competition than above-ground competition for this clone (Grams and Andersen 2007).

4.5.3 Fine roots distribution

Stratification of fine roots in mixed stands is supposed to reduce interspecific competition for soil resources such as nitrogen and water and consequently increase overall stand productivity (Jose et al. 2006; Man and Lieffers 1999). This was found, for example, in Norway spruce and European beech (*Fagus sylvatica*) mixed stands (Bolte and Villanueva 2006; Schmid and Kazda 2002) and in larch-ash (*Larix gmelini-Fraxinus mandshurica*) mixtures (Qing-Cheng 2002; Xiaoyang 1997). Results in this study showed a similar trend in fine root distribution in all treatments with a greater fine root density at the soil surface and less in deeper soil (20-40 cm). The slow growth of spruces and low fine root density implies they have much lower demands in soil resources compared to the poplars in mixed plantings, and consequently exert low interspecific competition for belowground resources. Hence, the fact that roots of the two species occupied the same soil strata at this age of the plantation may only be the result of an absence or low interspecific competition. Perhaps stratification of the root systems will occur as the plantations age and interspecific competition increases (Casper and Jackson 1997; Rothe and Binkley 2001). Root stratification in mixed stand of Norway spruce and European beech for example, was generally observed in mature stands (Bolte and Villanueva 2006; Schmid and Kazda 2002).

4.5.4 Leaf nitrogen

Because leaf N reflects soil N availability, leaf N can be an indirect measure of belowground competition (Ordoñez et al. 2009). We did not find a change in leaf N in response to both mixture and spacing treatments for clone PBT, suggesting an absence of intra- or interspecific competition for soil N. In contrast, leaf N of clone PMB was very sensitive to both spacing and mixture treatment; This clone grew faster than clone PBT hence it probably had greater demands for soil N and resulted in a greater sensitivity to changes in spacing and mixture. Leaf N of clone PMB was greater when mixed with spruces, which probably results from the lesser need for N of the spruces hence more available soil N for uptake by poplars. Interestingly, in the 1×1 m spacing the spruce species also had greater leaf N in mixed plantings compared to monocultures. It could be argued that the presence of poplars increased N mineralization at the soil surface with its more-easily decomposed litter compared to spruce only litter (Gartner and Cardon 2004). However, since the plantations were mechanically tended (herbicide use is prohibited in forestry in Quebec) which does not remove all weeds close to the trees, we attribute this increase in leaf N in mixed plantings to the absence of weedy vegetation in these plots which was repressed by the presence of a dense poplar canopy in the 1×1 m spacing.

4.6 Conclusion

After 6 years, growth of spruces was not affected by mixture treatment or spacing, while poplars had slightly better growth in mixtures (especially for clone PMB), through reduced competition between poplars in the mixed plantings. Reduced spacing however affected the taper of spruces, which could be a desirable trait for the forest industry. The two poplar clones behaved somewhat differently and highlight the need to properly select genotypes; Clone PMB rapidly took advantage of the available space in the larger spacings or in the mixtures with the spruces, which could be a desirable trait (high productivity) for mixed plantings if the spruces can tolerate to be overtopped until the poplars are ready for harvest. If not, then perhaps a clone such as PBT would be a better choice because of its more modest response to decreased competition offered by the spruces. Fine roots stratification under mixed plots did not occur at this stage of plantation development, but inter- and intra-

specific competition caused by mixture treatments and spacings was well reflected in leaf N, especially for clone PMB.

4.7 Acknowledgements

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5. Chapitre V

A PROCESS-BASED MODEL OF GROSS PHOTOSYNTHESIS FOR TWO HYBRID POPLAR CLONES IN BOREAL CONDITIONS

Benomar, L., DesRochers, A. et Larocque, G.R (Soumis à *Photosynthetica*)

5.1 Abstract

Process based models of photosynthesis are increasingly used to improve predictions of the effects of environmental change on forest productivity. Scaling from leaf to canopy still remains a major challenge. The aim of this study was to develop a multilayer canopy model of gross photosynthetic rate for two hybrid poplar clones growing at three different spacings in two regions of western Quebec, Canada, differing in climatic conditions. The leaf level photosynthetic rate model component was based on the Farquhar model, coupled with the Ball model for stomatal conductance. Photosynthesis parameters such as Rubisco potential capacity for CO₂ fixation, V_{cmax} , and potential electron transport rate, J_{max} , were derived from leaf nitrogen and soluble and insoluble protein contents. Scaling up was conducted by subdividing the canopy into four layers; leaf area and biomass at each layer were simulated using a polynomial function. Photosynthetic active radiation was computed at each layer using a radiative transfer approach. Results showed that leaf mass area was a good predictor of both leaf nitrogen content per unit area and leaf soluble and insoluble protein concentrations, but not for chlorophyll binding factor. The model predicted photosynthesis at the leaf level satisfactorily. Simulated photosynthesis at the canopy level was greater for clone MB915 than for clone BT747 among spacings and slightly greater for the warmer site.

5.2 Introduction

Tree growth models are generally classified in two broad categories: empirical models and physiological models (Constable and Friend 2000; Landsberg and Sands 2011). Empirical models, so-called statistical models, are generally based on statistical relationships between growth parameters and site-specific conditions without any attention to the physiological or biophysical growth processes. Empirical models still remain unable to perceive the effects of changes in environmental growth conditions on tree and stand productivity. In contrast, physiological models, so-called process-based models, are designed to represent biophysical and biochemical understanding of growth processes (Corona et al. 2002). A process-based model is a mechanistic representation of the biological processes that govern the dynamics of carbon assimilation. This model type aims to mathematically represent the dynamic interaction between tree, as a complex and dynamic system, and changes in resources levels and environmental conditions, such as temperature, precipitations and air CO₂ concentration. Understanding and quantifying the impacts of environmental change on tree and stand productivity is critical to estimate the probable impacts of the future environment. Therefore, process-based models have seen their importance increase to improve our understanding of the mechanisms of tree growth, to predict the impact of climate change on forest productivity and to make forest management decisions (Battaglia and Sands 1998; Johnsen et al. 2001; Mäkelä et al. 2000).

Process based models are generally subdivided into three components: carbon assimilation, carbon allocation and resources uptake (Constable and Friend 2000; Landsberg and Sands 2011). Carbon assimilation at the leaf level was largely investigated and commonly simulated using the biochemical model of Farquhar, von Caemmerer and Berry (1980) and Farquhar and von Caemmerer (1981) with recent modifications (Harley et al. 1992; Sharkey et al. 2007; von Caemmerer 2000). This model is based on three limitations of photosynthesis rate, such as the activation state and kinetic properties of Rubisco, the regeneration of RuBP in the Calvin cycle, or the rate of phosphate release during triose phosphate utilization. If carbon assimilation at the leaf level is well modeled, scaling up approaches from leaf to canopy level still has limitations to reproduce the morphophysiological complexity of tree crowns (Ewert 2004). In this regard, three scaling up methods exist: i) big-leaf models ii) sun-shade leaf models and iii) multilayer models (Chen

et al. 1999; Raulier et al. 1999; Sellers et al. 1992). Big-leaf models consider the canopy as a big leaf in which physiological processes and photosynthesis parameters J_{\max} and V_{cmax} are linearly related to the amount of light intercepted by the entire canopy. Sun-shade leaf models may be considered as a big-leaf model type, but with a top sun big sunlit leaf and a bottom big shaded leaf. Several ecophysiological studies found a spatially explicit nonlinear variation in both morphological and physiological parameters of the foliage within the canopy (Casella and Ceulemans 2002; Hikosaka 2003). These simplified canopy representations may have limitations to simulate the complexity of the change in photosynthetic rate at the canopy level (Ewert 2004; Larocque 2002; Raulier et al. 1999). Scaling up problems of these two modeling approaches led to the development of multilayer models (Sellers et al. 1992; Zhang and Xu 2003). Multilayer models compute the canopy photosynthetic rate by integrating the spatial variation in foliage characteristics and environmental conditions within the canopy.

There are still few examples of the development of photosynthesis process-based models for hybrid poplars based on specific foliage and crown characteristics to determine the extent to which differences in a physiological process may be important, which may explain differences in productivity. The objective of this study was to develop a process-based model of gross photosynthetic rate at the canopy level for two hybrid poplar clones growing at three different spacings. Scaling up from leaf to canopy was conducted through the subdivision of the canopy into four layers in which leaf properties (mass, area and nitrogen, insoluble and soluble proteins and chlorophyll concentrations), photosynthetic active radiation (PAR) conditions and gross photosynthesis were simulated hourly during the sixth growing season of plantation.

5.3 Material and methods

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5.3.1 Model description

The model consists of linked sub-models of leaf photosynthesis, stomatal conductance, and change in leaf distribution and PAR penetration within the canopy (Fig. 5-1). The leaf level model was first simulated using Stella software (Stella V9.1 1; isee systems, USA) to

facilitate the validation of photosynthesis parameters. Then, the integral model was developed using the C language.

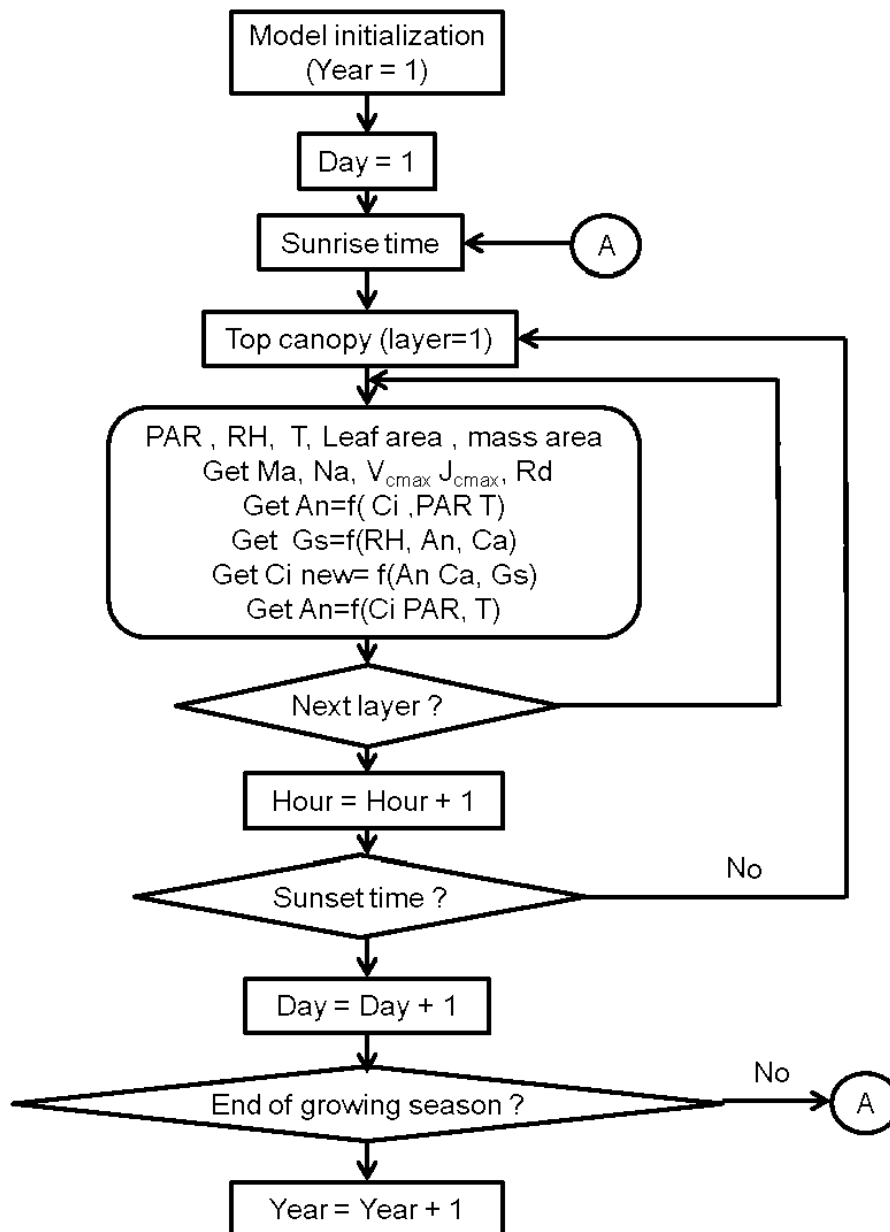


Figure 5-1: Schematic diagram of a gross photosynthesis model adapted from Larocque (2002).

5.3.1.1 Photosynthesis sub-model

The Farquhar and von Caemmerer's biochemical model for C_3 was used as modified by Harley et al. (1991) and von Caemmerer (2000). Farquhar and van Caemmerer's model assumes that the rate of CO_2 uptake (A_n), is limited: (i) by the Rubisco activity (A_c), (ii) the rate of regeneration of RuBP (A_j) and (iii) the rate of use of triose-P (A_p). The final rate, A_n , is the minimum of the three rates:

$$A_n = \min(A_c, A_j, A_p) \quad \text{Eq1}$$

The limitation by the rate of triose-phosphate utilization, A_p , was rarely observed so, it is not considered in the present study (von Caemmerer 2000).

The Rubisco-limited rate of CO_2 assimilation, A_c , was given by:

$$A_c = V_{cmax} \frac{C_i - I^*}{C_i + K_c(1 + [O]/K_o)} - R_d \quad \text{Eq2}$$

Where V_{cmax} ($\mu\text{mol } CO_2 \text{ m}^{-2} \text{ s}^{-1}$) is the maximum rate of carboxylation, C_i the intercellular partial CO_2 pressure, $[O]$ ($\mu\text{mol } O_2 \text{ mol}^{-1}$) the partial pressure of O_2 , and K_c and K_o the Michaelis-Menten constants for carboxylation and oxygenation, respectively. R_d is the dark respiration occurring in daylight and is assumed to be primarily mitochondrial respiration (see von Caemmerer (2000) for comprehensive details).

RuBP-limited rate of CO_2 assimilation is:

$$A_j = J \frac{C_i - I^*}{4(C_i + 2I^*)} - R_d \quad \text{Eq3}$$

Where J is the rate of electron transport and I^* the CO_2 compensation point, which is given by:

$$I^* = \frac{[O]}{2S_{c/o}} \quad \text{Eq4}$$

Where $S_{c/o}$ is the Rubisco specificity factor for CO_2 and O_2 . $S_{c/o}$ represents the evolutionary adaptation of plants to the evolutionary change of the atmospheric O_2 . von Caemmerer (2000) summarized published values of $S_{c/o}$ in photosynthesis modeling and concluded a marginal

variation in $S_{c/o}$ in C_3 plants. The Value 2342.3 ± 700 (bar bar^{-1}) from gas-exchange measurements for hybrid poplar by Manter and Kerrigan (2004) was used in this study.

The rate of electrons transport (J) was derived from the following quadratic equation (McMurtrie et al. 1992), which shows the relationship between electron transport and absorbed irradiance.

$$\Theta J^2 - (\alpha_p \varphi_p + J_{\max})J + \alpha_p \varphi_p J_{\max} = 0 \quad \text{Eq5}$$

Where: Θ is the concavity of the hyperbole. J_{\max} ($\mu\text{mol e}^- \text{m}^{-2} \text{s}^{-1}$) corresponds to maximum rate of electron transport and α ($\text{mol e}^- \text{mol quanta}^{-1}$) is quantum efficiency. The quantum efficiency α represents the initial slope of photosynthesis light response curve. It is a measure of the efficiency of light absorption by the leaf, which depends on leaf absorptance (Evans 1993).

$$\alpha = 0.292 \left(1 + \frac{0.076}{N_m M_a P_L C_b} \right)^{-1} \quad \text{Eq6}$$

Where N_m the leaf nitrogen concentration (g g^{-1}), M_a the leaf mass area (g m^{-2}), P_L the proportion of nitrogen in light harvesting and C_b the chlorophyll binding factor.

V_{cmax} , J_{\max} and R_d were modeled to account for the effect of leaf nitrogen and leaf morphology using the empirical model developed by Niinemets and Tenhunen (1997).

$$J_{max} = 8.06 J_{mc} M_a P_{et} N_m \quad \text{Eq7}$$

$$V_{cmax} = 6.25 V_{cr} M_a P_r N_m \quad \text{Eq8}$$

$$Rd = 0.5 R_{coe} V_{cmax} \quad \text{Eq9}$$

Where J_{mc} the potential rate of photosynthetic electron flow per unit of cytochrome f (mol electrons ($\text{mol cyt. f}^{-1} \text{s}^{-1}$), V_{cr} the maximum rate of RUBP carboxylation per unit Rubisco protein ($\mu\text{mol CO}_2$ ($\text{g Rubisco}^{-1} \text{s}^{-1}$), P_{et} the proportion of nitrogen in electron transport and P_r the proportion of nitrogen in carboxylation and M_a the leaf mass area.

The proportion of nitrogen in carboxylation and light harvesting was derived from allometric equations between soluble and insoluble proteins and M_a for each clone and site. Both linear and exponential form were tested.

As in Harley et al (1992), the temperature dependences of V_{cr} and J_{mc} were modelled as:

$$V_{cr} \text{ or } J_{mc} = \frac{e^{\left(\frac{c-\Delta H_a}{RT_k}\right)}}{1+e^{\left(\frac{\Delta S_k-\Delta H_d}{RT_k}\right)}} \quad \text{Eq 10}$$

Where c scaling constant, ΔH_a the energy of activation, ΔH_d the energy of deactivation, ΔS an entropy term, T_K the leaf temperature in degree Kelvin and R the gas constant.

The temperature dependence of the kinetic parameters was modeled according Jordan and Oregon (1984).

$$Parameter = e^{\left(\frac{c-\Delta H_a}{RT_K}\right)} \quad \text{Eq11}$$

5.3.1.2 Stomatal conductance sub-model

The semi-empirical model of Ball et al. (1987) was chosen in this study to derive stomatal conductance.

$$Gs = g_0 + m A_n \frac{RH}{Ca} \quad \text{Eq12}$$

Where Ca is the atmospheric CO_2 partial pressure ($\mu\text{mol/mol}$), RH the ambient relative humidity (%) and g_0 and m the intercept and the slope of the linear relationship between GS and the product of light saturated photosynthesis (A ; $\mu\text{mol m}^{-2} \text{s}^{-1}$) and relative humidity (RH) divided by Ca ($360 \mu\text{mol mol}^{-1}$) and g_0 the residual stomatal conductance.

Leaf intercellular CO_2 concentration (C_i) was computed from measured stomatal conductance and net photosynthetic rate.

$$Ci = Ca \frac{A_n 1.6}{Gs} \quad \text{Eq13}$$

5.3.1.3 Leaf area and biomass distribution

The crown was subdivided into four layers and the vertical distribution of both leaf area and biomass were modeled using a second order polynomial equation.

$$Y = a X^2 + b X + c \quad \text{Eq 14}$$

Where Y is the relative leaf area or biomass, X the relative crown height, and a, b and c parameters.

5.3.1.4 Light attenuation within the canopy

The distribution of light within the canopy was modeled using the simplified approach of Hassika et al (1997).

$$I_n = I_{n-1} e^{\left[\frac{-\cos(F_a)k_a LAI_n}{\sin(S_a)} \right]} \quad \text{Eq 15}$$

Where LAI_n the leaf area index within the canopy layer at layer n, n varying from 1 to 4 (number of layers in the present study), k_a the extinction coefficient (0.42), I_{n-1} the PAR above the canopy layer at depth n, I_n the PAR in layer n, S_a Sun elevation angle, and F_a the leaf angle relative to the horizontal plan.

5.3.2 Study area and physiological measurements

5.3.2.1 Study area

The study was conducted in two young hybrid poplar plantations located in the boreal region of Abitibi-Témiscamingue, western Quebec, Canada. The plantations were established in 2003 at Amos (48°36'N, 78°04'W) and Nédelec (47°45'N, 79°22'W). The Amos site was an abandoned farmland with heavy clay soils. The Nédelec site had been previously forested with a sandy-loam soil texture. The mean numbers of growing degree-days (above 5°C; 30-year average) were 1,387 for Amos and 1,480 for Nédelec, respectively (Environment Canada 2008). Precipitation during the growing season of 2008 averaged 620 mm (Ministère du Développement Durable de l'Environnement et des Parcs 2009). The plantation included two hybrid poplar clones, MB915319 (MB915; *P. maximowiczii* A. Henry × *P. balsamifera* L.) and BT747215 (BT747; *Populus balsamifera* L. × *P. trichocarpa* Torr. & Gray), growing at three initial square spacings, 1×1 m, 3×3 m, and 5×5 m. Details of plantations establishment and maintenance are given in Benomar et al. (2011). The basic characteristics of the experimental sites for model simulation are given in table 5-1.

Tableau 5-1: Basic characteristics of the experimental sites and selected trees for model parameterization and average climatic conditions in 2008.

Clone		Amos			Nédelec		
		Spacing (m)			Spacing (m)		
		1x1	3x3	5x5	1x1	3x3	5x5
BT747	Leaf area index	3.10	0.81	0.35	3.07	0.69	0.45
	Foliage biomass (kg ha ⁻¹)	2,939	922	422	2,893	602	448
	Mean height (m)	4.15	3.20	2.90	3.71	3.77	3.65
	Mean N _m (mg g ⁻¹)	18.80	19.40	19.97	18.52	18.81	20.75
MB915	Leaf area index	3.70	1.90	0.91	3.8	2.57	1.7
	Foliage biomass (kg dry mass ha ⁻¹)	3,160	1,724	839	3,058	2,234	1,547
	Mean height (m)	5.40	5.85	5.78	5.90	6.82	6.76
	Mean N _m (mg g ⁻¹)	18.31	19.42	20.34	18.56	19.77	20.54
Mean daylight temperature (°C)		17			16		
Mean daylight PAR (μmol m ⁻² day ⁻¹)		17,681			18,309		

N_m : Leaf nitrogen concentration (mg g⁻¹); PAR: Photosynthetic active radiation.

5.3.2.2 Meteorological data

Hourly climatic conditions throughout the growing season of 2008 (from 150 to 250 Julian days) were monitored on each site. The meteorological station was equipped with a shielded temperature and relative humidity sensor (HMP50, Vaisala, Helsinki, Finland), PAR sensors (Li 190 Campbell Scientific, Logan, Ut, USA) and an anemometer (Li 190 Campbell Scientific, Logan, Ut, USA) for wind speed. Data were continuously recorded hourly using datalogger (CR10X, Campbell Scientific, Logan, Ut, USA).

5.3.2.3 Gas exchange measurements

The crown of two randomly selected trees within each treatment (site×spacing×clone) was divided vertically into four layers from the bottom to the top of the crown. The first layer consisted in the top 10% of the crown. The other layers were located in 3 equal sections of the remaining 90% of the crown. One leaf from three points corresponding to horizontal

subdivisions (inner, middle and outer leaves) was sampled in the second, third and fourth layers, while one leaf from the terminal shoot was sampled from the top layer. Gas exchange, leaf mass area (M_a) and leaf N were measured during the summers of 2008. All measurements were conducted between July 15 and August 15 (Benomar et al. 2011). Measurements of light-saturated photosynthesis (A_{max}) and stomatal conductance (Gs) were performed using a portable infra-red gas analyser (IRGA), operating in an open mode (CIRAS-2, PP-Systems, Amesbury, MA, USA). The IRGA was equipped with a broadleaf cuvette that was illuminated using a LED light unit (PLC6-broad, PP Systems). Photosynthetically active radiation (PAR), flow rate and CO_2 concentration in the leaf cuvette were maintained, respectively, at $1600 \mu\text{mol m}^{-2} \text{s}^{-1}$, 300 mL min^{-1} , and $360 \mu\text{mol mol}^{-1}$.

5.3.2.4 A-C_i response curve

Photosynthesis parameters such as maximum rates of carboxylation (V_{cmax}), maximum rate of electron transport (J_{max}) and R_d were derived from A-C_i response curve. The A-C_i response curve measurements were carried out during the period between 15 July and 20 August 2008. This period is assumed to be physiologically optimal (LAI reached his plateau at this period). The measurements were taken after 10 min steady state at atmospheric CO_2 partial pressure; $C_a=360 \mu\text{mol mol}^{-1}$. Thereafter we applied the following variation in C_a : 360, 300, 200, 100, 80, 60, 40, 20, 360, 500, 600, 700, 800, 900, 1000, 1250, 1500 and $1750 \mu\text{mol mol}^{-1}$ (Long and Bernacchi 2003). The leaf chamber was maintained at $T= 25 \text{ }^\circ\text{C} \pm 0.5$, $VPD=10 \pm 0.2 \text{ mba}$ and $PAR=1500 \mu\text{mol m}^{-2} \text{ s}^{-1}$. V_{cmax} , J_{max} and R_d were estimated using nonlinear regression (Photosyn Assistant software Dundee Scientific Scotland UK) based on Farquhar's model modified later by Harley et al (1992). The limitation of the Rubisco was assumed to be below $250 \mu\text{mol mol}^{-1}$ (Wullschleger 1993). Following A-C_i measurements, leaves were immediately harvested, placed in plastic bags and refrigerated on dry ice. Thereafter at the laboratory, the leaves were placed at $-85 \text{ }^\circ\text{C}$ for chlorophyll and proteins determinations.

5.3.2.5 Chlorophyll content

Frozen leaf material (0.1g) was ground in mortar and pestle using liquid nitrogen. The ground material was homogenized with 6 ml ice-cold *N,N*-Dimethylformamide and the homogenates were incubated in the dark for 24 h. The homogenates were then centrifuged at 4000 g for 5 min. Supernatants absorbance at 647 and 663 nm were immediately measured by spectrophotometer (Inskeep and Bloom 1985; Porra 2002). Total chlorophyll content, chlorophyll a and chlorophyll b were determined according to Porra et al. (1989). All analyses were conducted in duplicate at two dilution levels (1 and ½). Chlorophyll content was reported on a leaf area basis (g m^{-2}).

5.3.2.6 Protein content

Frozen leaf material (0.1 g) was ground under liquid nitrogen in a mortar and pestle, which had been placed on ice (0°C). The ground material was immediately suspended in 3 ml of extraction buffer (pH=7.2, Tes-NaOH (20mM), Sorbitol (330mM), PVP (1.5 % w/v), PVPP (1.5 % w/v) and MgCl_2 (5mM)). The homogenate was centrifuged at 1600g for 10 min at 4°C . The supernatant was recovered as a first part of soluble proteins. The pellets were homogenized in the same buffer without PVP and PVPP and centrifuged at 2800 g. The supernatants were recovered as the last part on soluble proteins. Then, the pellet was re-suspended in 2ml of TCA (10% w/v) and centrifuged at 15000g and resuspended in 2 ml of NaOH (1M) and centrifuged 15000 g. The supernatant was recovered as insoluble proteins. Both soluble and insoluble proteins concentrations were measured spectrophotometrically using the Bradford method (Kirazov et al. 1993; Lauerer et al. 1993).

5.3.3 Statistical analysis

Simple linear regression without intercept was used to compare measured and model photosynthesis parameters, photosynthesis and stomatal conductance. Relationship between the three photosynthesis parameters and leaf nitrogen content per unit leaf area (Narea) was assessed by simple linear regression using proc reg (SAS). The relationship between model parameters (Soluble and insoluble protein content, Narea and Cb) with Ma was derived iteratively by an exponential function, except for chlorophyll binding factor which was fitted

using a linear function. The iteration was done using proc NLIN (SAS V9.2). The functions were fitted for each clone and site to take into account the variation in photosynthetic nitrogen use efficiency, as indicated by Benomar et al. (2011).

5.4 Results

5.4.1 Photosynthesis parameters (V_{cmax} , J_{max} and R_d) in relation to N_{area}

The relationship between the three key photosynthesis parameters and N_{area} was positive and log-linear (Fig. 5-2). This relationship was stronger for both V_{cmax} and J_{max} and moderate for R_d . The slope of this relationship was significantly different between clones and similar among spacing for the three photosynthesis parameters; within each clone the slope was similar among spacings.

The relationship between J_{max} and V_{cmax} was highly significant ($R^2=0.98$; $P<0.0001$) for both clones (Fig. 5-3). ANCOVA analysis showed a similar slope of the relationship for the two clones, indicating that the $J_{\text{max}}:V_{\text{cmax}}$ ratio was not significantly different between the two hybrid poplar clones.

5.4.2 Relationships between M_a and proteins content, N_{area} and C_b

Nitrogen content per unit leaf area increased exponentially with an increase in M_a . The relationship was highly significant for both clones on each site, with a coefficient of determination ranging from 0.63 to 0.94 (Table 5-2). Both soluble and insoluble proteins also increased exponentially with an increase in M_a . The coefficients of determination ranged from 0.41 to 0.67 (Table 5-2). The chlorophyll binding factor (C_b) decreased linearly with an increase in M_a and the coefficients of determination for the two clones on both sites indicated that the relationships did not explain a strong proportion of the variation in C_b as a function of M_a (Table 5-3).

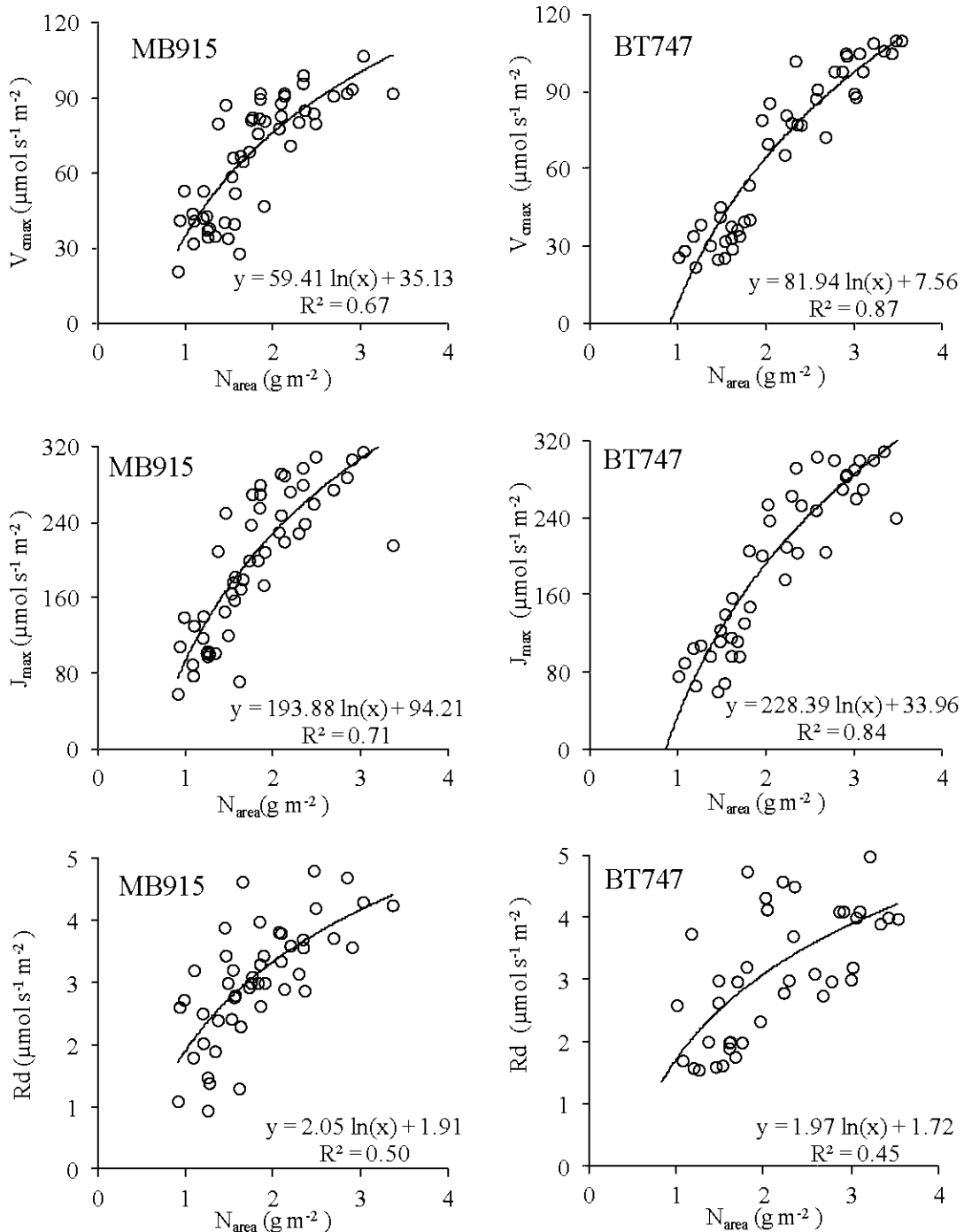


Figure 5-2: Relationships between the three key parameters of the photosynthesis (maximum rate of carboxylation V_{cmax} , light saturated rate of electron transport, J_{max} , and dark respiration rate, R_d) derived from A-Ci response curve and leaf nitrogen per unit leaf area, (N_{area}) for clones BT747 and MB915.

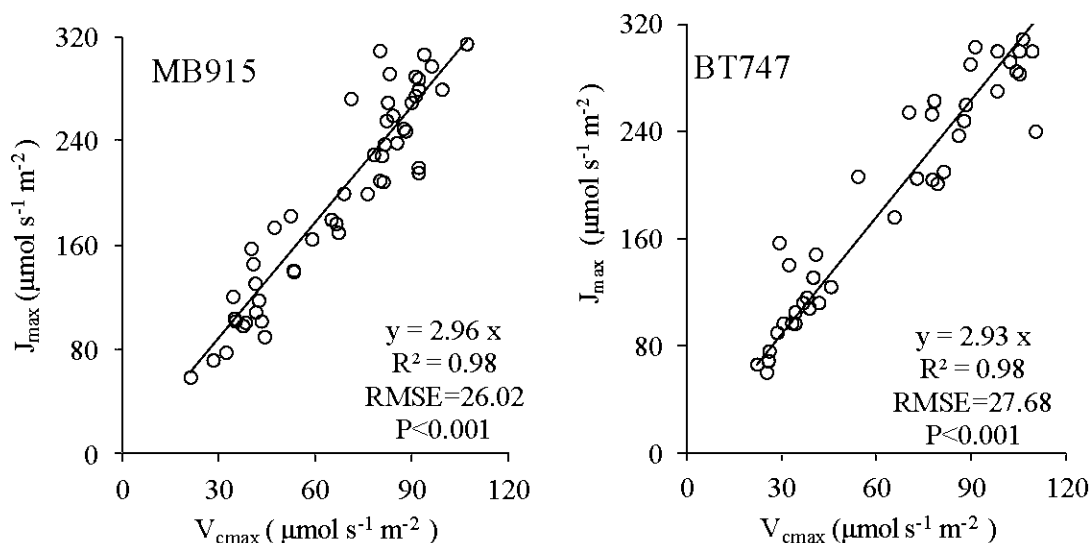


Figure 5-3: Relationship between the maximum rate of electron transport (J_{\max}) and maximum rate of RuBP carboxylation ($V_{c\max}$) at 25°C for clones BT747 and MB915. RMSE: Root mean square error.

Tableau 5-2: Soluble and insoluble proteins and leaf nitrogen per area as function of leaf mass area (M_a). The form of the relationship is $Y=a*\exp(b*M_a)$.

Clone	site	Y	a	b	R ²
BT747	Amos	P_s	0.4562	0.0159	0.67
		P_{ins}	0.5587	0.0169	0.52
		N_{area}	0.4715	0.0135	0.63
	Nédelec	P_s	0.6473	0.0131	0.56
		P_{ins}	1.4295	0.0108	0.51
		N_{area}	0.3143	0.0176	0.89
MB915	Amos	P_s	0.6812	0.0134	0.50
		P_{ins}	0.9103	0.0139	0.45
		N_{area}	0.383	0.0172	0.81
	Nédelec	P_s	0.6938	0.0138	0.55
		P_{ins}	0.9387	0.0138	0.41
		N_{area}	0.4774	0.014	0.94

P_s : Soluble proteins ($g\ m^{-2}$); P_{ins} : Insoluble proteins ($g\ m^{-2}$); N_{area} : Leaf nitrogen per area ($g\ m^{-2}$); M_a Leaf mass area ($g\ m^{-2}$)

Tableau 5-3: Chlorophyll binding factor (C_b :mmol g^{-1}) as a function of leaf mass area (M_a). The form of the relationship is $C_b = a + b * M_a$.

clone	site	a	b	R ²
BT747	Amos	0.2924	-0.0013	0.22
	Nédelec	0.2499	-0.0008	0.10
	Amos	0.2212	-0.0009	0.10
MB915	Nédelec	0.2725	-0.0014	0.28

5.4.3 Canopy light environment

The maximum above-canopy photosynthetic active radiation (PAR) observed for both sites exceeded 2000 $\mu\text{mol m}^{-2} \text{s}^{-1}$ several days during the growing seasons (Figs. 5-4). Mean Daily above canopy PAR in Nédelec varied from 8,841 to 29,172 with an average of 18,391 $\mu\text{mol m}^{-2} \text{s}^{-1}$. The variation in Amos was between 2,831 and 31,071 with an average of 17,681 $\mu\text{mol m}^{-2} \text{s}^{-1}$. The proportion of predicted PAR received at bottom of the canopy was greater for BT747 (Fig. 5-4a) than for MB915 (Fig. 5-4b). For clone BT747, the average PAR received at the bottom of the canopy was 15, 50, and 67% of available PAR in the 1x1, 3x3 and 5x5 m spacings, respectively. For clone MB915, the proportions were 11, 28 and 43% of available PAR in the 1x1, 3x3 and 5x5 m spacings, respectively.

5.4.4 Model validation

Simulated photosynthesis parameters (V_{cmax} , J_{max} and R_d) using the semi empirical model of Niinemets and Tenhunen (1997) were compared with the values calculated from the A- C_i response curves (Fig. 5-5). The slope of the regression between measured and simulated V_{cmax} was close to 1 for both clones, indicating a good fit between observations and predictions. The slope of the regression for J_{max} was close to 1 for clone BT747, but slightly greater than 1 for MB915, indicating a slight overestimation of J_{max} by the model for this clone. In general, the prediction error for both V_{cmax} and J_{max} was greater for BT747 than MB915. For both clones, dark respiration rate was underestimated (Fig. 5-5).

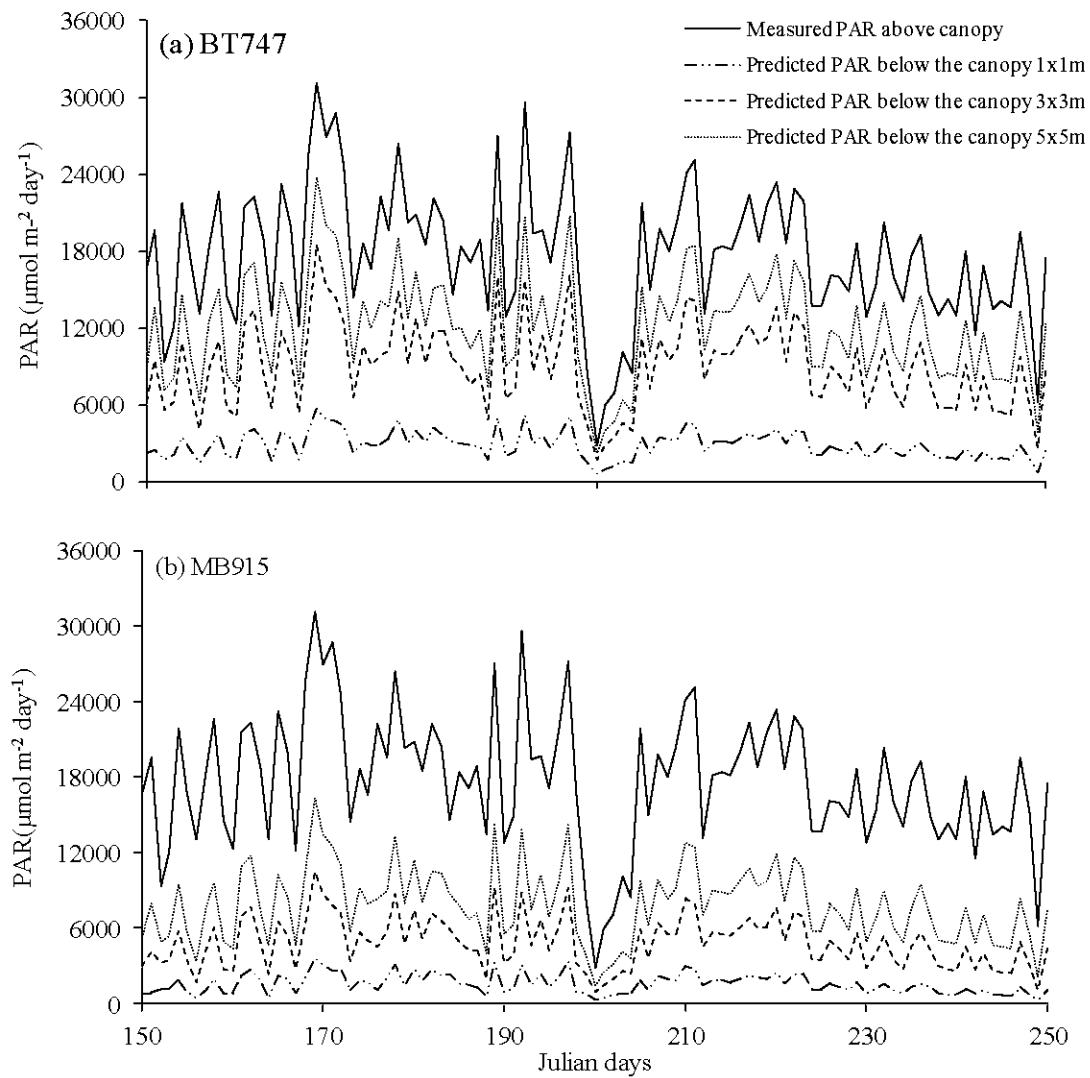


Figure 5-4: Measured above canopy and predicted below the canopy photosynthetically active radiation (PAR) at Amos for (a) BT747 and (b) MB915.

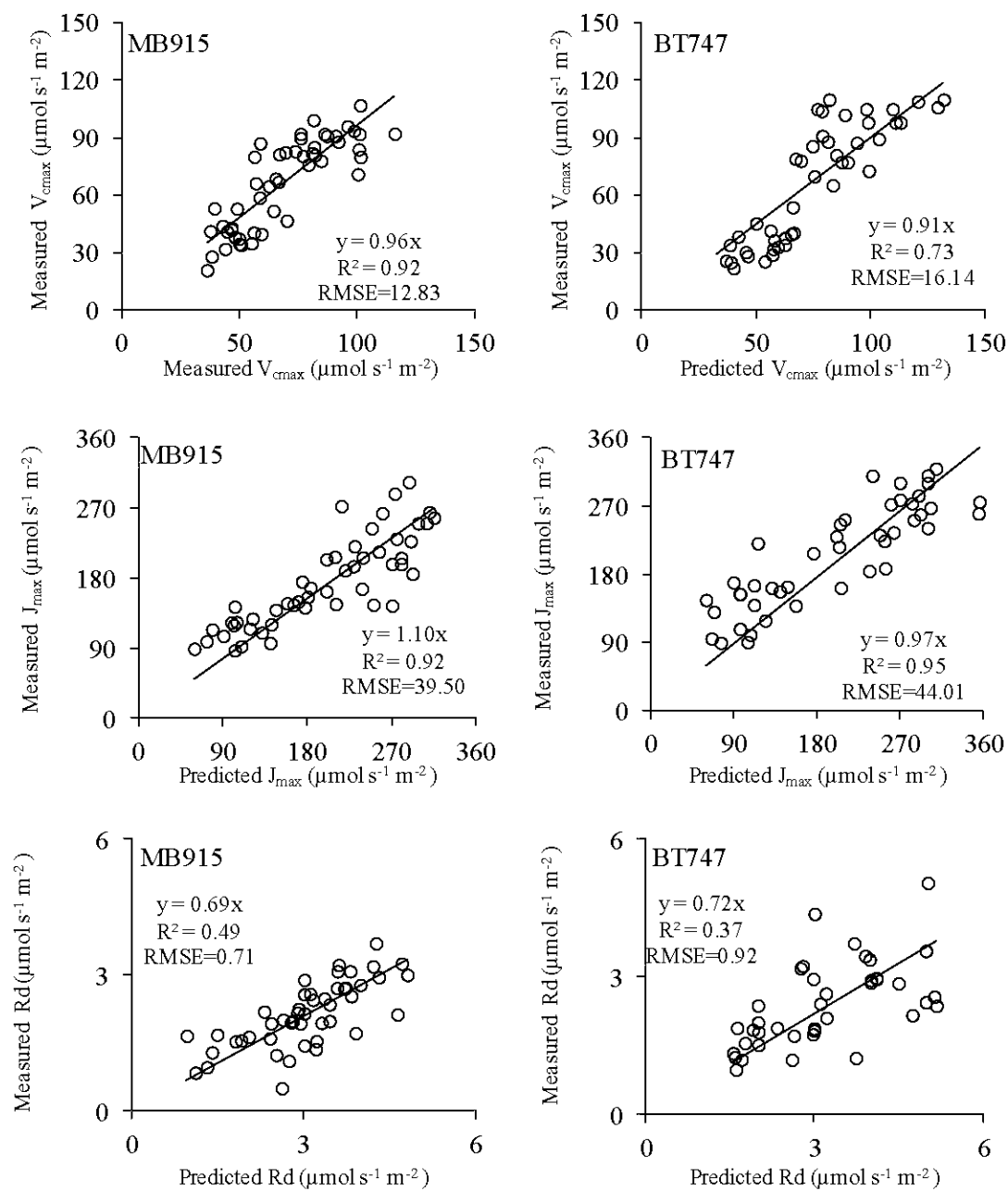


Figure 5-5: Linear regression with zero intercept of modeled vs measured V_{cmax} , J_{max} and R_d for clone BT747 and MB915. RMSE: Root mean square error.

The Ball model provided a good fit to stomatal conductance data, as indicated by the strong relationship between measured stomatal conductance and the product of photosynthesis (A) and relative humidity (RH) divided by external CO_2 concentration (C_a) ARH/C_a (Fig. 5-6). This relationship was affected only by site (similar within clones and spacings). The residual stomatal conductance in Amos ($170 \text{ mmol m}^{-2} \text{ s}^{-1}$) was much lower than in Nédelec ($270 \text{ mmol m}^{-2} \text{ s}^{-1}$).

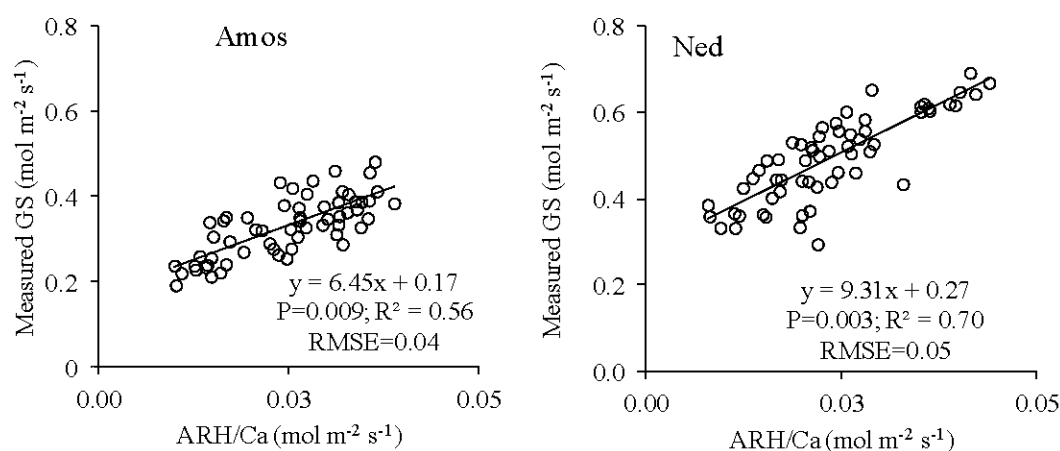


Figure 5-6: Relationship between measured stomatal conductance (GS) and the product of light saturated photosynthesis (A ; $\mu\text{mol m}^{-2} \text{ s}^{-1}$) and relative humidity (RH) divided by the ambient CO_2 (C_a ; $360 \mu\text{mol mol}^{-1}$). RMSE: Root mean square error.

The model predicted well light saturated photosynthesis (Fig. 5-7). The coefficient of determination for the relationships between observations and predictions was 0.73 and 0.68 for clones BT747 and MB915, respectively. The root mean square error (RMSE) was similar for both clones (Fig. 5-7) with value of $2.4 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$. The difference between predicted and measured values was at most $4 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$. This difference should not be attributed only to prediction error but also to measurement error (instrument errors). Plot residuals did not show any visible pattern indicating that the prediction errors by the model were, independent of leaf nitrogen content per unit leaf area and M_a .

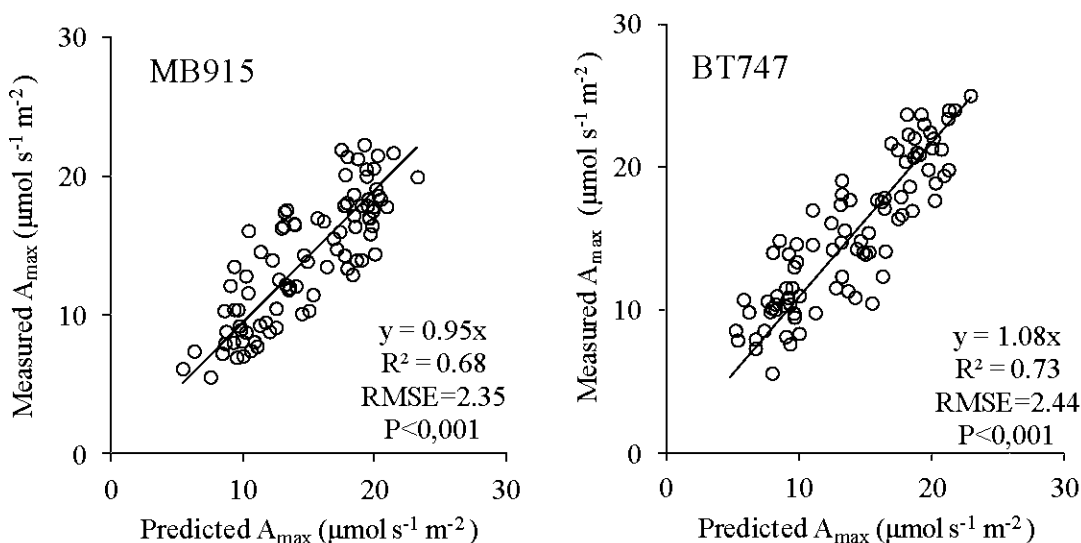


Figure 5-7: Validation of leaf photosynthesis model with measured data for clones BT747 and MB915.

5.4.5 Simulation of daily canopy photosynthetic rate

Simulated daily canopy photosynthetic rate was approximately 30% smaller for BT747 (Fig. 5-8a, b) than MB915 (Fig. 5-8c, d) across spacings and sites. Simulated canopy photosynthesis decreased by approximately 18 and 30% from the 1x1 to 3x3m spacings and from the 3x3 to 5x5m spacings, respectively, and was 9 and 30% greater on the Nédelec site (Fig.5-8b, d) than Amos (Fig.5-8a, c) for BT747 and MB915, respectively.

5.5 Discussion

The model developed in this paper produced a good fit to our data for both photosynthesis and stomatal conductance at the leaf level. The three key parameters of the photosynthesis submodel; V_{cmax} , J_{max} and R_d , were derived from leaf chemistry measurements (leaf proteins and chlorophyll concentrations) and their relationship with leaf mass area (M_a). Canopy photosynthesis was scaled up using a multilayer approach with a more realistic representation of canopy functions through a spatial distribution of leaf characteristics such as morphology (M_a) and chemistry (soluble and insoluble proteins, chlorophyll).

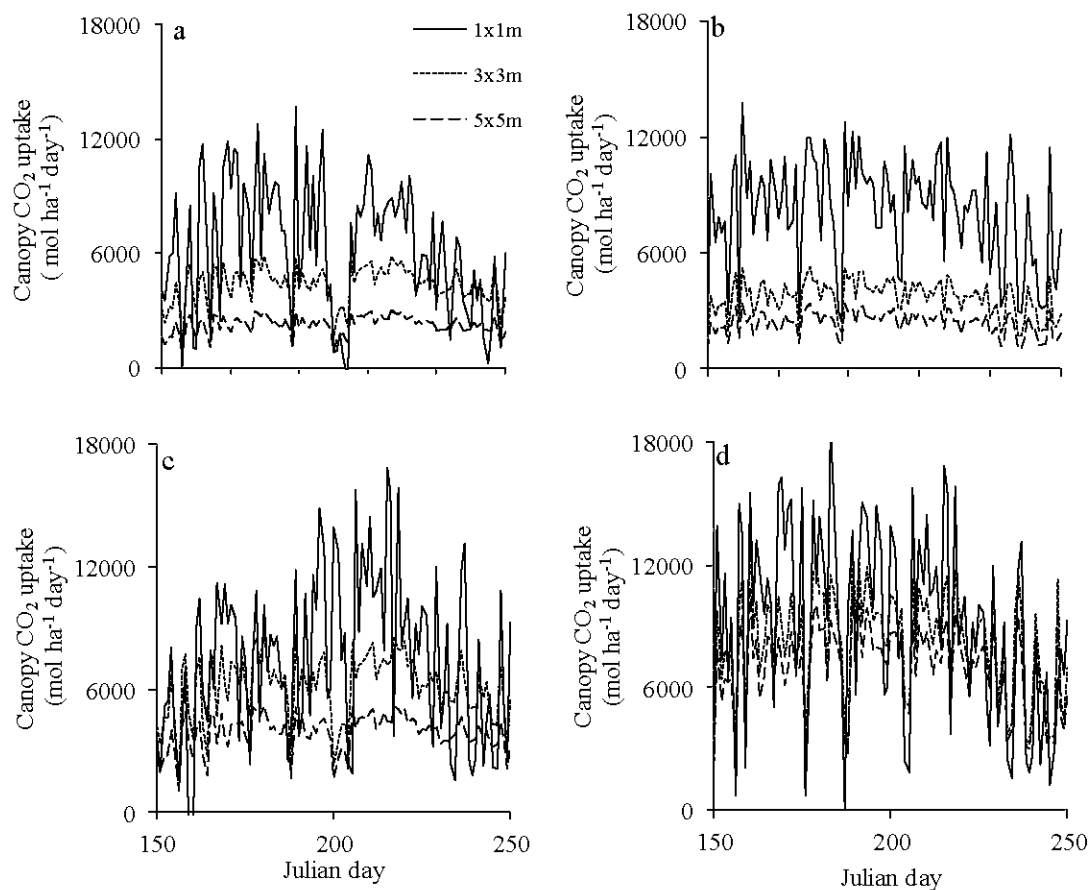


Figure 5-8: Daily simulated canopy CO₂ uptake during the 2008 growing season for clone BT747 (a and b) and clone MB915 (c and d) at Amos (a and c) and Nédelec (b and d).

5.5.1 Photosynthesis parameters measurement

Measured V_{cmax} , J_{max} and R_d were iteratively derived from A-C_i response curve using nonlinear least square regression. The A-C_i analysis assumes i) a smaller and insignificant resistance to CO₂ diffusion from the intercellular airspaces within the leaf through the mesophyll to the sites of carboxylation ii) a conservative aspect of the Michaelis-Menten constants K_c and K_o and also $S_{c/o}$ (von Caemmerer 2000) and iii) a constant value of C_i at which A-C_i switches from Rubisco to electron transport limitation. These assumptions may lead to an overestimation of both V_{cmax} and J_{max} . Mesophyll resistance to CO₂ diffusion,

which varies largely between species, may be substantial to reduce V_{cmax} for some species (Ethier and Livingston 2004; Flexas et al. 2007; Francesco and Angelo 2001; Manter and Kerrigan 2004; Sharkey et al. 2007). As stated by Von Caemmerer (2000), it may be suitable to include this factor to improve the estimation of the photosynthesis parameters from the A- C_i curve. The transition value of C_i is assumed to range from 20 to 25 Pa (Harley et al. 1992; Wullschlegel 1993). This conservative aspect of the transition results from the close correlation between V_{cmax} and J_{max} . Several authors support the finding that the transition from Rubisco limited state to the RuBP regeneration-limited state is not necessarily constant and can be greater than 25 Pa (Gu et al. 2010; Manter and Kerrigan 2004; Sharkey et al. 2007). The $J_{\text{max}}:V_{\text{cmax}}$ ratio in this study was greater than reported values for other species (Manter and Kerrigan 2004; Niinemets et al. 1998; Onoda et al. 2005). Plants acclimation to lower temperature conditions is governed principally by the activation energy of V_{cmax} and J_{max} , and the $J_{\text{max}}:V_{\text{cmax}}$ ratio (Hikosaka et al. 2006; Onoda et al. 2005; Wilson et al. 2000). Hence, the greater ratio of J_{max} to V_{cmax} in our study may be a consequence of plant adaptation to lower temperature in boreal conditions.

5.5.2 Photosynthesis sub-model

The three photosynthesis parameters increased log-linearly with increasing N_{area} , as reported by several studies (Harley et al. 1992; Le Roux et al. 1999; Le Roux et al. 2001). Hence, major published models use this simple linear relationship to model photosynthesis parameters. In this study, the semi empirical model of Niinemets and Tenhunen (1997) was chosen objectively to model photosynthesis parameters. This model predicted satisfactory both V_{cmax} and J_{max} . Thus, the changes in leaf stoichiometry and nitrogen allocation within leaf and leaf morphology (M_a) were both essential to predict a comprehensive change in leaf photosynthesis. The photosynthesis acclimation to environmental factors (nitrogen availability, water, light, temperature, and CO_2) must be considered in process-based models in order to predict a quantitative change in productivity in current and projected future climatic conditions. Photosynthesis capacity results from leaf stoichiometry and nitrogen partitioning between different parts of the photosynthetic apparatus is commonly used to explain leaf photosynthetic acclimation to its environment (Evans and Poorter 2001; Hikosaka and Terashima 1995; Niinemets and Valladares 2004; Ripullone et al. 2003). For

example, the proportion of nitrogen invested in soluble protein should be proportional to light and nitrogen in well acclimated leaves (Bunce 1991; Evans and Poorter 2001; Niinemets et al. 1998; Niinemets and Sack 2006; Niinemets and Tenhunen 1997; Poorter and Evans 1998). Also, nitrogen invested in soluble proteins is expected to decrease for the benefit of insoluble proteins under increasing atmospheric CO₂ (Drake et al. 1997; Rey and Jarvis 1998; Sicher and Bunce 1997; Sicher et al. 1994). In this regard, the photosynthesis model used in this study based on leaf acclimation through morpho-physiological adjustments may offer a possibility to predict a quantitative change in photosynthesis under different environmental conditions.

5.5.3 Stomatal conductance sub model

Stomatal conductance modeling suffers from the lack of a mechanistic approach that combines a mechanistic response of stomatal opening to water and CO₂ fluxes in the three dimensional space soil–plant–atmosphere. Currently, two semi-empirical models are extensively used to predict leaf stomatal conductance. The response function developed by Jarvis (1976) described the influence of leaf temperature, irradiance and leaf and soil water potentials on stomatal conductance. In contrast, the Ball model (Ball et al., 1987; Leuning, 1990) links stomatal conductance to rate of CO₂ assimilation and air humidity. Ball model has been found to be adequate under well-watered conditions (Damour et al., 2010; Liu et al., 2009; Tuzet et al., 2003; Wohlfahrt et al., 1998). Experimental sites of our study are characterized by relatively high levels of precipitation during the growing season of 2008 (Ministère du Développement Durable de l'Environnement et des Parcs 2009). This may explain a relatively greatest stomatal conductance observed in this study for both clones. In addition, these sites are characterized by low daylight temperatures and consequently a non limiting vapour pressure deficit to stomatal conductance. This may explain why this model described well the variation in stomatal conductance. Residual stomatal conductance (g_0) was greater in Nédelec than Amos due to higher level of precipitation at this site.

5.5.4 Canopy photosynthesis

Our result showed an increase in canopy photosynthesis in consequence of the increased LAI resulting from the decrease of spacing between trees. This supports the

relationship between LAI and canopy photosynthesis (Baldocchi and Harley 1995; Ewert 2004). Also, the difference in LAI and mean leaf nitrogen may explain a slight difference in canopy photosynthesis between Amos and Nédelec.

PAR at the bottom of the canopy was not measured, which makes validation of simulated PAR impossible. Nevertheless, several studies using the same approach had reported a satisfactory prediction capability of the model (De Pury and Farquhar 1997; Kull and Kruijt 1998; Larocque 2002). For example, Larocque (2002) reported a marginal difference of $100\mu\text{mol m}^{-2} \text{s}^{-1}$ between measured and predicted PAR using a similar approach.

Due to the one-hour time step used in our study, simulated canopy photosynthesis may differ from actual values since temperature, relative humidity and PAR vary substantially over this period. In consequence, models using shorter time steps might prove to be more realistic.

In conclusion, the present model was capable of predicting satisfactorily gas exchange at leaf level as function of PAR, temperature, relative humidity and CO_2 concentration. In this study, multilayer approach was used to scale from leaf to canopy level. This approach improves the representation of canopy photosynthesis compared to other models essentially by integrating (1) morpho-physiological acclimation of the foliage within the canopy, (2) spatial representation of leaf area within canopy and (3) leaf angle variations within the canopy. Several elements which could impact canopy photosynthesis were not considered in this study (1) leaf heterogeneity within each layer, (2) vertical variations in temperature and relative humidity, (3) leaf age influence in photosynthesis parameters and (4) LAI variation within a growth season.

5.6 Acknowledgements

We would like to thank Dr Manter for his statistical help. This research was funded by Canada Economic Development, Quebec's Ministry of Natural Resources and Fauna (MRNF), the Natural Sciences and Engineering Research Council of Canada through a Collaborative and Research Development grant to AD, and the Program on Energy Research and Development of Natural Resources Canada. We also thank Réseau Ligniculture Québec,

Norbord Inc., Alberta-Pacific Forest Industries Inc., CRSNG-UQAT-UQAM Industrial Chair in Sustainable Forest Management, Center for Forest Management (CEF) and Natural Resources Canada, Laurentian Forestry Centre for their support.

6. CONCLUSION GÉNÉRALE

La Foresterie à courte rotation (FCR) est une composante d'intérêt grandissant dans l'aménagement forestier durable au Québec. En effet, les plantations de peuplier hybride pourraient jouer un rôle important dans l'approvisionnement en matière ligneuse, tout en diminuant la pression des récoltes en forêt naturelle, ainsi que dans la restauration de friches agricoles abandonnées dans plusieurs régions du Canada, notamment en Abitibi-Témiscamingue. La faisabilité économique et la durabilité de ces plantations nécessitent une approche intégrale qui permet d'optimiser la productivité des plantations de peuplier hybride. La productivité comme ultime objectif en FCR est sous le contrôle de plusieurs interactions éco-physiologiques, notamment la structure de la canopée (contrôlée par l'espacement et le type de déploiement) et l'efficacité d'utilisation des ressources du site. De ce fait, la compréhension de ces interactions à l'échelle de l'individu facilitera la préconisation de pratiques sylvicoles adéquates ainsi que le choix de clones qui répondront aux besoins spécifiques à chaque situation, mais ouvrira aussi la voie vers de nouvelles pistes en amélioration génétique. D'autre part, l'avancement dans notre compréhension de ces interactions éco-physiologiques permettra d'améliorer notre approche de modélisation mécanistique de la productivité, outil incontournable pour la prédiction de l'effet à long terme des changements dans les conditions du milieu, notamment les changements climatiques.

La réduction de l'espacement entre les arbres a induit une diminution combinée de la lumière sous la canopée et de la teneur en azote foliaire. Par conséquent, on présume que les arbres ont expérimenté des conditions de compétition pour la lumière et l'azote. Ces conditions de compétition ont induit des changements notables dans la physiologie et la morphologie des arbres (Fig. 6-1). Au niveau morphologique, l'acclimatation des arbres à l'intensification de la compétition intraclonale s'est traduite par l'augmentation de la courbure des branches, l'allocation préférentielle de la biomasse à la croissance en hauteur par rapport au diamètre et la réduction de la fréquence, de la croissance et de la biomasse allouée aux branches. Ces changements ont contribué à une migration de la surface foliaire

vers le haut de la cime, ce qui a potentiellement amélioré l'efficacité d'utilisation de la lumière dans ces conditions. Ceci montre l'importance des caractéristiques des branches (dimension et orientation) dans la façon dont la surface foliaire est déployée pour maximiser le captage de la lumière. La théorie d'optimalité stipule que l'efficacité de l'utilisation photosynthétique de l'azote (PNUE) à l'échelle de la canopée augmente grâce à l'optimisation de la distribution spatiale de l'azote. Il n'en restera pas moins que la distribution spatiale de la surface foliaire joue un rôle quantitatif dans cette optimalité. Le ratio de biomasse alloué au feuillage a été affecté négativement par l'intensité de la compétition uniquement pour le clone MB915 à cause de la forte réduction de sa teneur en azote foliaire. Nos résultats suggèrent ainsi que l'allocation de biomasse au feuillage résulte plutôt de la compétition pour l'azote par rapport à la lumière. Au niveau physiologique, nos résultats ont mis en évidence l'importance de l'augmentation de surface foliaire spécifique (SLA) dans le maintien de la capacité photosynthétique en condition de compétition pour la lumière et l'azote. En effet, la surface foliaire spécifique a augmenté progressivement en parallèle à l'intensification de la compétition (réduction de l'espacement entre les arbres). Cette augmentation de SLA était corrélée positivement avec une augmentation de PNUE, la réduction du taux de respiration foliaire et le point de compensation à la lumière. Cette corrélation positive entre SLA et PNUE est attribuable à une augmentation de l'allocation de l'azote foliaire à la carboxylation par rapport au captage de la lumière. En effet, la réduction de l'épaisseur du parenchyme palissadique suite à l'augmentation de SLA augmente la pénétration de la lumière dans la feuille et par conséquent réduit les besoins en azote pour le captage de la lumière. Il est possible aussi, que cette corrélation soit associée à une augmentation de la conductance mésophyllienne de CO_2 suite à la réduction de l'épaisseur du parenchyme palissadique (Fig. 6-1). La distribution spatiale de la surface foliaire spécifique et de l'azote foliaire a été proportionnelle au taux de radiation à l'intérieur de la canopée. Nos résultats ont montré que la morphologie et la physiologie des feuilles étaient corrélées et que la SLA était un bon prédicteur de la physiologie de la feuille. Par ailleurs, la surface foliaire spécifique est une composante principale du taux relatif de croissance (RGR), et nombreuses données empiriques supportent la corrélation positive entre SLA et RGR (Reich et al 1998). Nos résultats ont montré que le clone le plus productif (MB915) avait une SLA et une

syllésie supérieure au clone moins productif. De ce fait, il est difficile de dissocier l'effet de SLA de celui de la syllésie.

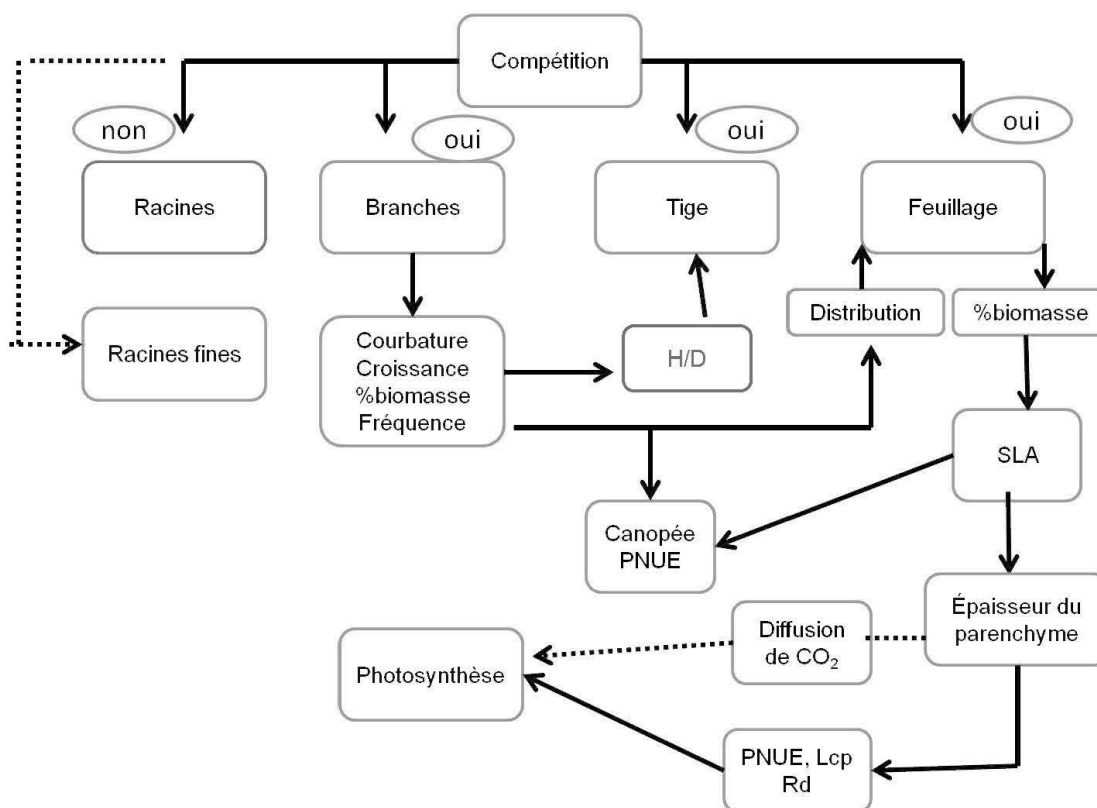


Figure 6-1: Schéma de la réponse morpho-physiologique des arbres à la compétition intraclonale.

Cette étude a mis en évidence l'importance des aspects morphologiques et physiologiques dans l'acclimatation des arbres au changement de l'intensité de compétition intraclonale. Ainsi, il semble évident que l'acclimatation à la compétition est un processus dynamique qui est mis en action à l'échelle de l'arbre grâce à une coordination spatiotemporelle des processus morpho-physiologiques. Ces résultats sont d'une importance capitale lorsqu'il s'agit d'améliorer nos connaissances sur la relation entre le développement morphologique et la physiologie des arbres ainsi que sur les processus biologiques qui permettent d'optimiser la croissance des arbres en fonction des conditions du site.

L'importance de l'acclimatation dans l'amélioration de l'efficacité d'absorption et d'utilisation des ressources du milieu serait ainsi à l'origine des variations importantes observées dans la réponse des clones de peuplier hybride à la compétition. La sélection des traits fonctionnels impliqués dans le processus d'acclimatation des arbres à la compétition (SLA, PNUE et l'orientation des branches) va permettre de produire des clones productifs et susceptibles de répondre efficacement à l'éclaircie et à la fertilisation.

Les résultats de cette étude permettent de consolider l'utilisation de l'approche multicouche pour améliorer l'aspect quantitatif et qualitatif des modèles écophysologiques. En effet nos résultats montrent que :

- (1) La distribution spatiale du feuillage dépend à la fois des conditions du milieu et du degré d'acclimatation morphologique du clone. De ce fait, la relation entre l'indice de la surface foliaire et la disponibilité de la lumière à l'intérieur de la canopée, n'est pas forcément linéaire et dépend surtout du degré d'acclimatation morphologique.
- (2) L'acclimatation morphologique a une influence quantitative sur la distribution spatiale de l'azote foliaire.
- (3) La photosynthèse ne dépend pas uniquement de l'azote foliaire mais aussi du degré d'acclimatation morpho-physiologique du feuillage à savoir SLA et PNUE. Les modèles écophysologiques doivent tenir ainsi compte du processus d'acclimatation morpho-physiologique du feuillage pour améliorer la sensibilité et la prédictibilité des modèles.

L'espacement optimal entre les arbres devrait théoriquement augmenter la productivité à l'échelle de la parcelle tout en concentrant la biomasse sur un nombre réduit d'arbres et sur une période de rotation courte. Nos résultats montrent qu'à ce stade relativement jeune de la plantation, la productivité à l'hectare a été maximisée avec l'espacement de 1×1 m entre les arbres. Le temps nécessaire pour l'occupation du site avec des espacements larges entre les arbres est lié aux conditions initiales du site, le taux de croissance relatif de l'espèce et l'âge de rotation. L'absence de données sur les plantations âgées dans les conditions de la région d'étude rend la décision difficile quant à l'intérêt des espacements très larges. Vu la courte saison de croissance et le faible taux de croissance comparativement aux régions tempérées, l'occupation complète des sites sera très tardive dans le développement de la plantation dans les grands espacements. La fermeture tardive de la canopée dans les espacements de 3×3 et

5×5 m a engendré, à court terme, une perte de fraction de la biomasse marchande liée à l'augmentation du taux d'allocation de biomasse aux branches. De ce point de vue, l'intérêt d'utiliser des espacements plus larges est à discuter quand il s'agit de maximiser la biomasse récoltée à l'échelle de la plantation, mais aussi la production de bois de qualité. Nous suggérons, donc, la favorisation des espacements initiaux étroits, suivis d'éclaircies. Le bois qui serait récupéré pendant les éclaircies pourrait être destiné à la bioénergie, et les arbres résiduels auraient une meilleure qualité pour le sciage.

Les plantations mixtes sont de plus en plus favorisées pour rendre les plantations forestières durables et acceptables socialement et écologiquement. Néanmoins, objectivement, l'amélioration de la productivité et la réduction des risques phytopathologiques demeurent les principaux motifs de cette argumentation. Cependant, on note un manque de données empiriques sur le déploiement de peupliers hybrides en plantations mixtes. Nos résultats montrent que la mixture entre le peuplier hybride et l'épinette a eu un effet positif sur la croissance en diamètre du peuplier hybride et un effet neutre sur la croissance des épinettes. L'effet bénéfique de cette mixture était intimement lié à l'espacement entre les arbres et au clone de peuplier utilisé dans la mixture. L'effet positif de la mixture sur la croissance du peuplier a résulté de la faible compétition interspécifique. En effet, la faible croissance des épinettes a contribué à la réduction de la compétition pour les ressources du sol mais aussi à la stratification de la canopée. La productivité des parcelles mixtes est cependant demeurée inférieure à celle des parcelles monoclonales du peuplier hybride, dans la plupart des cas. Le jeune âge des plantations laisse présager une productivité des plantations mixtes du moins égale à celle de peuplier hybride en monoculture puisque l'évolution de la compétition intraspécifique serait nettement plus intense par rapport à la compétition interspécifique. Cette tendance est aussi conditionnée par le degré de tolérance des épinettes à l'ombre. À ce stade jeune, l'interaction entre peuplier-épinette paraît à première vue comme étant un effet de sélection. Cependant, les traits fonctionnels des deux espèces à savoir la tolérance à l'ombre, la phénologie du feuillage, taux de croissance en hauteur supportent la complémentarité fonctionnelle entre le peuplier hybride et l'épinette. Cette complémentarité pourrait être stabilisée dans le temps par : (1) la réduction de la proportion du peuplier dans la mixture pour créer des conditions minimales de survie des épinettes en strate inférieure de la canopée. (2) L'utilisation des clones de peuplier hybride

comme BT747 caractérisés par des structures morphologiques moins compétitives. (3) La sélection des cultivars d'épinette dotés d'une meilleure acclimatation à l'ombrage.

Les plantations mixtes pourraient ainsi être une alternative prometteuse à l'utilisation des espacements larges en monoculture de peuplier hybride. Surtout qu'elles nous permettent à la fois de satisfaire les besoins liés à la productivité, l'amélioration de la qualité du bois et la réduction des risques abiotiques. Ainsi que, l'augmentation de la résilience de l'écosystème et l'amélioration de l'habitat faunique.

La modélisation est devenue un outil incontournable dans l'aménagement forestier durable. Les modèles écophysologiques sont basés sur les processus biologiques et peuvent donc être utilisés pour la prédiction de la productivité en dehors de la plage des données utilisées dans l'élaboration du modèle. Ces modèles peuvent être utilisés pour simuler la productivité sous différents sites, conditions culturales et climatiques. L'originalité du modèle développé dans cette étude réside dans l'amélioration de la représentativité de la canopée sur le plant (1) morphologique par une meilleure représentation verticale de la surface foliaire et (2) physiologique par le linkage des paramètres de la photosynthèse à l'acclimatation morpho-physiologique du feuillage au microclimat à l'intérieur de la canopée. Le modèle a été satisfaisant pour prédire les échanges gazeux à différents niveaux de la canopée. Néanmoins si l'on veut prédire d'une façon plus réaliste la productivité brute à l'échelle de la canopée, il faudrait inclure les variations de l'indice de surface foliaire et des paramètres de la photosynthèse à l'intérieur de la saison de croissance.

Dans la perspective de prédiction quantitative de l'effet de divers facteurs incluant les changements climatiques, le modèle devrait être bonifié par les données de respiration et d'allocation de carbone pour les différentes parties de l'arbre. Aussi, il serait important d'étudier (1) l'effet combiné de l'augmentation de CO_2 et de la température sur la physiologie du feuillage (taux d'assimilation et conductance stomatique), (2) l'influence de la conductance mésophyllienne sur la photosynthèse et (3) la relation entre conductance mésophyllienne et la morphologie foliaire (surface foliaire spécifique).

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