UNIVERSITÉ DU QUÉBEC À MONTRÉAL

RELATIONS ALLOMETRIQUES DE L'ÉPINETTE NOIRE (*PICEA MARIANA* (MILL.) B.S.P.) ET DE L'ÉPINETTE BLANCHE (*PICEA GLAUCA* (MOENCH) VOSS)

THÈSE

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Avertissement

AVANT-PROPOS

Le travail de la thèse a été réalisé sous la supervision et avec la collaboration de mon directeur et de mes co-directeurs. J'ai planifié, supervisé et exécuté la prise de donnée sur les sites du Lac-St-Jean et du Témiscamingue. J'ai participé à la prise de donnée sur le site de la forêt de recherche de Petawawa. La planification et le choix des peuplements et des arbres à échantillonner à la forêt de recherche de Petawawa a été effectué par l'étudiant à la maîtrise Adam Kuprivicius sous la supervision du Dr. John Caspersen de l'Université de Toronto. Les données provenant de l'Alberta proviennent des travaux de doctorat de Derek F. Sattler, travaux effectués sous la supervision du Dr. Phil Comeau à l'Université de l'Alberta.

La thèse, qui compte trois chapitres, est présentée sous forme d'articles scientifiques rédigés en anglais. Le premier chapitre qui porte sur la comparaison des dimensions de la cime vivante de l'épinette noire et de l'épinette blanche a été publié dans la Revue canadienne de la recherche forestière sous le titre: *Differences in crown characteristics between black (Picea mariana) and white spruce (Picea glauca)*. Les deuxièmes et troisièmes chapitres portant respectivement sur la comparaison de la biomasse foliaire des deux espèces et sur le modèle tubulaire de l'épinette blanche et de l'épinette noire seront soumis à des journaux avec révision par les pairs.

Cette thèse est le fruit de la collaboration avec différents chercheurs. Je tiens à remercier tout particulièrement mes deux co-directeurs les Drs. Frank Berninger et Valerie LeMay ainsi que mon directeur le Dr. Daniel Kneeshaw qui m'ont guidé tout au long de la réalisation de ce projet et qui ont fait preuve d'une grande disponibilité. Je voudrais également remercier le Dr. Robert Schneider pour sa fructueuse collaboration, Derek F. Sattler, la forêt de recherche de Petawawa et Adam Kuprivicius pour avoir rendu disponible leurs données permettant ainsi d'améliorer la portée du projet. Cette thèse n'aurait pu être réalisée sans le travail dévoué des étudiants chercheurs et des assistants de recherche qui ont participé au travail de terrain et à celui de laboratoire à un moment ou l'autre du projet.

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Bd	Branch basal diameter (mm)
Bl	Branch length (m)
Cd	Relative crown depth
Cl	Crown length (m)
Cr	Crown radius (m)
Crwf	Cumulative relative foliage biomass
Cs	Crown surface area (m²)
D/H	Diameter at breast height over total height ratio
DBH	Diameter at Breast Height (cm)
Df	Degree of freedom
DH	Dominant height (m)
Dm	Dummy variable for species (0 black spruce; 1 white spruce)
Dmp	Dummy variable for p parameter of beta function
Dmq	Dummy variable for q parameter of beta function
Fd	Foliage density (g/m²)
G	Stand basal area (m²/ha)
Gb	branch basal area (mm²)
Ht	Total tree height (m)
Hl	Horizontal branch length (m)
Hrel	Relative height on tree stem
PDBH	Plot mean diameter at breast height (cm)
PHt	Plot mean tree height (m)
PSP	Permanent sample plot

QDBH	Quadratic mean diameter at breast height (cm)
Rd	Pipe model ratio at disk level (g/cm^2)
RSSE	Residual sum of square
Rt	Pipe model ratio at tree level (g/cm^2)
Sd	Relative height between the base of the tree and crown base
SI	Site index, domiant height at 50 years old (m)
SPH	Stand density (stems/ha)
Wf	Foliage biomass (Kg)
Wfb	Branch foliage biomass (g)

RÉSUMÉ

L'étude des relations allométriques est depuis longtemps un élément important de la biologie, et ce, pour différentes raisons allant de la prédiction de la taille et du poids d'un individu à l'explication des processus physiologiques qui gouvernent sa croissance. Cette étude compare les relations allométriques qui unissent les différentes parties de la biomasse aérienne de deux espèces phylogénétiquement proches, l'épinette noire et l'épinette blanche. L'étude des relations allométriques des deux espèces d'épinettes a permis de mieux comprendre comment les caractéristiques écologiques du milieu dans lequel croissent les individus affectent leur développement morphologique et comment les traits fonctionnels propres à chaque espèce se reflètent dans leurs relations allométriques. Les résultats permettront de mieux caractériser la distribution de la biomasse aérienne de l'épinette blanche et de l'épinette noire et éventuellement d'utiliser ces relations dans des modèles de croissance à bases fonctionnelles. Ceci permettra de mieux comprendre la croissance et le développement de ces deux espèces écologiquement et économiquement importantes.

La thèse porte spécifiquement sur les relations allométriques entre les différentes parties de la cime vivante de l'épinette noire et de l'épinette blanche et sur la biomasse foliaire et sa distribution dans la cime vivante. La thèse porte également sur la relation entre la biomasse foliaire et la superficie d'aubier de l'arbre. L'hypothèse principale soutenant ce travail de recherche est que des différences entre les traits fonctionnels des espèces permettront d'expliquer les différences de relations allométriques et l'influence des conditions de croissance sur ces relations.

Afin de répondre à ces questions, un échantillonnage destructif d'épinettes noires et d'épinettes blanches a été effectué sur quatre sites en Alberta, en Ontario et au Québec. La mesure du diamètre des branches vivantes de même que leur positionnement à l'intérieur de la cime vivante a permis de reconstruire la cime vivante des arbres et d'en estimer la longueur et le profile. Un échantillonnage de feuillage a également été réalisé afin d'estimer la biomasse foliaire de l'arbre et sa distribution verticale dans la cime vivante. Finalement, des sections de tiges ont été échantillonnées le long du tronc afin d'estimer la superficie d'aubier à plusieurs endroits de l'arbre. Des régressions linéaires et non linéaires mixtes ont été utilisées afin de paramétrer les relations allométriques.

L'étude a permis de constater que la longueur de la cime vivante de l'épinette noire et de l'épinette blanche ne différait pas lorsque les dimensions des arbres et les conditions de croissance étaient prises en compte. Par contre, le profil des deux espèces s'est avéré différent. L'épinette blanche montre une cime plus large dont le profil est plus sensible à la compétition exercée par les autres arbres du peuplement. De plus, l'indice de qualité de station a un effet différent chez les deux espèces laissant supposer une différence en termes d'allocation des ressources. Des différences ont également été remarquées quant à la

biomasse foliaire des deux espèces. En présence de conditions de croissance similaires, l'épinette noire supporte une plus grande quantité de feuillage que l'épinette blanche. De plus, l'épinette noire montre une plus grande densité de feuillage. Cette différence pourrait être reliée à la plus grande tolérance à l'ombre de l'épinette noire. Pour les deux espèces, la distribution verticale du feuillage a varié de façon similaire en fonction de l'âge et de la vitesse de croissance en hauteur. La relation allométrique entre la biomasse foliaire et la superficie d'aubier s'est avérée différente entre les deux espèces. L'épinette noire maintient une plus grande quantité de feuillage par surface d'aubier que l'épinette blanche. Cette différence pourrait être reliée à un besoin en eau diminué pour le feuillage de l'épinette noire compte tenu de sa plus faible productivité.

La thèse permet de révéler des différences entre les relations allométriques de l'épinette noire et de l'épinette blanche et des différences concernant l'influence des conditions de croissance sur celles-ci. Ces différences laissent supposer que les stratégies d'investissement des ressources et que la relation face à la compétition diffère entre les deux espèces.

INTRODUCTION GÉNÉRALE

0.1 Relations allométriques et traits fonctionnels

Depuis longtemps, les relations allométriques ont fait l'objet de travaux, et ce, dans plusieurs domaines de la biologie (Beuchat *et al.*, 1997 ; Niklas, 1994 ; Schmidt-Nielsen, 1984 ; West, Brown et Enquist, 1997). L'allométrie peut être définie comme l'étude des corrélations entre différentes mesures reliées à la taille, à la forme ou au métabolisme des êtres vivants (Niklas, 1994). Les relations allométriques peuvent être abordées empiriquement ou physiologiquement. L'étude empirique s'intéresse exclusivement à la relation mathématique entre deux variables alors que l'étude physiologique se préoccupe des origines de la relation (Niklas, 1994). Les relations allométriques peuvent donc être utiles pour explorer les liens entre les différentes parties ou caractéristiques d'un organisme. Elles peuvent également être utiles pour comprendre comment le changement de dimension d'une partie d'un organisme induit le changement d'une autre partie et comprendre les processus physiologiques qui gouvernent ces relations (Niklas, 1994 ; Schmidt-Nielsen, 1984). Les traits fonctionnels d'une plante, qui lui permettent de tirer avantage du milieu et de la position qu'elle occupe dans ce milieu (Wright *et al.*, 2004), se reflètent dans les relations allométriques qui unissent ses différentes parties. On pourrait donc penser que les relations allométriques peuvent être différentes selon les milieux de croissance et selon les espèces, permettant à la plante d'utiliser les ressources de manière optimale et aux espèces de se distinguer quant à leur comportement dans un milieu donné.

L'épinette noire et l'épinette blanche sont deux des espèces arborescentes les plus répandues de la forêt boréale nord-américaine (Cauboue et Malenfant, 1988). Leurs

caractéristiques morphologiques sont généralement considérées comme étant différentes (Marie-Victorin, 1995). Bien que très peu d'études, à notre connaissance, comparent directement l'allométrie des deux espèces, il semble probable que les différences morphologiques se traduisent par des différences de relations allométriques. Étant donné que les exigences du milieu de croissance influencent les traits physiologiques et par le fait même l'allométrie des arbres (Berninger et Nikinmaa, 1997 ; Vanninen et Mäkelä, 2005), la variété des sites colonisés par ces deux espèces pourrait expliquer des différences de relations allométriques entre elles.

L'influence du milieu sur les relations allométriques s'observe entre autres pour le modèle tubulaire (Pipe model theory; Shinozaki *et al.*, 1964b). Cette relation qui unit la biomasse foliaire à la superficie d'aubier change avec le stress hydrique imposé à la plante. Les arbres poussant sur des sites sujets au stress hydrique maintiennent une plus petite quantité de feuillage par unité de surface d'aubier, prévenant ainsi la rupture de la colonne d'eau (Mencuccini et Bonosi, 2001). Cependant, l'influence de l'environnement ne saurait expliquer à elle seule les différences de relations allométriques et des traits fonctionnels spécifiques à l'espèce demeurent. En reprenant l'exemple du modèle tubulaire, on constate que les arbres d'essences intolérantes à l'ombre montrent des rapports entre la masse de feuillage et la surface d'aubier plus petits que les arbres d'essences tolérantes, permettant ainsi d'acheminer une plus grande quantité de sève par unité de feuillage (Waring, Schroeder et Oren, 1982). Il est ainsi plausible qu'une portion des différences entre les relations allométriques de l'épinette noire et de l'épinette blanche provienne directement de différences associées à leurs traits fonctionnels et au rapport que chaque espèce entretient avec son environnement.

Plusieurs équations allométriques ont mis en relation différentes parties de l'arbre. Parmi les relations ayant des bases physiologiques, Shinozaki et *al.* (1964a), avec la théorie du modèle tubulaire, mettent en relation la superficie du tronc à la base de la cime vivante et la biomasse foliaire de l'arbre, établissant ainsi un lien de conduction hydraulique entre ces deux parties de l'arbre. Enquist et *al.* (1999) établissent quant à eux une relation liant la masse des arbres à la photosynthèse brute, Farnsworth et Van Gardingen (1995) étudient la

relation entre la longueur et le diamètre des branches en apportant des explications de nature hydraulique et mécanique à la relation. Le bois de la branche a deux principales utilités, soit servir de milieu de conduction de la sève et de support mécanique permettant au feuillage de se déployer dans un environnement lumineux adéquat. La relation allométrique entre le diamètre de l'arbre mesuré à 1,3 m (DHP) et la hauteur totale de l'arbre a également été analysée sous l'angle des exigences hydrauliques et des exigences de support mécanique (e.g. Alves et Santos, 2002 ; King, 2005 ; McMahon et Kronauer, 1976 ; O'Brien *et al.*, 1995). En plus de subir des tensions hydraulique plus forte avec l'augmentation de la hauteur (Tyree et Zimmermann, 2002) l'arbre doit également accroitre son diamètre afin d'assurer sa stabilité mécanique (McMahon, 1973).

Les espèces montrant des différences au point de vue de leur autoécologie (e.g. espèces sciaphiles versus héliophile) alloueront différemment leurs ressources afin de satisfaire les exigences de leur milieu de croissance (Cannell, 1985 ; King, 2005 ; Wiemann et Williamson, 1989). Le schéma de distribution de la biomasse variera donc entre les espèces et entre les milieux de croissance. Il est alors essentiel d'analyser l'ensemble de l'arbre et tenir compte des conditions de croissance lorsque l'on compare la productivité de deux espèces différentes.

0.2   Autoécologie de l'épinette noire et de l'épinette blanche

L'épinette noire et l'épinette blanche sont deux espèces arborescentes possédant une distribution générale dans la portion nord-américaine de la forêt boréale, un biome qui occupe près de 310 millions d'hectares et qui représente 10% de la superficie forestière mondiale (Canadian Forest Service, 2005). La distribution presque identique des deux espèces couvre le continent d'est en ouest et s'étend du nord des États-Unis d'Amérique jusqu'à 69° de latitude nord au Canada et en Alaska. Par contre, la distribution commerciale des deux espèces est considérablement plus réduite (Burns et Honkala, 1990 ; Vincent, 1965). L'importance économique des deux essences est manifeste, particulièrement celle de

l'épinette noire qui est l'essence la plus employée en Amérique du nord dans la fabrication des pâtes et papiers (Burns et Honkala, 1990), qui est également employée dans le bois de construction et qui est une espèce de choix pour les bois structuraux en dans l'est du Canada (Butos *et al* 2008).

L'épinette noire et l'épinette blanche forment toutes deux des peuplements purs et mélangés. L'épinette noire se retrouve très souvent en peuplements purs dans le domaine bioclimatique de la pessière à mousses ou sur les sols organiques dans le reste de sa distribution (Cauboue et Malenfant, 1988). L'épinette noire s'associe également à l'épinette blanche, au pin gris (*Pinus banksiana* Lamb.), au sapin baumier (*Abies balsamea* (L.) Mill.), au mélèze laricin (*Larix laricina* (Du Roi) K. Koch), au peuplier faux-tremble (*Populus tremuloides* Michx.) et au bouleau à papier (*Betula papyrifera* Marshall) pour former des peuplements mélangés (Burns et Honkala, 1990 ; Cauboue et Malenfant, 1988 ; Vincent, 1965). L'épinette blanche quant à elle forme plus rarement des peuplements purs et est généralement associée à l'épinette noire, au sapin baumier, au peuplier faux-tremble, au bouleau à papier, au bouleau jaune (*Betula alleghaniensis* Britton) et au pin tordu (*Pinus contorta* Douglas ex Loudon) au sein de peuplements mélangés (Burns et Honkala, 1990 ; Cauboue et Malenfant, 1988 ; Sutton, 1969).

L'épinette noire et l'épinette blanche peuvent toutes deux se retrouver sur plusieurs types de stations, allant des sols minces sur les sommets de collines aux sols organiques localisés dans les dépressions (Cauboue et Malenfant, 1988 ; Sutton, 1969 ; Vincent, 1965). Malgré leur présence sur une variété de stations, les deux espèces se développent à leur plein potentiel sur des sols profonds, de texture moyenne et bien drainés (Burns et Honkala, 1990 ; Cauboue et Malenfant, 1988 ; Vincent, 1965). Cependant, l'épinette noire, grâce à son système racinaire superficiel, réussit à mieux croître sur les stations où la nappe phréatique se situe à proximité de la surface du sol (Burns et Honkala, 1990 ; Larsen, 1980 ; Vincent, 1965).

L'épinette noire atteint des hauteurs de 12 à 25 m alors que l'épinette blanche peut atteindre plus de 30 m (Burns et Honkala, 1990). La forme de la cime de l'épinette noire est généralement considérée étroite, avec les branches tombantes. On note également la présence d'un houppier au sommet de l'arbre sur les sites de mauvaise qualité (Marie-Victorin, 1995 ; Vincent, 1965). À la différence de l'épinette noire, la forme de la cime de l'épinette blanche est généralement obtuse et arrondie (Sutton, 1969). La forme de la cime vivante des deux espèces varie en fonction de la qualité du site sur lequel elles poussent. Le volume de bois à maturité atteint de 100 à 300 m³/ha pour l'épinette noire alors qu'il peut être beaucoup plus grand et atteindre 400 m³/ha pour l'épinette blanche (Burns et Honkala, 1990). Sur des sites de même fertilité, l'épinette blanche produit plus de bois que l'épinette noire (Pothier et Savard, 1998 ; Thiffault *et al.*, 2003) bien que le bois de l'épinette noire soit plus dense et ait une meilleure résistance mécanique (Jessome, 1977). Ces différences de caractéristique pourraient donc représenter des stratégies d'investissement différentes entre les deux espèces, l'épinette noire favorisant un tronc moins volumineux mais plus résistant à la rupture assurant ainsi sa fonction de soutient mécanique.

L'épinette noire et l'épinette blanche sont considérées comme des espèces qui sont modérément à tolérantes à l'ombre (Burns et Honkala, 1990). L'épinette blanche atteint son plein potentiel de croissance en hauteur sous 50% de pleine lumière mais cette tolérance diminue avec l'âge et avec la taille (Cauboue et Malenfant, 1988 ; Kneeshaw *et al.*, 2006). L'épinette noire est considérée comme étant plus tolérante à l'ombre que l'épinette blanche et son feuillage atteint un point de saturation lumineuse en situations plus ombragées que l'épinette blanche (Grossnickle, 2000 ; Lamhamedi et Bernier, 1994 ; Man et Lieffers, 1997). De plus, l'épinette noire produit une réaction positive de plus grande envergure que l'épinette blanche à l'augmentation de CO_2 en conditions ombragées (Marfo et Dang, 2009), confirmant sa plus grande tolérance à l'ombre.

Le feuillage de l'épinette noire et de l'épinette blanche se ressemblent à plusieurs points de vue. Les deux espèces possèdent des aiguilles quadrangulaires persistantes. Cependant, les feuilles de l'épinette blanches (1.5 à 3 cm) sont plus grandes que celles de l'épinette noire

(0.5 à 1.5 cm). (Marie-Victorin, 1995) mais elles ont un ratio surface poids plus petit que celles de l'épinette noire (Dang et Cheng, 2004). Ces résultats sont conséquents avec les résultats de Messier *et al.* (1999) selon lesquels le ratio surface/poids de feuillage est plus grand pour les espèces tolérantes à l'ombre que pour les espèces intolérantes.

0.3   Implications pratiques de l'étude

Les implications pratiques de l'étude des relations allométriques sont nombreuses. En foresterie, la relation entre le diamètre et la hauteur de l'arbre est utilisée afin d'estimer le volume des arbres à l'aide de l'unique mesure du diamètre (e.g. Perron, 1985). De nos jours, avec l'utilisation du LIDAR aéroporté, la relation inverse (prédire le diamètre à l'aide de la hauteur totale de l'arbre) peut également être utilisée (Vepakomma *et al.,* en préparation). De nombreuses relations allométriques sont également utilisées par les modèles de croissance intégrant des éléments physiologiques (Mäkelä, 1997). L'utilisation de ces modèles devient de plus en plus pertinent dans le contexte des changements climatiques et de l'estimation des effets de nouveaux traitements sylvicoles (Weiskittel *et al.*, 2011). Les relations allométriques présentées dans la thèse pourront être utilisées afin de mieux comprendre comment chacune des deux espèces investit ses ressources et quel impact cette stratégie d'investissement a sur la productivité de l'arbre.

0.4   Objectif général de la thèse

L'objectif principal de la thèse est de modéliser et comparer les dimensions et la biomasse de différentes parties de l'épinette noire et de l'épinette blanche afin de mieux comprendre comment des espèces phylogénétiquement proches se distinguent quant à leurs relations allométriques lorsque les conditions de croissance sont prises en considération. Les différences entre les deux espèces peuvent indiquer des différences de traits fonctionnels influençant leur autoécologie. Les relations allométriques pourront par la suite être utilisées

par des modèles de croissance afin de mieux prédire la croissance de l'arbre et de ses différentes parties.

0.5   Objectifs spécifiques de la thèse

Spécifiquement, parce que les caractéristiques morphologiques de la cime vivante sont souvent mises en relation avec la biomasse foliaire et avec la croissance de l'arbre, la thèse vise à modéliser et à comparer la longueur, le profil et la superficie latérale de la cime vivante de l'épinette noire et de l'épinette blanche.

Parce que le feuillage est le moteur de croissance de l'arbre, la thèse a également pour objectif de modéliser et comparer la biomasse foliaire à l'échelle de l'arbre, sa distribution verticale et son lien avec la surface de la cime vivante pour l'épinette noire et l'épinette blanche.

En dernier lieu, parce que cette relation est importante afin de caractériser la distribution de la biomasse de l'arbre, la thèse vise à établir et comparer la relation entre la surface transversale d'aubier et la biomasse foliaire à l'échelle de l'arbre et à plusieurs endroits dans la tige de l'arbre pour l'épinette noire et l'épinette blanche. Pour l'ensemble des objectifs précédemment mentionnés, la thèse vise également à caractériser l'effet des conditions de croissance sur ces relations. L'analyse de l'effet des conditions de croissance permettra de mieux comprendre comment les traits fonctionnels propres à une espèce lui permettent de croître de façon optimale dans un milieu donné.

CHAPITRE I

DIFFERENCES IN CROWN CHARACTERISTICS BETWEEN BLACK (*PICEA MARIANA*) AND WHITE SPRUCE (*PICEA GLAUCA*)

Hugues Power, Valerie LeMay, Frank Berninger, Derek F. Sattler et Daniel Kneeshaw

1.1 Résumé

L'épinette noire (*Picea mariana* (Mill.) B.S.P.) et l'épinette blanche (*Picea glauca* (Moench)) sont deux espèces phylogénétiquement proches l'une de l'autre mais dont la productivité diffère. Malgré l'importance de ces deux espèces au sein de la forêt boréale canadienne et malgré l'importance de la cime des arbres afin de mieux comprendre et modéliser leur croissance, les connaissances sur les caractéristiques des cimes vivantes des épinettes noires et des épinettes blanches demeurent partielles. Dans cet article, nous avons caractérisé et comparé la longueur, le profil, la forme et la surface latérale de la cime vivante des deux espèces d'épinettes. Ce travail a été effectué grâce à l'échantillonnage destructif de 57 épinettes noires et 65 épinettes blanches provenant des provinces canadiennes de l'Alberta de l'Ontario et du Québec. La longueur de cime vivante a été mesurée sur chaque arbre échantillon et le profile de cime a été obtenu à la suite de la reconstruction de la cime vivante à l'aide de mesures de longueur de branches. Notre étude montre que la longueur de cime ne diffère pas entre les deux espèces lorsque les dimensions des arbres ainsi que les conditions dans lesquelles ils croissent sont prises en compte. Cependant, l'épinette noire et l'épinette blanche croissent généralement dans des milieux différents entrainant des différences en termes de longueur de cime vivante. Nous avons cependant trouvé des différences entre les espèces quant au profil de la cime vivante. L'épinette blanche a montré une cime plus large qui passe d'une forme parabolique à une forme conique en présence d'une forte compétition. Ces différences se reflètent dans la surface latérale de la cime vivante des deux espèces.

1.2   Abstract

Black (*Picea mariana* (Mill.) B.S.P.) and white spruce (*Picea glauca* (Moench) Voss) are phylogenetically proximal species that differ in productivity. Crown characteristics of these two species have not been extensively studied, in spite of the importance of these two species to the Canadian boreal forest and the importance of tree crowns for understanding and modelling tree growth.   In this paper, we characterize and compare crown lengths, crown profiles (i.e, radii), shapes and surface areas of these two species using 65 white spruce and 57 black spruce trees destructively sampled in the provinces of Alberta, Ontario and Québec, Canada. Crown length was measured on every sample tree while crown profile was obtained by reconstructing crowns from branch measurements. Our results showed that crown lengths did not differ between these two species given the same tree size and growth conditions. However, these two species establish under different growth conditions resulting in crown length differences. Further, differences in crown radii and profiles were found even under the same growth conditions. White spruce had wider crown radii and profiles changed from a parabola to a cone shape under increased density.   As a result, differences in crown surface areas were found.

1.3   Introduction

Black (*Picea mariana* (Mill.) B.S.P.) and white spruce (*Picea glauca* (Moench) Voss) are two important coniferous species of North America and they share a similar geographical distribution. The shade tolerance of black spruce is considered to be intermediate to high, whereas white spruce is generally considered to be slightly less shade tolerant (Burns and Honkala 1990). The maximum crown width of black spruce has been reported as being narrower than that of white spruce (Marie-Victorin 1995). Black spruce generally grows to heights between 12 and 25 m, while white spruce can reach heights of 30 m or more (Burns and Honkala 1990). The volume at maturity for primarily black spruce stands varies from 100 to 300 m^3 ha^{-1}, while predominantly white spruce stands can approach 400 m^3 ha^{-1}. Differences in maximum volume between these two species on similar sites may be explained by a number of factors including differences in the crown characteristics and architecture.

Crown characteristics refer to changes in morphology, in particular, crown length, maximum width, shape or profile, surface area, volume, and biomass, whereas crown architecture refers to the arrangement and distribution of branches and foliage within tree crowns. Crown characteristics and architecture affect photosynthetic rates of tree via light interception and, therefore, affect forest productivity (Cannell et al. 1987). Oker-Blom and Kellomäki (1983) studied effects of crown shape on light interception in a simulated stand of Scots pine (*Pinus sylvestris* L.) and found that interception varied not only with stand characteristics but also with the foliage distribution within trees. Wang et *al.* (1990) studied the light interception of Sitka spruce (*Picea sitchensis* (Bong.) Carr.) using model of photosynthesis and found that crown shape was less important for affecting light interception than the individual effects of total leaf area, foliage distribution within the crown, and leaf angles. The lesser impact of crown shape on light interception was also reported by Duursma and Mäkelä (2007); their model for Scots pine light interception was influenced more by

crown surface area than by crown shape. However, since crown shape and crown surface area are strongly correlated, likely both characteristics affect light interception.

Von Gadow and Hui (1999) stated that tree crown characteristics both determine and respond to shading and physical constraints between neighboring trees. As a result, crown characteristics are commonly used in growth models at the tree level (e.g., TASS, Mitchell 1975; CROBAS, Mäkelä 1997) and are important variables in process-based or hybrid forest growth models (Valentine and Mäkelä 2005). Consequently, many authors use maximum crown radius or crown shape to develop competition indices (e.g. Hegyi 1974; Daniels et al. 1986; Biging and Dobbertin 1992; Nepal et al. 1996). In some models, leaf area index (LAI) defined as the ratio between total leaf area and the ground surface area, has been used as an indicator of photosynthetic productivity (Landsberg and Waring 1997). However, LAI and crown characteristics are strongly related.

Overall, crown architecture and characteristics are strongly related to photosynthetic capability and, therefore, to tree productivity. These characteristics have been shown to vary among species and growth conditions. Characterizing and comparing the differences in crowns of two of the most abundant tree species of the Canadian Boreal Forest is essential for improving understanding of growth and productivity in this large forest area.

In this study, differences between black and white spruce crown characteristics were examined. As noted, crown characteristics have not been extensively studied for these two species, in spite of their importance. The specific crown morphological characteristics studied in this paper were crown length, profile, and surface area. Since growth conditions are known to affect tree crowns, we examined species differences in the context of stand density and site productivity differences. A second objective was, therefore, to examine how changes in growth conditions affect crowns of these two important spruce species.

1.4   Materials and methods

1.4.1   Data

The study dataset included 65 white spruce and 57 black spruce trees. The white spruce data were obtained from sites located in Ontario and Alberta, Canada, whereas data for the black spruce trees were collected in Québec, Canada (Table 1.1). Sampling at the various sites took place during the growing season (May through September) in 2008 through 2010.

The sampling sites in Alberta were spruce-dominated stands that contained a minor component of trembling aspen (*Populus tremuloides* Michx.) within the Central Mixedwood Natural Sub-region (Beckingham and Archibald 1996) and had existing 0.1 ha permanent sample plots (PSPs). These stands developed from natural regeneration and were not influenced by silvicultural treatments. The three PSPs represented a range of stand densities; however, all were located on sites with mesic soil moisture and medium soil fertility. At each location and adjacent to the existing PSP, a minimum of four dominant or co dominant trees with undamaged crowns were selected as sample trees. Using the selected tree as the plot centre, local competition from neighbouring trees was measured by establishing a 5.64 m radius circular plot. Within the plot, the diameter outside bark at 1.3m above ground (DBH) and total tree height (Ht) were measured and species was recorded for all live trees ≥ 7.5cm DBH. Unlike sampling in the other two provinces, smaller trees from 1.1 to 7.5 cm DBH were not measured. However, plots selected from Alberta sites were all in mature stands (85 to 140 years old), and there were few trees of this size. The mean of sample tree ages was calculated at each location (hereafter termed stand age). The data from the fixed-radius plots, including the subject tree, were used to calculate plot-level variables presented in Table 1.2.

White spruce trees from Ontario were sampled from existing plantations that received spacing or thinning treatments; however, the last thinning was done in 1982 and growth was assumed to be similar to that of natural white spruce-dominated stands. Sample trees from the

Petawawa site were taken inside or from the periphery of existing PSPs ranging in size from 0.03 to 0.08 ha. For all live trees $\geq$ 1.1 cm DBH in the PSP, species was recorded and the DBH was re-measured; heights of the previously measured trees were re-measured. To obtain a distribution of samples across tree size, trees were purposively sampled by selecting one tree from each of small and large DBH classes and two trees from the medium DBH class, resulting in four trees per plot. Each DBH class included the same number of trees. Sample trees were limited to those with undamaged crowns. Stand age was the plantation age adjusted to age at 1 m above ground, using estimates provided by Pothier and Savard (1998). The measures for all live trees in each PSP were used to calculate the plot-level variables presented in Table 1.2.

Black spruce trees from Québec were selected from even-aged stands that naturally regenerated following clearcutting or a stand-replacing fire. Stands of different ages, densities (i.e. trees per ha), and site indices were selected. For each selected stand, a variable-radius plot with basal area factor of 1 m^2 ha^{-1} was established at a location previously determined on the forest map. Species was recorded and DBH was measured for all live trees $\geq$ 1.1 cm DBH. As with white spruce from Ontario, trees in the plot were divided into small, medium and large DBH classes each class including the same number of trees. Height was measured for 20 to 90 trees across the DBH classes. For each plot, one sample tree was selected from each DBH class resulting in three trees per plot. Age at 1 m above ground for three dominant and undamaged trees of the target species was recorded. The mean age of the three dominant trees was used as stand age. The information from the variable-radius plot was used to calculate the plot-level summary statistics (Table 1.2).

For all sites, selected sample trees were hand-felled. Information about the selected sample trees is presented in Table 1.3. Height and height to live crown were measured on trees after felling. Height to live crown was considered as the height of the lower branch that presented green foliage and above which all the whorls included at least one living branch. The vertical position of each live branch along the tree bole (i.e., main stem) was recorded. Branch basal diameter, branch insertion angle, and whether the branch was a nodal or an inter-nodal branch were recorded for each living branch.

For the trees sampled in Ontario and Québec, the crown was divided into 10 sections of equal length and one living branch from each section was randomly selected with the use of a random table and measured for branch length. For the trees from Alberta, the crown was divided in two sections of equal length and branch length was measured on 10 randomly selected branches from each section. A random selection of branches was made from a random sampling performed after the measurement of all living branches.

1.4.2   *Calculations of plot- and tree-level variables including imputations of missing heights*

Sample data were compiled to obtain the plot- and tree-level variables used in modeling and examining crowns (Table 1.2). All plot-level variables were expanded to per ha measures. No attempt was made to correct for the difference in minimum DBH between Alberta and other sites in calculating plot-level variables, since all plots from Alberta were in mature stands with few stems in the 1.1 to 7.5 cm DBH range. Also, for all models, random-effects at the site-, plot-, tree, and branch-level (where appropriate) were included, thereby accounting for correlation and heteroscedasticity due to the four-level (or three-level) sampling hierarchy.

Unmeasured heights of trees in each plot from Québec and Ontario were imputed using the following models for black spruce (Eq. 1.1) and white spruce (Eq. 1.2):

(1.1)
$$Ht_{ijk} = -8.5523 + 0.6216DBH_{ijk} - 0.0184DBH_{ijk}^2 + 1.6978PDBH_{ij} - 0.0619PDBH_{ij}^2 + 0.0005PHT_{ij} + 0.0298DBH_{ijk}PDBH_{ij} + \varepsilon_i + \varepsilon_{j(i)} + \varepsilon_{k(ij)}$$

(1.2)
$$Ht_{ijk} = 8.5477 + 0.2638DBH_{ijk} - 0.0079DBH_{ijk}^2 + 0.2660PDBH_{ij} - 0.0163PDBH_{ij}^2 + 0.0659PHT_{ij} + 0.0182DBH_{ijk}PDBH_{ij} + \varepsilon_i + \varepsilon_{j(i)} + \varepsilon_{k(ij)}$$

Where: *PDBH* is the plot mean *DBH*, all live trees; *PHt* is the plot mean height, height-measured trees only; *ijk* are the subscripts for tree k in plot j in site i and ε_i, $\varepsilon_{j(i)}$, and $\varepsilon_{k(ij)}$ are the random error terms at the site, plot within site and tree within plot levels, respectively.

Eq. 1.1 and 1.2 were fitted using the height and DBH measured on the adjacent sample plot and the lme function of R (Pinheiro et al. 2010). Subject-specific (i.e., site and plot nested in site levels) random effects on the intercept were added to each predicted total height. Tree height predictions were used in imputing any missing heights in each plot. The error terms at the site and plot levels were assumed to follow normal distributions with the hierarchical structure of plots within sites accounting for any correlation between plots. The final error term at the tree level was also assumed to follow a normal distribution with the hierarchical structure accounting for correlations of trees within plots. Tree-level error terms were also checked for homogeneity of variance using residual plots and for normality using normality plots. Where heteroscedasticity of the tree-level errors was detected, a function to model the variance of the tree-level residuals was added to the model (Pinheiro et al. 2000). Further, the chosen models were linear in the parameters, but nonlinear in the variables (i.e., a linear model) to address the expected curvilinear relationship of height with DBH. Therefore, since these height predictions equations were only used to impute unmeasured heights and should not be used with other datasets, these linear were not further discussed.

The dominant height (DH) for each plot was calculated by averaging the height of the 100 largest trees (by DBH) per hectare. Quadratic mean DBH (QDBH, cm), density (stems ha^{-1}), and basal area (m^2 ha^{-1}) were calculated for each plot using only the trees that

comprised the main cohort of the stand. We excluded saplings as part of the regeneration cohort for all stands except for three young stands of black spruce (i.e., 20 to 30 years old) where saplings were considered as part of the main cohort. The site index (SI; site height at 50 years total age) for each plot was calculated using the HD, stand age and SI equations by Pothier and Savard (1998).

1.4.3   Crown reconstruction

In order to analyze the crown characteristics, we reconstructed the crowns of each sample tree. Crown reconstruction involved two steps: first, the lengths of all living branches were imputed by fitting models using measured branch lengths (*Bl*); and second, horizontal distances between the bole of the tree and the tip of each branch (*Hl*) were calculated using the branch lengths and branch angles (Fig. 1.1).

To estimate the lengths of the living branches, nonlinear mixed-effects models were fitted using sampled branches separately for black and white spruce using the nlme function in R (Pinheiro et al. 2000). To fit these models, first models of branch length using branch diameter (*Bd*) and relative crown depth (*Cd*) as predictor variables and assuming a single error term were developed, where relative crown depth was the relative position in the living crown equal to 0 at the top of the tree and equal to 1 at the base of the living crown. The residuals at the plot, tree and branches level from these models were graphed against the tree- and plot-level variables presented in Table 1.2 for each species and these graphs were used as a guide for selecting additional predictor variables. Each additional predictor variable was entered in the model and the new models were tested against the original model (i.e., *Bd* and *Cd* only) using likelihood ratio tests ($\alpha=0.05$).

Once predictor variables were selected, random effects at the site, plot, tree and branch levels were used to modify all fixed-effects parameters with a single error term at the branch level. Errors at all four levels in the hierarchy (i.e., site, plot, tree, and branch) were initially considered. However, these additional error terms are equivalent to adding an intercept to the model for subject-specific branch length estimates. Since this could result in negative

estimated branch lengths, only the error term at the branch level was retained. All random effects were considered normally distributed with equal variances; these assumptions were verified for the branch-level error term using the same methods as for 1.1 and 1.2.

The final models included the predictor variables *Cd*, *Bd* and *SI* for black spruce (Eq. 1.3) and only *Cd* and *Bd* for white spruce (Eq. 1.4).

$$(1.3) \quad Bl_{ijkl} = \beta_1 Bd_{ijkl}^{(\beta_2+b_i+b_{j(i)}+b_{k(ij)})} Cd_{ijkl}^{\beta_3} SI_{ij}^{\beta_4} + \varepsilon_{l(ijk)}$$

$$(1.4) \quad Bl_{ijkl} = \beta_1 Bd_{ijkl}^{(\beta_2+b_i+b_{j(i)}+b_{k(ij)})} Cd_{ijkl}^{\beta_3} + \varepsilon_{l(ijk)}$$

Where *ijkl* is the subscript for branch *l* in tree *k* in plot *j* in site *i*; β are fixed-effects parameters; *b* are random-effects parameters at the site, plots within site, and trees within sites levels; and $\varepsilon_{l(ijk)}$ is the random error at the branch level.

Eq. 1.3 and 1.4 included random effects on β_2 at the site, plot nested in site and tree nested in site and plot levels for tree-specific estimates of the parameter β_2 only. These final tree specific branch length models were applied to each tree and living branch position to obtain the subject-specific estimated branch length.

In the second step of the crown reconstruction, we calculated the estimated horizontal distance (*Hl*) between the tree bole and the tip of the living branch using the estimated *Bl* and the measured branch angle (θ) (Eq. 1.3,1.4, 1.5).

$$(1.5) \quad \hat{Hl}_{ijkl} = \hat{Bl}_{ijkl} \sin\theta_{ijkl}$$

Where *ijkl* is the subscript for branch *l* in tree *k* in plot *j* in site *i*.

1.4.4   Crown length

To study differences in crown lengths between the two spruce species, first, a nonlinear mixed-effects model was fitted using the nlme function of R (Pinheiro et al. 2010) using the pooled data for both species (hereafter termed the base model). Once the base model was selected, dummy variables were used to alter the parameters of the model to be species-specific. The test for species differences was then performed by comparing the base model to the species-specific model using a likelihood ratio test (α=0.05). The modeling approach permitted the use of non-linear forms of equations, forms of equations frequently used in allometry, this can be compared to the analysis of co-variance where the relationship between the co-variables and the dependent variable is linear.

For the base model using pooled data for both species, different nonlinear model forms from Davies and Pommerening (2008), Antos et al (2010), Thorpes et al. (2010), and Sattler and LeMay (2011) along with different predictor variables were fitted and compared using Akaike's information criterion (AIC; Akaike 1973) as a measure of model fit. The Akaike information criterion allows us to compare the likelihood of two models while penalizing for the number of parameters included in the model. This method can be used to compare two models built with the same dataset and the same random structure but with differences in their fixed effects. However, the Akaike information criterion does not provide an evaluation of the fit of the models to the data. Random effects at the site, plot and tree levels were included in all models, with the same distributional assumptions as for the height imputation models. Eq. 1.6 was selected as the base model for the pooled data of both species. This model was then modified by including a dummy variable for species (*Dm* is 0 for black spruce and 1 for white spruce) to alter all fixed-effects parameters (Eq. 1.7).

(1.6) $Cl_{ijk} = Ht_{ijk} * \exp^{(\beta_1 D/H_{ijk}{}^{\beta_2} + \beta_3 QDBH_{ij})} + \varepsilon_i + \varepsilon_{j(i)} + \varepsilon_{k(ij)}$

(1.7) $Cl_{ijk} = Ht_{ijk} * \exp^{((\beta_1 + \beta_4 Dm)D/H_{ijk}{}^{(\beta_2 + \beta_5 Dm)} + (\beta_3 + \beta_6)QDBH_{ij})} + \varepsilon_i + \varepsilon_{j(i)} + \varepsilon_{k(ij)}$

Where D/H is the ratio of DBH over tree height; ijk is the subscript for tree k located in plot j located in site i; β are fixed-effect parameters; and ϵ represents the error terms (i.e. random-effects) of the model at the site (ϵ_i), plot within site ($\epsilon_{j(i)}$) and tree within plot ($\epsilon_{k(ij)}$) levels.

A likelihood ratio test (α=0.05) was then used to determine whether there were differences between the two species by comparing Eq. 1.6 (reduced model) and Eq. 1.7 (full model). The likelihood ratio test allows us to perform a hypothesis test on the fit of two models where one of the two models is a special case of the second one. To further examine differences between the two species, graphs of the predicted crown length using fixed effects only (i.e., population-averaged level) versus combinations of predictor variables were used.

1.4.5   Crown profile

For our study, crown profiles were defined by crown radii (Cr) calculated as the average of the four longest horizontal branch lengths within each inter-whorl segment defined by the nodal and inter-nodal branches beginning with whorls at the top of the segment. For these models, crown depth was redefined using the position of the mid-point of the whorl segment.

A nonlinear mixed-effects model fitted using the nlme function in R (Pinheiro et al. 2010) was used to model the crown radii representing the tree crown profile. The random effects were errors at the site, plot and tree and whorl levels, with similar assumptions as for the branch length imputation models.

Initially, the same methods used to fit the crown length models (i.e., full versus reduced models) were used for the crown profile model. However, difficulties were encountered in fitting the species-specific model. As a result, separate crown profile models were fitted for

each species (Eq. 1.8) and then for the two species combined. Because the comparison of the three models could not be done with the likelihood ratio test or the Akaike criterion, the residual sum of squares (RSSE; all levels of errors included) for the model using the pooled data was compared to the sum of RSSEs for separate black and white spruce models. Large differences were used to indicate that the crown profiles differ between species.

$$(1.8) \quad Cr_{ijkl} = \frac{Cd_{ijkl}}{\beta_1 + \beta_2 Cl_{ijk} + (\beta_3 + \beta_4 Cl_{ijk})Cd_{ijkl} + \beta_5 SI_{ij} + \beta_6 SPH_{ij}} + \varepsilon_i + \varepsilon_{j(i)} + \varepsilon_{k(ij)} + \varepsilon_{l(ijk)}$$

Where $ijkl$ is the subscript for whorl l in tree k in plot j in site i; β_1 to β_5 are fixed-effects parameters; SPH is the stems per ha; and ε represents the error terms of the model at the site ($\varepsilon_{j(i)}$), plot within site ($\varepsilon_{j(i)}$) tree within plot ($\varepsilon_{k(ij)}$) and branch within tree ($\varepsilon_{l(ijk)}$) levels; and all other variables were previously defined.

This model provided better results than a power or exponential models (i.e., lower AIC) using the pooled data for both species. The same method as with crown length was used to examine differences between species. Further, subject-specific crown radii predictions (i.e., tree-level branch predictions) were used in calculating crown surface areas.

1.4.6 Crown surface area

The crown surface area (Cs) was also compared between the two species. Crown surface area was obtained by integrating the crown circumferences from the base of live crown to the tree tip. The subject-specific estimated radii from the crown profile equation were used in the equation provided in Husch et al. (2003) for a parabola shape(Eq. 1.9).

$$(1.9) \quad \hat{Cs}_{ijk} = 2\pi \int_{Cb}^{Ht} \hat{Cr}_{ijkl} \sqrt{1 + (\frac{d\,\hat{Cr}_{ijkl}}{dx_{ijkl}})^2} \, d(x_{ijkl})$$

Where x is the distance from the base of live crown (*Cb*) to a maximum at tree height (*Ht*); *ijkl* is the subscript for whorl *l* in tree *k*, plot *j* and site *i*; and $\widetilde{Cr}$ is the predicted crown radius.

The crown surface areas were compared between species using graphs of the crown surface area plotted against crown length.

1.5   Results

1.5.1   Crown reconstruction

The root mean squared error (RMSE) including all errors of the branch length model (Eq. 1.4) combined (i.e., site+plot+tree+branch errors) was 16.77 cm for black spruce (Eq. 1.3) and 22.31 cm for white spruce. As expected, branch diameter was the most important variable in estimating branch lengths (Eq. 1.3 and 1.4) with longer branches associated with larger branch diameters. For a given branch diameter, branch lengths increased from the tree top with a crown depth of 0 to the crown base with a crown depth of 1 (Table 1.4). Site index had a slightly positive effect on black spruce branch lengths, but this effect was not detected for white spruce where site index was not statistically significant (α=0.05).

1.5.2   Crown length models

The RMSE of all errors combined was only slightly larger for the reduced model without species (2.090 m) (Eq. 1.6) than for the full model with species (2.058 m) (Eq. 1.7). Also, the likelihood ratio test (α=0.05) for the reduced model versus the full model with species indicated no differences between species (log L=-242.3017 for Eq. 1.6 versus -240.5087 for

Eq. 1.7, p-value = 0.3098). Crown lengths did not vary between black and white spruce after accounting for effects of height, D/H and QDBH on crown length (Table 1.4).

Using the fitted crown length model, a positive, monotonically increasing relationship between crown length and tree height was observed (Fig. 1.2 A). Crown length also increased with D/H, indicating a longer crown length for trees with greater taper. Conversely, crown length decreases with QDBH.

Although differences between the two species were not detected given the same height, D/H, and QDBH values, the sample data and previous literature indicate that the two species grow in different characteristics. Using the sample data, the 1st and 3rd quartiles of the D/H and QDBH distributions were lower for black spruce (i.e., lower than for the pooled data) than for white spruce (i.e., higher than for the pooled data). Using these species-specific D/H and QDBH values, for a given height, black spruce crowns were longer than white spruce crowns (Fig. 1.2 B and C).

1.5.3   Crown profile models

The crown profile model (Eq. 1.8) fitted using the pooled data resulted in a larger RSSE (i.e., all errors pooled) (313.925) than the sum of the RSSE obtained by fitting separate equations for the two species (282.7454), indicating that crown profiles differ between species (Table 1.4). For both species, the maximum predicted crown radius was located at the base of the crown.

Given the same crown depth and crown length, black spruce crowns were generally narrower than white spruce crowns except for stands of high density and site index (Fig. 1.3). Site index had a small negative effect on white spruce crown radius while showing a small positive effect on black spruce crown radius. Stand density showed a stronger negative influence on crown radii for white spruce than for black spruce.

To compare the crown shape of both species, the relative crown radius was graphed against the relative crown depth (Fig. 1.4). Black and white spruce both had parabolic shapes for stands with low stand density; however, white spruce crown shapes were more sensitive to changes in stand density. That is, an increase in stand density induced a shift from a parabolic to a conical shape for white spruce.

1.5.4   Crown surface area

The noted differences in crown profiles between the two spruce species resulted in differences in crown surface areas (Fig. 1.5). The crown surface area increased nonlinearly with crown length for both species. White spruce tended to have a larger crown surface area than black spruce under low stand density, while black spruces had larger crown surface area under high stand density. As for crown profile, white spruce crown surface area decreased with site index while black spruce crown surface area showed the opposite trend.

1.6   Discussion

1.6.1   Crown length

Crown length dynamics are a result of the interaction of two processes, crown recession and height growth. Crown recession occurs when the branches located at the base of the living crown die. The rate of crown recession is known to be largely influenced by light availability at the crown base (Sorrensen-Cothern et al. 1993), by stand density, and by height growth (Valentine et al. 1994; Kantola and Mäkelä 2004). Physical interactions between branches of neighboring trees are also known to influence the crown recession rates (Putz et al. 1984). Trees that are growing in stands with higher stem densities or trees with larger crowns may experience more physical interactions with crowns of their neighbouring trees resulting in increased crown recession. Given these considerations, we would expect that white spruce

trees with a larger maximum crown radius and lower shade tolerance would have shorter crown length than black spruce.

However, no significant differences were found between black and white spruce after accounting for differences in D/H and QDBH (i.e., using model predicted values given D/H and QDBH). The negative relationship between crown length and QDBH (Fig. 1.2 A) coupled with larger values of QDBH for white spruce (Table 1.2) could explain the shorter crowns of white spruces under species-specific growth conditions (Fig. 1.2 B and C). As trees grow, heights increase resulting in increases in potential crown lengths. As a result, tree height was an important variable for estimating crown length for both species.

Davies and Pommerening (2008) reported that the addition of spatial and non-spatial competition indices improved the prediction of crown length for Sitka spruce. In our models, the plot-level variable QDBH was an important variable. QDBH can be mathematically interpreted as: i) the diameter of the tree with average basal area; ii) the mean of squared diameters, hence the term "quadratic mean DBH"; or iii) a measure of basal area per hectare relative to stems per ha. As such, QDBH is indicative of competition at the plot level. The inclusion of D/H in the model can be interpreted as an indicator of tree social position and competitive environment as noted by Clyde and Titus (1987), factors known to influence crown length (Maguire and Hann 1990). In our sample data, dominant trees had higher D/H values than co dominant and intermediate trees. Once D/H and QDBH were included in the model, other measures of plot-level competition (i.e., stems per ha) and non-spatial tree-level competition (i.e., basal area of larger trees) did not improve the model.

1.6.2   Crown profile

Site quality also impacts the crown profile (Gillespie et al. 1994). In our study, the opposite effect of site index on crown radius between the two species may be attributed to the difference in the expected ranges of site index values for black and white spruce as reflected in our dataset. Black spruce is better adapted to grow on poorer sites than white spruce

(Burns and Honkala 1990); in this study, sampled black spruce stands had lower site indices than sampled white spruce stands. The trend towards shorter branches for black spruce trees (with implied shorter crown radii) in stands with lower site indices may reflect a choice in resource allocations where investing less carbon in branches may allow the tree to invest more in the root system, a common trend for trees growing on poor sites (Cannell 1985). Conversely, for white spruce that grows on better sites, an increase in site index may be associated with an increase in competition (Husch et al. 1982) and therefore less space for growing large branches.

Competition (Ducey 2009) and social class (Hann 1999) are factors that are known to affect maximum crown radius. In our model, density was included as a measure of competition in crown profile models. The stronger effect of stand density on white spruce may be attributed to both lower shade tolerance and to wider crowns, since wider crowns are more subject to physical interactions and increased crown recession rates (Putz et al. 1984).

Other variables representing the inter-tree competition were absent from the crown profiles models. However, since crown length was shown to be impacted by D/H and crown length was the most important predictor variable in the crown profile models, the impacts of competition on crown profile may be reflected in changing crown lengths. Deleuze et al. (1996) proposed that trees may slow their branch growth and consequently conserve long crowns even under high competition. However, the positive association of crown length and crown radius in our models is consistent with results obtained by Valentine et al. (1994) for Sitka spruce, Gilmore and Seymour (1997) for balsam fir (*Abies balsamea* (L.) Mill.) in Maine, US, and with Sattler and LeMay (2011) for white spruce in mixed-species stands of British Columbia, Canada.

1.6.3   *Crown shape*

Shape can be defined as the relationship between two different measures of an object (Niklas 1994). In our case, crown shape was defined as the relationship between crown radius

and crown depth. Our results showed that black spruce crown shape was parabolic and appeared to be little affected by stand density. However, white spruce crown shape was parabolic for lower stand densities and approached a more conical shape as density increased. Hann (1999) noted that suppressed Douglas fir trees (*Pseudotsuga menziesii* var. *menziesii* (Mirb.) Franco.) have a more parabolic and less conical crown shape than dominant trees, which may be viewed as a contradiction of the results in this study. However, plot or stand level competition as measured by stand density is not equivalent to tree level competition resulting in differential social classes. Further, stand density is confounded with age in that densities are higher in younger stands (Assmann 1970). Baldwin and Peterson (1997) reported different crown shapes between loblolly pine trees of 15 versus 30 years old, with older trees showing a more pronounced parabolic shape than younger trees.

1.6.4 Crown surface area

Because crown surface area depends of both crown radius and crown length, variables that were associated with differences in crown profile and length also impact crown surface area. Since crown surface area is strongly related to foliage biomass (Mäkelä and Albrektson 1992) and photosynthesis (Duursma and Mäkelä 2007), it is interesting to note that white spruce presented a larger crown surface area for low versus high densities for the same crown length (Fig. 1.5). Under high density, the conical crown shape of white spruce with narrow branch lengths resulted in smaller crown surface areas. As noted, crown profiles of black spruce were not directly affected by stand density, but may be indirectly affected via impacts of density on crown length. As a result, changes in surface area for different densities would be expected for black spruce also. These differences in crown surface areas may partly explain the differences in productivity between the two species. Also, since white spruce crowns appeared to be more affected by changes in stand density, the crown form of white spruce may be more plastic and respond more readily to changes in the competitive environment.

1.6.5   Constraints of the study

In this study, we combined samples from three provinces. As a result, there were slight differences in sampling protocols among studies. In particular, no intermediate trees were sampled in Alberta. Also, since the plot-level variables were based on different plot sizes, the spatial extents represented by the plot-level measures of competition were not exactly the same. Small differences in sampling protocols are common in observational studies, but these also provide information on a wider range of growth conditions than is possible with field experimental studies. To address differences variances among samples due to sampling protocols, a hierarchical error structure was included in each model and models were examined for any remaining level-one (i.e, smallest spatial extent) heteroscedasticity.

1.7   Conclusions

In our study, we found differences between crown characteristics of black and white spruces, two important species in the Canadian Boreal Forest. Black and white spruce crowns differ in terms of radii, shape and surface area for a given site productivity and level of competition. Because of larger crown radii, for a given tree size, site productivity, and competition level, white spruce generally had a larger crown area. Since crown area is related to overall tree-level productivity, white spruce may be more productive than black spruce on a given site. However, black spruce is better adapted to areas of low productivity. In terms of plantation management, a reduction in stand density is expected to increase crown width to a greater extent in the less shade-tolerant white spruce. Overall, differences in these two related species indicate that models to forecast growth, along with management to meet growth and value objectives should be species-specific.

Table 1.1 Characteristics and locations of sample sites

Site	Location	Species	Number of plots	Age (years)	Density (stems ha^{-1})	Number of sample trees
Lac La Biche Alberta	55° 00'N 112° 00'W	White spruce	3	85-140	800-1500	15
Petawawa, Ontario	45°59'N, 77° 25'W	White spruce	12	40-75	130-2500	50
Lac-St-Jean, Québec	49°00'N, 72° 40'W	Black spruce	12	30-120	900-7000	36
Témiscamingue, Québec	46°45'N, 78° 20'W	Black spruce	7	30-120	1500-4500	21

Table 1.2 Summary statistics for plot and tree level variables (65 white spruce trees in 17 plots, 57 black spruce trees in 19 plots)

Variable	Black spruce				White spruce			
	Min.*	Mean†	Max‡.	Std. dev.	Min.	Mean	Max.	Std. dev.
Diameter at breast height (cm), DBH	5.4	14	26.8	5.6	10.8	26.39	42.2	7.9
Diameter at breast height / Total height, D/H	0.64	1.05	1.48	0.17	0.79	1.32	2.20	0.30
Total tree height (m), Ht	5.5	13.2	20.8	4.4	13.3	20.4	32.3	4.7
Dominant Height (m), HD	9.2	15.6	20.5	3.6	15.6	22.9	31.6	4.4
Quadratic mean DBH (cm), QDBH	5.8	11.4	26.8	3.7	15.4	25.4	35.2	5.9
Site index (height in m at 50 years old), SI	9.5	14.6	17.7	2.1	15.8	20.3	27.5	3.0
Stand age (years at 1m height), age	20	70	120	28.4	45	73	140	26.3
Stand basal area (m²/ha), G	10.0	29.8	47	9.8	13.2	29.8	68.2	14.4
Stand density (stems ha⁻¹), SPH	921	3697	11263	2478	136	912	3657	953

*Min. = minimum; †Max. = maximum; and ‡Std. dev. = standard deviation.

Table 1.3 Branch and crown characteristics for sample trees (774 branches from 65 white spruce trees, 565 branches from 57 black spruce trees)

Branch/Crown characteristic	Black spruce				White spruce			
	Min.*	Mean†	Max‡.	Std. dev.	Min.	Mean	Max.	Std. dev.
Crown length (m)	1.5	6.4	14.5	2.8	1.7	8.1	16.7	3
Branch angle (°)	10	75	180	19	0	76	170	20
Branch diameter (mm)	1	7	40	5	1	13	72	10
Branch length (cm)	3	82	350	52	7	145	482	86
Estimated branch length (cm)	0	49	288	40	4	86	487	71

*Min. = minimum; †Max. = maximum; and ‡Std. dev. = standard deviation.

Table 1.4 Parameter estimates for branch length equations (Eq. 1.3 and Eq. 1.4), crown length equation (Eq. 1.6) and crown radius equation (Eq. 1.8)

Parameters	Parameter Estimates (p-Values)				
	Eq. 1.3 Black spruce	Eq. 1.4 White spruce	Eq. 1.6 Black and white spruces	Eq. 1.8 White spruce	Eq. 1.8 Black spruce
β_1	8.9515 (0.0091)	17.1253 (0.0000)	-0.4752 (0.0000)	-0.1257 (0.001)	0.7582 (0.0000)
β_2	0.6768 (0.0000)	0.7623 (0.0000)	-1.9270 (0.0001)	-0.0091 (0.0000)	-0.0191 (0.0000)
β_3	0.04605 (0.0000)	0.3008 (0.0000)	-0.0237 (0.0000)	0.3467 (0.0000)	0.5549 (0.0000)
β_4	0.03501 (0.0193)	NA	NA	-0.0124 (0.0000)	-0.0216 (0.0000)
β_5	NA	NA	NA	0.0159 (0.0000)	-0.0213 (0.0000)
β_6	NA	NA	NA	0.0002 (0.0000)	0.000017 (0.0000)
σ^2site	0.0000	0.0362	0.4170	0.0151	0.0005
σ^2plot	0.0005	0.0186	1.4978	0.0188	0.0005
σ^2tree	0.0028	0.0327	NA	0.0293	0.0114
$\sigma^2\varepsilon$	630.9642	1026.0939	34.6018	0.2200	1.8904
RMSE (all errors combined)	16.77	22.31	2.09	0.3478	0.1864

* NA = not applicable
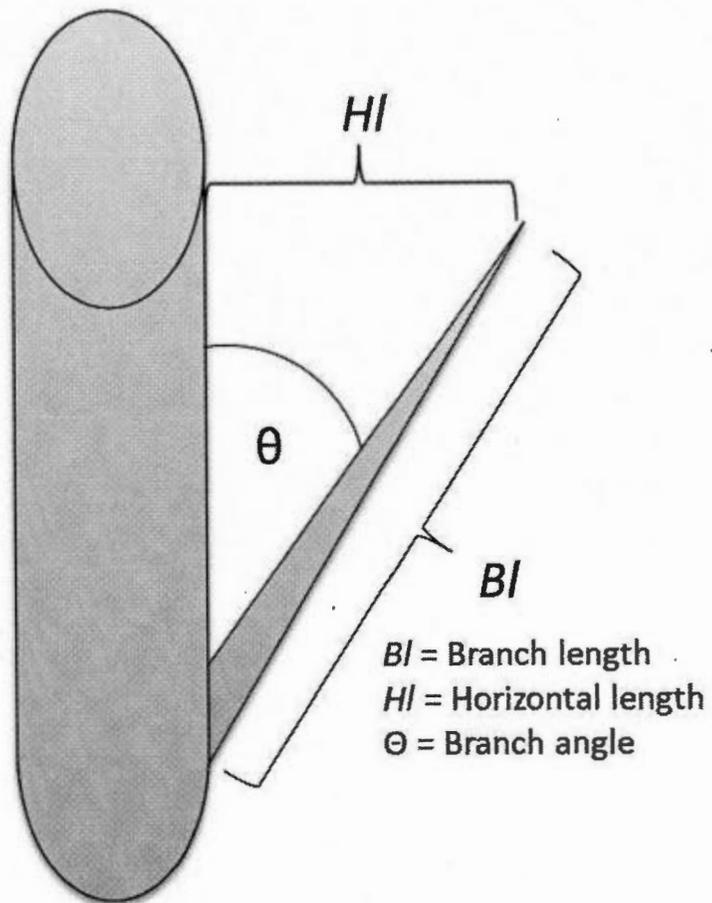
Figure 1.1 Relationship between horizontal length, branch length and branch angle.
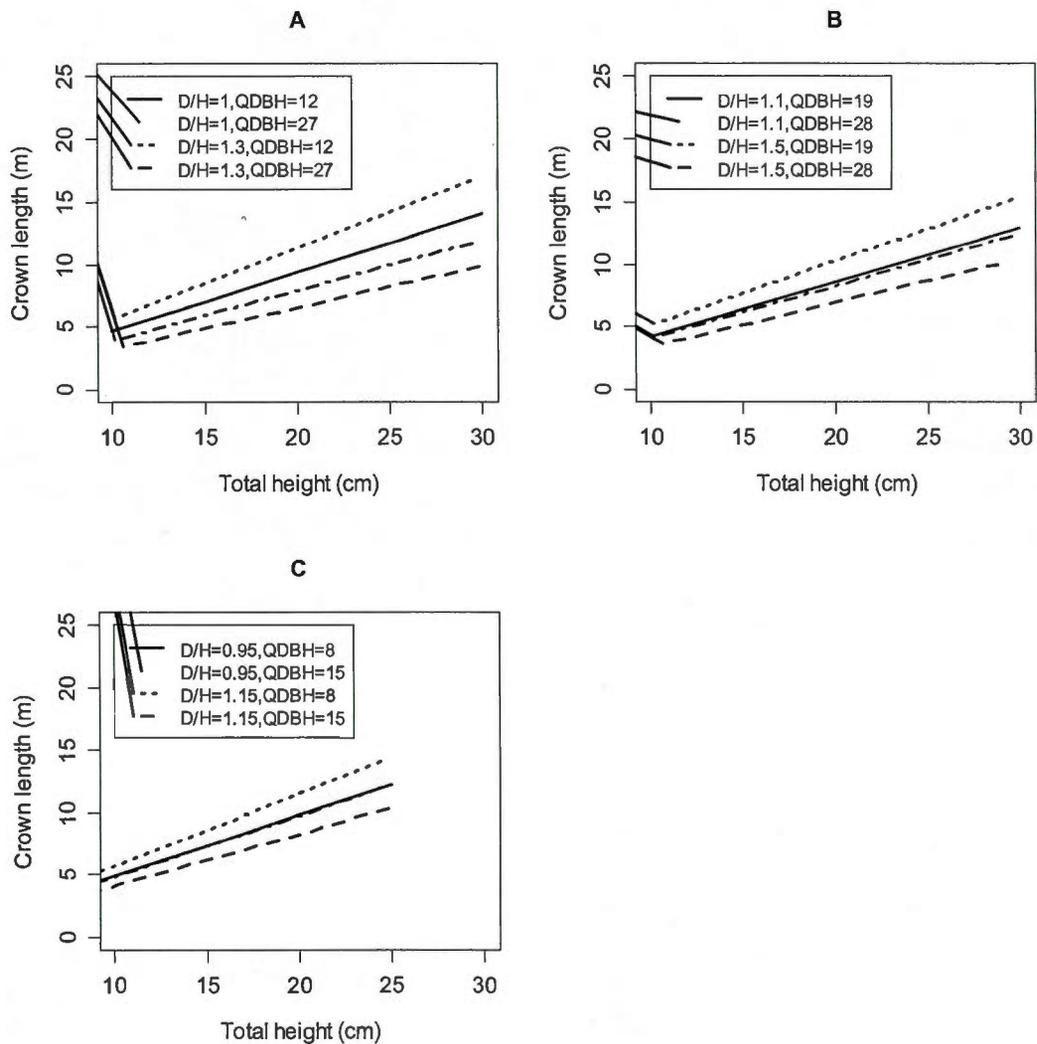
Figure 1.2 Crown length models A) Crown length model under comparable growth condition; B) Crown length model under white spruce specific growth condition; C) Crown length model under black spruce specific growth condition.
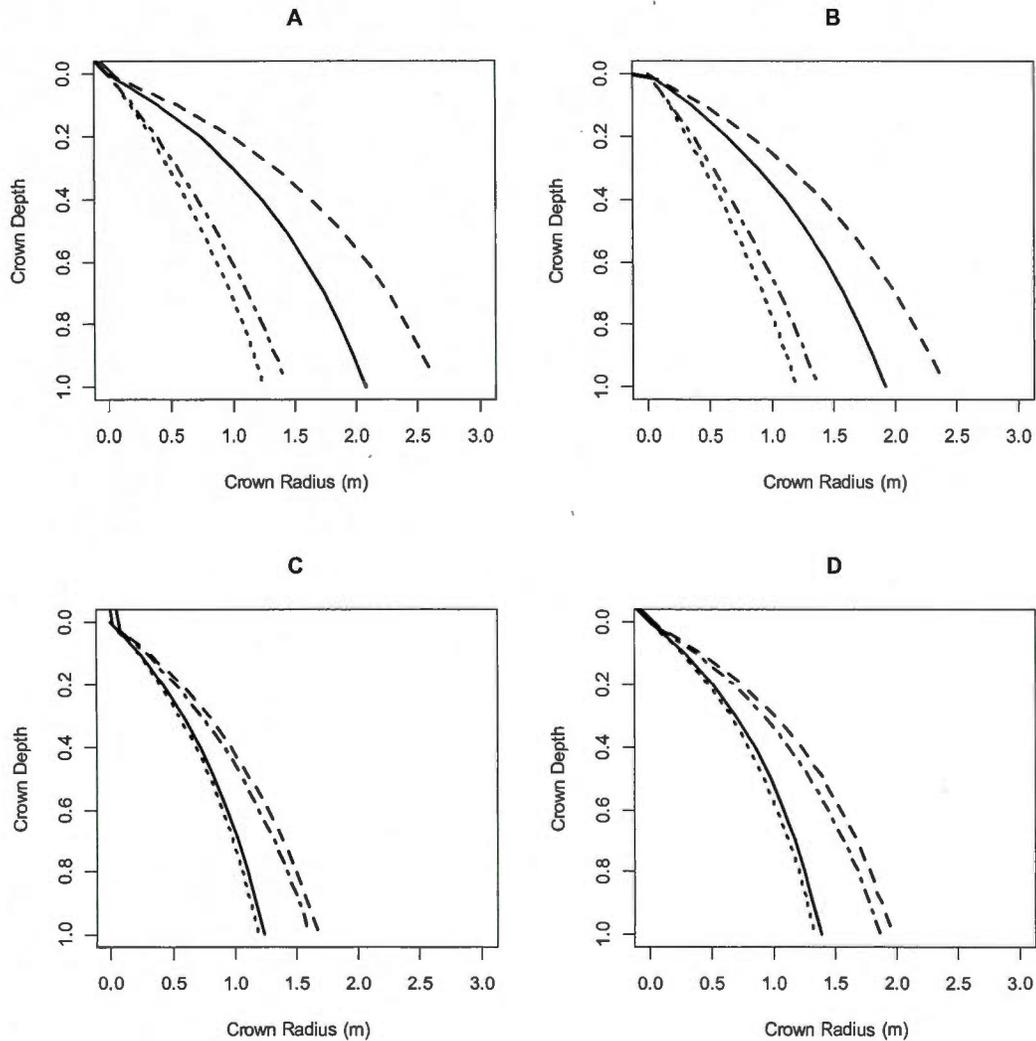
Figure 1.3 Crown radius over depth for crown lengths and stand density of 5 m and 500 stems ha^{-1} (solid line), 10 m and 500 stems ha^{-1} (dashed line), 5 m and 2500 stems ha^{-1} (dotted line), 10 m and 2500 stems ha^{-1} (dashed with dots) for: A) white spruce, site index (SI)=15 m; B) white spruce, SI=20 m; C) black spruce, SI=15 m; and D) black spruce, SI=20 m.
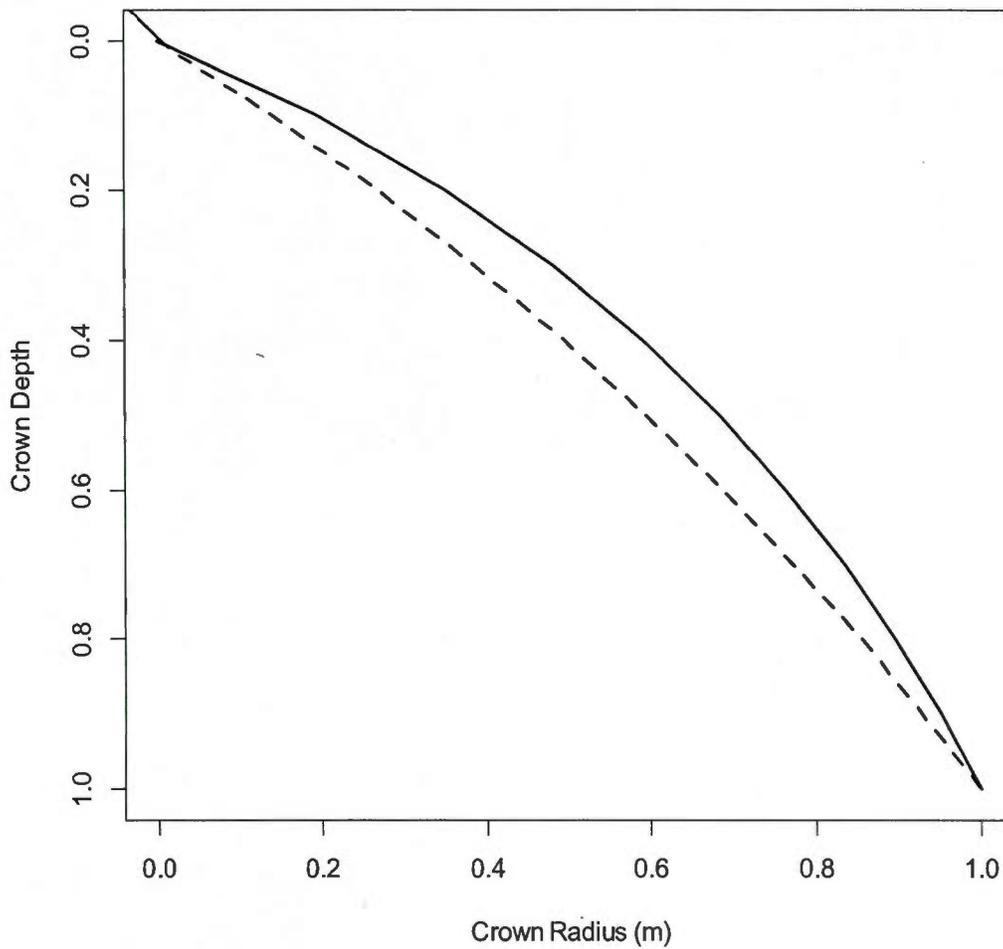
Figure 1.4 Relative crown radius over crown depth for black spruce with stand density of 500 stems ha^{-1} , 2500 stems ha^{-1} and for white spruce with stand density of 500 stems ha^{-1} (solid line), relative crown radius over crown depth for white spruce with stand density of 2500 stems ha^{-1} (dashed line).
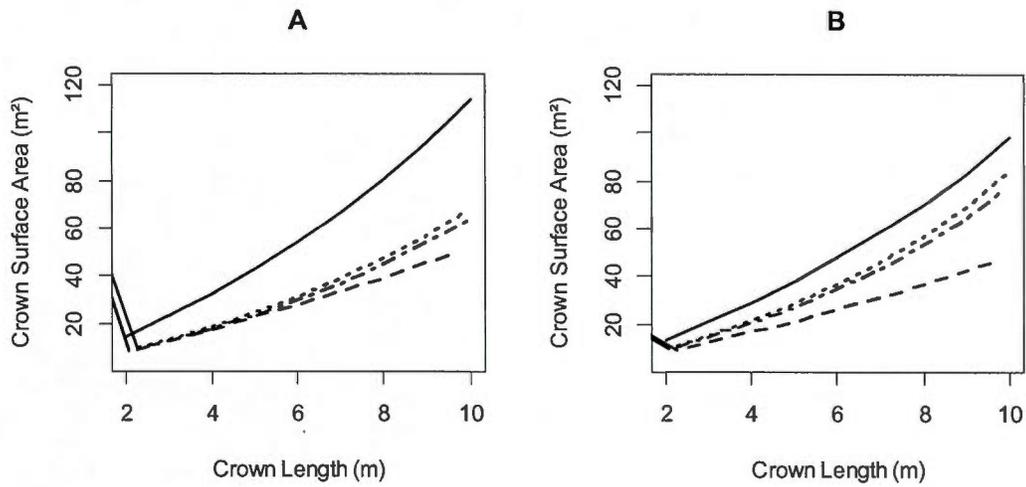
Figure 1.5 Crown surface area for white spruce with 500 stems ha^{-1} (solid line) and 2500 stems ha^{-1} (dashed), black spruce with 500 stems ha^{-1} (dotted) and 2500 stems ha^{-1} (dashed and dotted) for: A) site index (SI) = 15 m and B) SI = 20 m.

CHAPITRE II

COMPARISON OF THREE DIFFERENT FOLIAGE BIOMASS

CHARACTERISTICS OF BLACK (*PICEA MARIANA*) AND WHITE

SPRUCE (*PICEA GLAUCA*)

Hugues Power, Robert Schneider, Frank Berninger

2.1   Résumé

Notre étude vise à modéliser et à comparer la biomasse foliaire totale, la densité de la biomasse foliaire et la distribution verticale relative de l'épinette noire (*Picea mariana* (Miller) BSP) et de l'épinette blanche (*Picea glauca* (Moench)Voss). Un total de 57 épinettes noires et de 65 épinettes blanches ont été échantillonnés de manière destructive sur quatre sites localisés en Alberta, en Ontario et au Québec. Des modèles linéaires et non linéaires mixtes ont été utilisés pour modéliser et comparer les caractéristiques du feuillage des deux espèces. Nos résultats ont montrés que l'épinette noire avait une biomasse foliaire totale plus grande que l'épinette blanche lorsque les conditions de croissance étaient prises en compte. Pour les deux espèces, une augmentation du rapport entre le diamètre de la tige et la hauteur totale de l'arbre et de la profondeur dans la cime vivante a amené une augmentation de la biomasse foliaire totale. La densité de feuillage s'est avérée plus grande pour l'épinette noire reflétant sa plus grande tolérance à l'ombre. Aucune différence n'a été trouvée entre les espèces quant à la distribution verticale relative de biomasse foliaire, et ce, même si l'âge de l'arbre entrainait un déplacement de la distribution vers le sommet de l'arbre et que l'indice de qualité de station produisait l'effet inverse.

2.2   Abstract

Our study modelled and compared black (*Picea mariana* (Miller) BSP) and white (*Picea glauca* (Moench) Voss) spruces in terms of their total foliage biomass, foliage biomass density, and foliage biomass relative vertical distribution. A total of 65 white spruce and 57 black spruce trees were destructively sampled at four different locations in Alberta, Québec and Ontario, Canada. Linear and non-linear mixed-models were used to model and compared the foliage biomass characteristics of the two species. Our results show that black spruce had a larger total foliage biomass than white spruce, even when accounting for growth conditions. For both species, an increase in stem diameter, total height ratio, and crown depth induced an increase in tree total foliage biomass. The foliage biomass density was also found to be higher for black spruce, tending to affirm its higher shade tolerance. No differences were found between species in their cumulative relative vertical foliage biomass distributions, even if tree age skewed foliage distributions toward the tops of the trees while site index had the opposite effect.

2.3   Introduction

Black spruce (*Picea mariana* (Miller) BSP) and white spruce (*Picea glauca* (Moench) Voss) are two prominent conifer species of the North American boreal forest (Burns and Honkala, 1990), a biome that occupies 310 million hectares and represents 10 percent of the world's forest cover (Canadian Forest Service 2005). The ranges of the two species extend from 69°N in Canada to 35°N in the US states of New York, Vermont and New Hampshire, and from the Atlantic coast in the east to the Bering Sea at their westernmost boundaries. Both species also grow to their full potential on cool and moist mineral soils, but black spruce has adapted to wet organic soils that are commonly found in more northerly locations (Burns and Honkala, 1990; Larsen, 1980). Although they have the same geographical distribution and can grow on the same type of soil, the two species have different functional traits.

Differences have been noted between black and white spruce with regards to leaf form, shade tolerance and crown characteristics. Both species have quadrangular needles, although white spruce needles are about twice as long as those of black spruce (Marie-Victorin, 1995). The shade tolerance of black spruce is considered to be intermediate to high, while white spruce is generally considered slightly less shade-tolerant (Burns and Honkala 1990). Black spruce reaches photosynthetic light saturation under more shaded conditions than does white spruce (Grossnickle, 2000; Man and Lieffers, 1997). Moreover, black spruce shows a stronger growth response to increased CO_2 concentrations under shaded conditions (Marfo and Dang, 2009), indicating higher shade tolerance. The maximum crown width of black spruce has been reported as narrower than that of white spruce (Power et al., 2012).

Differences in wood production have also been reported. On sites of the same quality, stem wood production is higher in white than in black spruce (Pothier and Savard, 1998; Thiffault et al., 2003). Stem growth and tree productivity, in turn, can be linked to foliage biomass via photosynthesis (Landsberg and Gower, 1997). Moreover, in carbon allocation models, allometric relationships with foliage biomass are central and necessary to predict growth of all tree components (Mäkelä, 1997).

Total foliage biomass of black and white spruce can be compared using tree-level biomass equations. The equations of Ung et al. (2008) predict greater foliage biomass for white spruce than for black spruce when taking stem diameter at breast height (DBH) and total tree height (Ht) into account. However, Alemdag's equations (1982) predict the opposite trend. These differences could be explained by tree and stand characteristics that were not included in the studies.

For various tree species of the boreal forest, including black spruce, Bond-Lamberty et al. (2002) added tree age as a covariate along with DBH to predict tree total foliage biomass. Porte et al. (2000) used the same two variables to model leaf area in maritime pine (*Pinus pinaster* Aiton). The authors of both studies found that tree total leaf area increased with DBH and diminished with tree age. In another study, Maguire and Bennett (1996) used crown length, together with the ratio between DBH and total height (i.e., D/H), to model total foliage biomass in coastal Douglas-fir (*Pseudotsuga menziessi* var. *menziesii* (Mirbel) Franco). As expected, foliage biomass increased with crown length and D/H. The increase of foliage biomass with D/H can be associated with an increase in foliage biomass density. Foliage biomass density has been known to vary with species and tree social class. Indeed, Zeide and Pfeifer (1991) found differences in foliage biomass density among species; shade-intolerant species tended to have lower quantities of foliage biomass per unit of crown surface than shade-tolerant species. Messier et al. (1999) found that shaded trees have lower foliage biomass densities. In addition to species and tree position within the stand, silvicultural treatments have been found to influence total tree foliar biomass. Gillespie et al. (1994) noted an increase in total foliar biomass for a given DBH after thinning and fertilization.

Because the interception of photosynthetically active radiation by the tree is directly related to photosynthesis (Oker-Blom et al., 1989) and because the light interception is not only influenced by the quantity, but also by the distribution of foliage within the tree (Oker-Blom and Kellomaki, 1983), another characteristic of foliar biomass, i.e., its vertical distribution, has also been the subject of research. A shift in foliage towards the base of the tree has been noticed for dominant trees, demonstrating the effect of the social class on

vertical foliage biomass distributions (Garber and Maguire, 2005; Gillespie et al., 1994; Maguire and Bennett, 1996; Mäkelä and Vanninen, 2001). Shade tolerance of the species and stand density are two other characteristics that can interact to influence the vertical distribution of foliage biomass. Intolerant species can exhibit an upwards shift in foliage biomass distribution when competition increases (Garber and Maguire, 2005). Stand age can also skew cumulative relative foliage biomass distributions towards the tops of the trees (Schneider et al., 2011).

Many studies have looked at foliage biomass, but only a few authors, to our knowledge, have reported results for black and white spruce. This paucity of information is surprising because the two species are both ecologically and economically important. Further, characterization of foliage biomass is important in understanding tree growth. In this study, we characterized and compared the foliage biomass of black and white spruce in three steps. First, we constructed a model to compare the total foliage biomass of black and white spruce trees. Second, we constructed a model to compare the foliage biomass density of the two species. Third, we compared the relative cumulative vertical distribution of foliage biomass between species. Since growth conditions are known to influence foliage biomass characteristics, we also analyzed and compared their effects on foliage biomass characteristics for each species.

2.4   Materials and methods

2.4.1   Data

The data set includes 65 white spruce and 57 black spruce trees, which were sampled between the 2008 and 2010 growing seasons. The white spruce data were obtained from sites that were located in Ontario and Alberta, Canada, whereas data for black spruce were collected in Quebec, Canada (Table 2.1).

At the Alberta site, sampled stands were pure white spruce or spruce-dominated stands that contained a minor component of trembling aspen (*Populus tremuloides* Michaux). The stands were located in east-central Alberta, north of Lac La Biche, within the central mixedwood natural sub-region (Beckingham and Archibald, 1996), and included 0.1 ha permanent sample plots (PSPs). These stands had developed from natural regeneration and were not influenced by silvicultural treatments. The three selected stands represented a range of densities; however, all stands were located on mesic soils with medium fertility. A minimum four dominant or co-dominant trees that had undamaged crowns and were adjacent to the PSPs were selected at each location for the collection of crown measurements. Each selected tree served as the centre of a circular plot (5.64 m radius). Within the plot, the outside bark-DBH (diameter at breast height, 1.3 m) and total tree height were measured and species was recorded on all live trees $\geq$ 7.5cm DBH. Because the Alberta stands were mature stands, the number of stems with a DBH < 7.5cm was minimal and these stems did not compete with the trees from the main cohort. Stand age for each sample location was calculated as the mean of sample tree ages. The data from the fixed-radius plots were used to calculate plot-level variables that are summarized in Table 2.2.

White spruce trees from Ontario were sampled from existing plantations in Petawawa Research Forest. The stands had received spacing or thinning treatments; however, the last thinning was done in 1982 and growth was assumed to be similar to that of nearby natural white spruce-dominated stands. Sample trees from the Ontario site were taken inside or along the periphery of existing square PSPs, which ranged from 0.03 to 0.08 ha in size. For all live trees $\geq$ 1.1 cm DBH in the PSP, the species was recorded and the DBH was re-measured; heights of the previously measured trees were re-measured. Trees were divided into small, medium and large classes by DBH, each class including the same number of trees. One tree was selected from each of the small and large DBH classes and two trees were selected from the medium DBH class, resulting in four trees per plot. Sample trees were limited to those with undamaged crowns. Stand age was the plantation age adjusted to an age at 1 m above-ground, using estimates provided by Pothier and Savard (1998). The measurements for all live trees in each PSP were used to calculate the plot-level variables summarized in Table 2.2.

Black spruce trees from Quebec were selected from stands that had naturally regenerated following clear-cutting or a stand-replacing fire. Stands of different ages, densities (i.e., trees per ha), and site indices were selected using forest stand maps from Québec's government for Lac-St-Jean and Temiscamingue regions. For each selected stand, a variable-radius plot with basal area factor of $1 \text{ m}^2 \text{ ha}^{-1}$ was established at a location that had been previously determined on the forest map. The species was recorded and DBH was measured for all live trees ≥ 1.1 cm DBH. As was the case with white spruce from Ontario, trees in the plot were divided into small, medium and large trees by DBH. For each plot, one sample tree was selected from each DBH class, resulting in three trees per plot. Also, height was measured for 20 to 90 trees across DBH classes. The ages at 1 m height above-ground for three dominant and undamaged trees of the target species were recorded, averaged, and used as the estimate of stand age. Information that had been gathered from the variable-radius plots was used to calculate the plot-level summary statistics (Table 2.2).

For all sites, selected sample trees were felled. Height and height to live crown were measured on trees after felling. Height to live crown was considered as the height of the lowest branch that displayed green foliage and above which all whorls included at least one living branch. The vertical position of each live branch along the tree bole (i.e., main stem) was recorded. Basal diameter, insertion angle, and nodal or inter-nodal status were recorded for each living branch.

The crowns of the felled trees from Quebec and Ontario were divided in 10 sections of equal length. In each of the sections, one sample branch was randomly selected among the living branches with the use of a random table. The length of each sample branch was measured. For one section over two (odd or even) the selected sample branch was collected for biomass study. The crowns of the felled trees from Alberta were divided in two parts of equal length. Ten living branches were randomly selected in each section for length measurement. The random selection of the branches was made from a random sampling performed after the measurement of all the living branches. In each section, three of the ten sample branches were randomly selected and collected for the biomass study. After being transported in paper bags from the field to the laboratory and drying at room temperature for

several weeks, the needles of the sample branches were removed and oven-dried (24 h at 60°C) before being weighed.

Sample data were compiled to obtain the plot and tree variables used in modeling and examining foliage biomass (Table 2.2). All plot-level variables were expanded to per ha measures. Although minimum DBH that was measured differed between the plots from Alberta ($\geq$ 7.5 cm DBH) and those from Ontario and Quebec ($\geq$ 1.1 cm DBH), no attempt was made to correct for this difference in calculating plot-level variables, since all trees on these plots from Alberta were mature individuals. Therefore, the numbers of stems from 1.1 to 7.5 cm DBH were expected to be small and their effect on quadratic mean DBH or stand density was considered negligible. Further, since a model-based approach, rather than a design-based approach, was used in this study to compare and contrast tree crowns of the two spruce species, no weights were included to account for differences in plot sizes in any models. Hierarchical mixed-effects models were performed to estimate site-, plot- and tree-level variances, thereby accounting for correlations of plots within-sites, trees within-plots and heteroscedasticity due to different levels of sampling.

Heights (HT) of the remaining trees in each plot were estimated with a species-specific model that has been already published by Power et al. (2012) and reproduced in the Appendix, using plot-specific predictions.

For all sites, dominant height (HD, m) was calculated by averaging the height of the 100 largest trees per hectare. Quadratic mean DBH (QDBH, cm), stand density (stems ha^{-1}), and stand basal area (m^2 ha^{-1}) were calculated for each plot, excluding saplings that did not compete with the main cohort of the stand. The site index (SI; site height at 50-years-old) for each plot was calculated using HD and stand age within SI equations estimated by Pothier and Savard (1998).

To estimate foliage biomass of all living branches, we applied a mixed-model of foliage biomass at the branch level, using tree- specific foliage biomass predictions. The foliage biomass model at the branch level is presented in the Appendix. Total foliage biomass was

calculated for each tree by summing predicted foliage biomass of all its living branches. Cumulative foliage biomass was estimated by summing estimated foliage biomass of every living branch that was located between the apex and any vertical position inside the living crown of the sample trees. Height to live crown was considered as the height of the lowest branch that displayed green foliage and above which all whorls included at least one living branch. In the case where living branches were located below the crown base, foliage biomass was reported at crown base.

We applied two different methods for estimating crown surface area (Cs, m^2). First, the surface area of each crown section was estimated with Eq. 2.1. Crown sections were defined as a crown segment that included the nodal branches of a whorl and the inter-nodal branches located between the section's whorl and the next whorl below the section's whorl.

$$(2.1) \quad Cs_{ijk} = \sum_{l=1}^{l=n} \pi(Cr_{ijkl} + Cr_{ijkl+1}) * a_{ijkl}$$

where Cr_{ijkl} is the crown radius (m) of the lth crown section in tree k in plot j in site i; Cr_{ijkl+1} is the crown radius of the section below the lth section; a_{ijkl} is the apothem between the lth and $l^{th}+1$ crown section in tree k in plot j in site i, and n is the number of crown sections in the sample tree.

The second method for estimating crown surface area attempted to fit a crown radius equation and integrate it over the crown length of the sample trees. The methods used to parameterize the crown radius equation and to calculate the crown surface area from the crown radius equation are presented in Power et al. (2012) and have been reproduced in the Appendix.

2.4.2 Foliage biomass analysis models

Parameterization of the linear and non-linear mixed-effects models was respectively performed with the lme and nlme functions of R (Pinheiro et al. 2010). For all models, the error terms at the site-, plot- and tree-level were each assumed to follow normal distributions with the hierarchical structure of trees nested in plots and plots nested in sites accounting for any correlations. The final error terms were assumed to be "white-noise" errors that were independent and identically normally distributed. However, the assumption of equal variance was checked using residual plots and a function to model the variance of the residuals was added to the mixed-effects model when warranted (Pinheiro et al. 2010).

For each mixed-model, an initial equation was parameterized after first consulting the literature and graphically examined the relationship between the predicted variable and the tree and stand variables in Table 2.2. The residuals and random effects of the initial equation were graphed against the remaining plot- and tree-level variables that are presented in Table 2.2. Plot- and tree-level variables that showed non-random pattern with random effects at the tree levels of tree-, plot or site levels were added to the model in an additive or multiplicative form. A likelihood-ratio test was performed to assess whether the added variable improved model fit. The likelihood ratio test allows us to perform a hypothesis test on the fit of two models in which one of the two models is a special case of the other. We adopted $\alpha = 0.05$ as our level of significance for determining if a given model performed better than another model. Models that used the same number of explanatory variables were ranked using the AIC (Akaike Information Criterion; Akaike 1973) in order to select the model to be retained.

A power function using stem DBH was first fitted to the pooled data for both species. After finding the best model for predicting total foliage biomass (Wf) of the pooled black and white spruce data (Eq. 2.2), we introduced dummy variables coding for species (0, 1) onto each parameter in Eq. 2.2. Non-significant dummy variables were withdrawn one at a time, beginning with the least significant one. At each subsequent step, the model was re-parameterized and compared using a likelihood-ratio test against the model containing all of

the dummy variables. If the likelihood-ratio test was non-significant, we retained the model with fewer variables and repeated the operation until only significant dummy variables remained (Eq. 2.3). The final model that included dummy variables was compared against the pooled data model with a likelihood-ratio, to test for differences between black and white spruces. This modeled based approach allowed the use of non-linear equations, which are frequently used in allometry, to compare the two species.

$$(2.2) \qquad Wf = \beta_1 DBH^{\beta_2} * Ht^{\beta_3} * Cl^{\beta_4} + \varepsilon_i + \varepsilon_{j(i)} + \varepsilon_{k(ij)}$$

$$(2.3) \qquad Wf = (\beta_1 + \beta_{11} Dm) DBH^{\beta_2} * Ht^{(\beta_3 + \beta_{33} Dm)} * Cl^{\beta_4} + \varepsilon_i + \varepsilon_{j(i)} + \varepsilon_{k(ij)}$$

where Cl is the tree crown length (m); Dm is a dummy variable with a value of 0 for black spruce and 1 for white spruce; ijk is the subscript for tree k in plot j in site i; β_1 to β_{33} are fixed-effect parameters; ε represents the error terms of the model at the site- (ε_i), plot-within-site ($\varepsilon_{j(i)}$), and trees-within-plot levels ($\varepsilon_{k(ij)}$).

We defined crown foliage biomass density as the ratio between foliage biomass and crown surface area (Mizoue and Masutani, 2003). Before estimating crown foliage biomass density, the two methods of crown surface area estimation were compared for their ability to predict tree foliage biomass. A linear mixed-effect model that predicted foliage biomass was fitted separately to each $\log_e$-transformed estimator of crown surface area (Eq. 2.4). We used the logarithmic transformation because it more efficiently corrected for heteroscedasticity and non-normality of the residuals than any variance function of the tree-level residuals that was added to the model. The predictions of Eq. 2.4 for each estimator, using the fixed effects only, were re-transformed back to the original scale used before the comparison. The predictions were corrected to account for bias that is incurred during back-transformation from a logarithmic scale (Sprugel, 1983). The efficiency of the two variables in predicting foliage biomass was compared on the basis of their root-mean-square-errors (RMSE).

$$(2.4) \quad \ln Wf = \beta_1 + \beta_2 \ln Cs + \varepsilon_i + \varepsilon_{j(i)} + \varepsilon_{k(ij)}$$

where $\ln Wf$ is the natural logarithm of total foliage biomass for an individual tree; $lnCs$ is the natural logarithm of the sample tree's crown surface area; ijk are the subscripts for the kth tree

in plot j in site i; β_0 and β_1 are fixed effect coefficients; ε represents the error terms of the model at the levels of site (ε_i), plot-within-site ($\varepsilon_{j(i)}$), and trees-within-plots ($\varepsilon_{k(ij)}$).

The crown surface area estimator exhibiting the best performance in estimating foliage biomass was used to calculate and analyze foliage biomass density. This estimator was used, assuming that it provided a better estimate of Cs. Using the selected crown surface area estimator, the same method of model construction and model selection for Eq. 2.2 and Eq. 2.3 was applied to modeling foliage biomass density. Equations 2.5 and 2.6 are, respectively, the pooled data and dummy species variable models for foliage biomass density (*Fd*).

$$(2.5) \quad Fd = \beta_1 + \beta_2 D / H + \varepsilon_i + \varepsilon_{j(i)} + \varepsilon_{k(ij)}$$

$$(2.6) \quad Fd = (\beta_1 + \beta_{11} Dm) + (\beta_2 + \beta_{22} Dm) D / H + \varepsilon_i + \varepsilon_{j(i)} + \varepsilon_{k(ij)}$$

where *Fd* is foliage biomass density (g/m²); *Dm* is a dummy variable for species (0 for black spruce, 1 for white spruce); β_0 to β_1 are fixed coefficients; *ijk* is the subscript for the kth tree in plot *j* in site *i*; ε represents the error terms of the model at the level of site (ε_i), plot-within-site ($\varepsilon_{j(i)}$), and trees-within-plot ($\varepsilon_{k(ij)}$).

Foliage biomass of each crown section was first estimated, after which relative cumulative foliage biomass (Crwf) was calculated, assuming that it followed a beta cumulative density function (Eq. 2.7). For each sample tree, a beta cumulative distribution function (Eq. 2.8) was fitted to cumulative relative foliage biomass. The beta distribution was fitted with the gnls function in the nlme package of R (Pinheiro et al. 2010). One outlier was removed from the data set. The outlier, which was a white spruce from Alberta, had the

deepest crown of the data set. The estimated value of the q parameter for this individual was 18.2, while the next largest estimate of q was 4.33.

$$(2.7) \quad Crwf_{l(ijk)} = \frac{\sum_{l}^{n} Wfs_{l(ijk)}}{\sum_{0}^{n} Wfs_{l(ijk)}} = F(Cd \mid p,q) + \varepsilon_{ijkl}$$

$$(2.8) \quad F(Cd \mid p,q) = \frac{\int_{0}^{Cd_{ijkl}} Cd^{p-1}(1-Cd)^{q-1} dCd}{\int_{0}^{1} Cd^{p-1}(1-Cd)^{q-1} dCd}$$

where *Crwf* is the cumulative relative foliage biomass; *Wfs* is the crown section foliage biomass; n is the first crown section at the top of the tree; *Cd* is relative crown depth, which has a value of 0 at the top of the tree and 1 at crown base; the subscripts *ijkl* are the subscripts for crown section l in tree k, in plot j in site i; p and q are shape parameters of the distribution; and ε is the random error term.

In order to estimate the effect of species and growth conditions on the two parameters of the beta distribution, a mixed-model of p and q parameters was simultaneously parameterized with a two-member equation using dummy variables for the parameters p and q (Eq. 2.9).

$$(2.9) \; Y_{ijk} = Dmp(b_{ip} + b_{jp(i)} + \beta_1 SI^{\beta_2} + \beta_3 Age) + Dmq(b_{iq} + b_{jq(i)} + \beta_4 SI^{\beta_5} + \beta_6 Age) + \varepsilon_{ijk}$$

where Y is alternatively the p or q parameter of the beta function; *Dmp* is a dummy variable equal to 1 when Y is a p parameter, and 0 when Y is a q parameter; *Dmq* is a dummy variable equal to 1 when Y is a q parameter, and 0 when Y is a p parameter; β_0 to β_5 are fixed-effect parameters; b_p is a random parameter used to estimate the p parameter; bq is a random parameter used to estimate the q parameter; ε is the random error term; and *ijk* are the subscripts for the kth tree in plot j in site i.

After obtaining estimates of the parameters from Eq. 2.9 where data for both species were pooled, Eq. 2.9 was parameterized for each species individually. The predicted parameters p and q from the pooled and species-specific equations were inserted into the beta function to predict cumulative foliage biomass. The predictions of cumulative foliage

biomass were then compared with the observed data. The sums-of-squares error (SSE) for the equation with the pooled species equation was compared to the SSE that was obtained for the predictions made with the species-specific equations to assess differences between species.

2.5   Results

2.5.1   Total foliage biomass

Total foliage biomass relationship differed significantly between black and white spruce (log-likelihood ratio test: χ^2 = 15.55, df = 2, P = 0.004), as indicated by the respective likelihood estimates for Eq. 2.2 (-1118.964) and Eq. 2.3 (-1111.166). The RMSE of final model of foliage biomass at the tree level (Eq. 2.3) was 3 578 g (Table 2.3). For the same values of DBH, Ht and Cl, black spruce has a greater foliage biomass than does white spruce (Fig. 2.1). For both species, tree foliage biomass increases non-linearly with DBH, showing a much faster increase in foliage biomass for trees with large DBH (Fig. 2.1). Moreover, for specified values of DBH and crown length, foliage biomass of both species diminishes greatly with total height, while an increase in crown length for fixed values of DBH and height implies an increase in foliage biomass (Fig. 2.1).

The accuracy of foliage biomass predictions differed between the two methods of crown surface area estimation. Crown surface area that was estimated using the summation of crown section surfaces (Eq. 2.1) showed the best values of RMSE (4 kg) and AIC (80.2), while the method using the crown radius function produced, for the same statistics, values of 5.2 kg and 145.16. Predictions of foliage densities with the first method had means (and standard deviations) of 127.8 g/m² $\pm$ 43.7 g/m² for black spruce and 106.2 g/m² $\pm$ 34.9 g/m² for white spruce, respectively.

2.5.2   Foliage biomass density

Foliage biomass density differs between the two species (Log-likelihood-ratio test: $\chi^2 =$ 10.95, df = 2, P = 0.0042), based on the respective likelihood estimates for Eq. 2.6 (likelihood = -603.9045), which included species dummy variables, and Eq. 2.5 (likelihood = -609.3810), which was our null or pooled species model. The RMSE of Eq. 2.6 was 36.2 g/m² (Table 2.3). Black spruce generally has a higher foliage biomass density than white spruce (Fig. 2.2). Increasing values of D/H positively influence the foliage biomass density of both species, but the slope of the relationship is steeper for black spruce, implying a faster increase in foliage density with D/H for this species.

Our results suggest that there is no appreciable difference between black and white spruce in their vertical distributions of cumulative relative foliage biomass, when SI and age were taken into account. Indeed, the SSE for the pooled species cumulative relative foliage biomass distribution was only slightly higher than the sum of its values for black and white spruce species-specific equations (23.00 and 22.98, respectively). RMSE for the prediction of cumulative relative foliage biomass vertical distribution is 0.081, regardless of whether both species were pooled or its value is calculated from the separate equations for each species.

2.5.3   Cumulative relative foliage biomass vertical distribution

Both p and q parameters of the beta distribution have a positive relationship with site index and a negative relationship with tree age (Table 2.3, Fig. 2.3), implying that trees located on richer sites have a cumulative relative foliage biomass vertical distribution that is skewed toward the base of the trees, while older trees have a cumulative relative foliage biomass vertical distribution that is skewed towards the top of the trees (Fig. 2.3).

2.6   Discussion

A wide range of tree sizes, densities, and site indices contributed to our results. However, even if the sample method differed between sites, standardization of the stand-level variables and the use of mixed-models allowed us to analyze the combined data from different sites. To our knowledge, no other study has directly compared black and white spruce foliage characteristics. This comparison is useful, given the importance of these two species and the importance of characterizing foliage to better understand growth, biomass distribution, and resource allocation.

2.6.1   *Variation in foliage biomass and foliage biomass density*

Our model of total foliage biomass showed that, for a given value of DBH, height and crown depth, black spruce had a greater quantity of foliage biomass than did white spruce. This result was consistent with that of Alemdag (1982) but contrary to that predicted from the biomass equations of Ung et al. (2008). This difference in results was surprising given that the study of Ung et al. (2008) included 1591 black spruce and 931 white spruce, which were located all over Canada, while Alemdag's (1982) study only included 74 black and 77 white spruce from two locations in Ontario. Both of these studies only used DBH and height to model foliage biomass, while our model also took into account crown length. Differences in the explanatory variables that the previous authors used and those that we used have complicated comparisons between the models. This was especially true in our case because the multiplicative form of the models implied strong correlations among the effects of the explanatory variables. Moreover, the biomass of twigs was included with the foliage in the two previous studies, while foliage biomass only included needles in our study. These differences in the definition of foliage biomass likely explained to a great extent differences in the results. Consequently, a larger quantity of needle biomass per unit twig length for black spruce could also explain, in part, the overall greater foliage biomass density for black spruce compared to that of white spruce.

The larger amount of total foliage biomass for black spruce when accounting for DBH, total height, and crown length could be interpreted as a greater foliage biomass density. This result was confirmed by Eq. 2.6, as represented in Figure 2.2. The greater foliage density of black spruce could be explained by the difference in shade tolerance exhibited by the two spruce species. This explanation was consistent with that of Zeide and Pfeifer (1991), who found that shade-tolerant species tended to have a higher foliage biomass density than shade-intolerant species. Our result was also consequent with those of Popma and Bongers (1988), who found that tolerant species had a higher leaf area ratio than that of intolerant species.

Our predictions that total foliage biomass would increase with DBH and crown length but diminish with total height were in agreement with the findings of Maguire and Bennett (1996). This result can be interpreted as an effect of tree canopy position and dominance class. Lower total height values that were associated with constant values of crown length and stem DBH have implied increases in D/H and crown ratio, two variables that are known to be larger for dominant trees than for co-dominant and intermediate trees (Oliver, 1990). This result was consistent with the effects of DBH and tree height on foliage biomass that were observed by Ung et al. (2008). We could assume that some differences in foliage biomass could be attributed to changes in foliage density (Fig. 2.2). Moreover, lower foliage densities of shaded trees have been estimated by Messier et al. (1999). The steeper slope for black spruce in the foliage biomass density model has suggested a more rapid increase of foliage biomass density with D/H than for white spruce, explaining the stronger negative effect for the former species of tree height on total foliage biomass (Fig. 2.1).

Different explanations can be proposed for the change in total foliage biomass and foliage biomass density that were associated with tree dominance class. Horn (1976) claimed that under shaded conditions monolayer of foliage are more effective than multilayer for photosynthesis. Horn based his theoretical model on the nonlinear response of photosynthesis to light. A lower foliage density for shaded trees can limit the effects of self-shading (Messier et al., 1999). Because photosynthetically active radiation diminishes from the top to the

bottom of the canopy (Ellsworth and Reich, 1993), trees in lower strata can access only a part of the radiation that trees in higher strata can access, and which consequently cannot maintain the same foliage density. Moreover, the lower value of total foliage biomass for trees in lower forest strata can be explained by a reduction in crown width and depth with increased competition (Antos et al., 2010; Harper, 2008; Thorpe et al., 2010). Smaller crown width and depth would imply diminishing crown surface and crown volume, which would limit the allowable space for foliage.

2.6.2   *Relative cumulative foliage biomass vertical distribution*

Cumulative foliage biomass distributions were very similar between the two species. The RMSE estimated for the pooled data was similar to the sum of RMSE for species-specific equations. This meant that, even though black spruce maintained a greater quantity of foliage biomass than did white spruce, their vertical foliage distribution did not differ. Pronounced between-species differences in vertical foliage distributions have been previously described by Garber and Maguire (2005) for grand fir (*Abies grandis* (Douglas ex D. Don) Lindley), lodgepole pine (*Pinus contorta* Douglas ex Loudon ssp. *contorta*), and ponderosa pine (*Pinus ponderosa* Douglas ex C Lawson), and Weiskittel et al. (2009) for northern white cedar (*Thuja occidentalis* (L.)) and other conifers. In the present study, because white spruce was generally located on better sites than black spruce, it would have been difficult to distinguish differences between species when site index is included in the equation, as this variable expressed a large component of the variation that was associated with the species.

Our model predicted a shift in foliage distribution towards the lower crown when the site index was high. A similar shift for black spruce and jack pine (*Pinus banksiana* Lambert) was detected by Goudiaby et al. (2012) as a response to increased site fertility due to fertilization. This phenomenon could be explained by the growth of trees on better sites that were larger and which had more greatly differentiated crowns, thereby receiving more direct light at their bases. For these trees, canopy closure and physical contact with other crowns, for which there is an implied loss of foliage (Putz et al., 1984), would occur at a lower

relative height. Further, greater resource availability on better sites would allow lower branches to maintain a greater foliage biomass (Gillespie et al., 1994), implying a shift in foliage biomass distribution towards the tree bases..

A shift in cumulative relative foliage biomass towards the tops of the trees with age was consistent with observations made by Schneider et al. (2011) for jack pine. These authors attributed this upward shift in foliage distribution with age to stand closure. However, in our data set, most stands (with exception of a few black spruce stands) were well past the canopy closure stage. An alternative explanation could be related to the slowdown in height growth with age. In trees with rapid height growth, young branches that have yet to develop all of their foliage biomass can occupy a larger proportion of the crown. A reduction in height growth rates in older trees (Assmann, 1970) can limit the young branches to a smaller proportion of the living crown depth, thereby inducing a shift in the cumulative relative distribution of foliage biomass towards the top of the tree. This explanation is consistent with observed changes in crown shape, from a conical form in young trees to ellipsoids in older trees (Baldwin and Peterson, 1997). This change in crown shape has been attributed to a decrease in the apical control with age (Deleuze et al., 1996), which can allow faster development of lateral branches at the top of the tree and explains the shift in cumulative relative foliage biomass.

Saito et al. (2004) demonstrated that large shifts in foliage density distribution occurred with changes in the dominance class of the broad-leaved evergreen *Castanopsis cuspidata* (Thunberg Schottky). They observed a large shift in foliage distribution towards the uppermost parts of the canopy. Schneider et al. (2011), as well as Xu and Harrington (1998), showed smaller and opposite effects of competition status (note that results are not directly comparable since vertical foliage distribution was defined differently in the publications). Our results indicated that foliage distribution was not sensitive to competition status. We had assumed that tree growth in northern forests with relative low light angles and a large proportion of light passing between trees could explain these results, or alternatively, our spruce species have a rather fixed foliage density distribution (Oker-Blom et al., 1989).

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2.7   Conclusion

Our study showed that black spruce maintained greater foliage biomass than did white spruce, even when accounting for tree size and growth conditions. Moreover, we found that black spruce has a higher foliage density than white spruce. Analysis of the relative cumulative vertical foliage biomass distribution, however, did not reveal differences between species, perhaps due to the confounding effect of site index. The differences in the amount of foliage biomass and foliage biomass density between black and white spruces may be attributed to their differences in shade tolerance. The social status or canopy position of the trees affected the foliage biomass of the two spruce species. There were indications that less competitive trees exhibited greater total foliage biomass and foliage biomass density. Trees that grew on better sites, together with younger trees, also had a vertical foliage biomass distribution that was skewed toward the base of the crown. The greater foliage biomass and higher foliage biomass density for black spruce tended to confirm the higher shade-tolerance of black spruce. However, the spatial distribution of the study sites did not represent the full geographic range of the two species and, thus, confirmation of our results over a greater number of sites across the entire species ranges would be desirable.

Table 2.1 Characteristics and locations of sample sites

Site	Location	Species	Number of Plots	Age (years)	Density (stems ha^{-1})	Number of Sample Trees
Lac La Biche Alberta	55° 00'N 112° 00'W	White spruce	3	85-140	800-1500	15
Petawawa, Ontario	45° 59'N, 77° 25'W	White spruce	12	40-75	130-2500	50
Lac-St-Jean, Quebec	49° 00'N, 72° 40'W	Black spruce	12	30-120	900-7000	36
Témiscamingue, Quebec	46° 45'N, 78° 20'W	Black spruce	7	30-120	1500-4500	21

Table 2.2 Summary statistics for plot- and tree-level variables (65 white spruce trees in 15 plots; 57 black spruce trees in 19 plots)

Variable	Black spruce				White spruce			
	Min.	Mean	Max.	Std. Dev.	Min.	Mean	Max.	Std. Dev.
Crown length (m) Cl	1.5	6.4	14.1	2.7	3.8	9.3	16.7	2.9
Crown ratio Cr	0.13	0.51	0.97	0.18	0.24	0.46	0.82	0.13
Diameter at breast height (cm), DBH	5.4	14	26.8	5.6	10.8	26.39	42.2	7.9
Diameter at breast height / Total height, D/H	0.64	1.05	1.48	0.17	0.79	1.32	2.20	0.30
Foliage biomass (Kg), Wf	0.9	6.3	23.0	5.2	2.0	14.0	44.0	9.4
Total tree height (m), Ht	5.5	13.2	20.8	4.4	13.3	20.4	32.3	4.7
Dominant Height (m), DH	9.2	15.6	20.5	3.6	15.6	22.9	31.6	4.4
Quadratic mean DBH (cm), QDBH	5.8	11.4	26.8	3.7	15.4	25.4	35.2	5.9
Site index (height in m at 50 years old), SI	9.5	14.6	17.7	2.1	15.8	20.3	27.5	3.0
Stand age (years at 1m height), age	20	70	120	28.4	45	73	140	26.3
Stand basal area (m^2/ha), G	10.0	29.8	47	9.8	13.2	29.8	68.2	14.4
Stand density (stems ha^{-1}), SPH	921	3697	11263	2478	136	912	3657	953

Min. = minimum value of the variable

Max. = maximum value of the variable

Std. dev. = standard deviation of the variable

Table 2.3 Parameter estimates and their associated *P*-values and error term for equations 2.3, 2.6 and 2.9

	Parameter estimate *P*-Values									Variance components				
Model	β_1	β_2	β_3	β_4	β_5	β_6	β_{11}	β_{22}	β_{33}	σ^2site	σ^2plot	σ^2tree	$\sigma^2\varepsilon$	RMSE
Eq.2.3	115.6	2.19	-1.27	0.74	NA	NA	-86.33	NA	0.39	3.61	7.53	NA	522.6	3579
	0.000	0.000	0.000	<0.001			<0.001		0.011					
Eq.2.6	-19.37	138.8	NA	NA	NA	NA	NA	78.82	-95.89	165.33	$2.9e^{-6}$	NA	1107	36.2
	0.000	0.000						0.040	0.003					
Eq.2.9	0.4314	-0.0045	0.523	1.029	-0.005	0.311	NA	NA	NA	*p* $2.07e^{-9}$	0.002	0.091	0.001	0.081
	<0.001	<0.001	<0.001	0.020	<0.001	<0.001				*q* $127e^{-8}$	0.022	0.318		

Note: NA = not applicable

Figure 2.1 Total foliage biomass for black spruce with crown length values of 5 m (solid line) and 10 m (dashed line), and for white spruce with crown length values of 5 m (dotted line) and 10 m (dashed and dotted line), for A) Total height =13 m and B) Total height = 21 m.
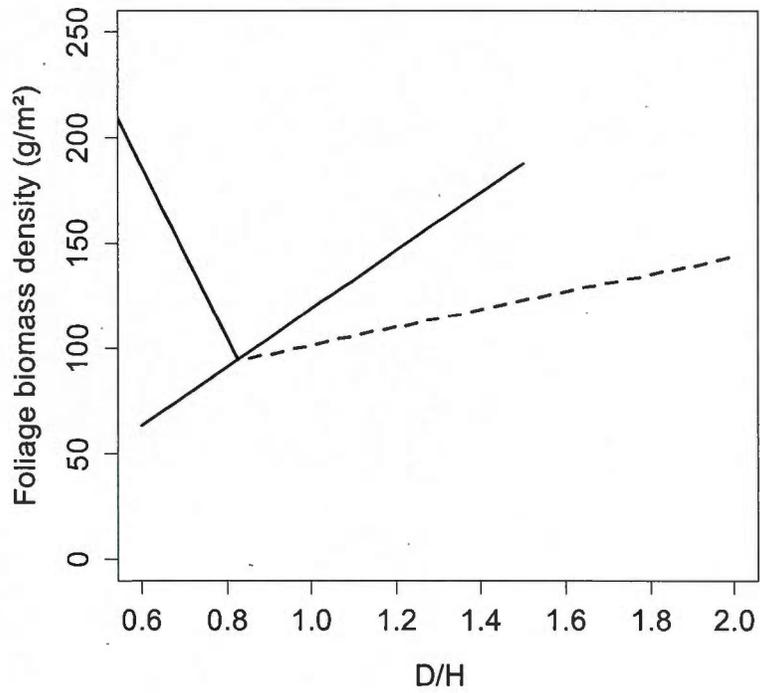
Figure 2.2 Foliage biomass density for black spruce (solid line) and white spruce (dashed line). D/H = ratio between diameter at breast height and tree's total height.
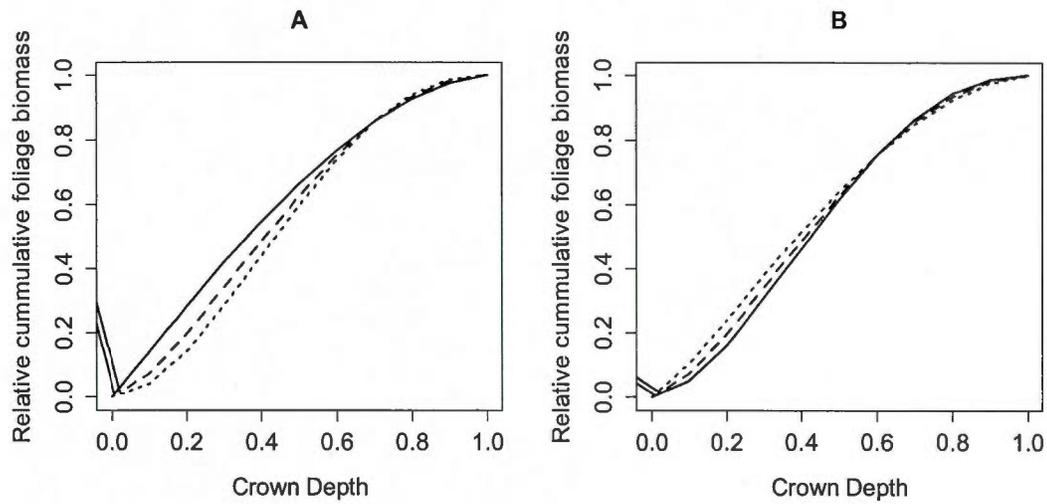
Figure 2.3 Relative cumulative foliage biomass. A) Age = 80 years and SI = 10 m (solid line), 17 m (dashed line) and 25 m (dotted line). B) SI = 17 m and Age = 20 y (solid line), 80 y (dashed line) and 140 y (dotted line).

2.8   Appendix

2.8.1   Total height imputation

Imputation of the missing heights was done with Eq. A1 for black spruce and Eq. A2 for white spruce. The site and plot nested in site random effects on the intercept were added to the prediction in order to obtain tree specific predictions.

(A1)
$$Ht_{ijk} = -8.5523 + 0.6216DBH_{ijk} - 0.0184DBH_{ijk}^2 + 1.6978PDBH_{ij} - 0.0619PDBH_{ij}^2 + 0.0005PHt_{ij} + 0.0298DBH_{ijk} * PDBH_{ij} + \varepsilon_i + \varepsilon_{j(i)} + \varepsilon_{k(ij)}$$

(A2)
$$Ht_{ijk} = 8.5477 + 0.2638DBH_{ijk} - 0.0079DBH_{ijk}^2 + 0.2660PDBH_{ij} - -0.0163PDBH_{ij}^2 + 0.0659PHt_{ij} + 0.0182DBH_{ijk} * PDBH_{ij} + \varepsilon_i + \varepsilon_{j(i)} + \varepsilon_{k(ij)}$$

where: Ht is the tree total height (m); $PDBH$ is the plot mean DBH of all live trees (cm); PHt is the plot mean height of height-measured trees only (m); ijk are the subscripts for the kth tree in plot j in site i; and ε_i, $\varepsilon_{i(i)}$, $\varepsilon_{k(ij)}$ are the respective random error terms at the site, plot-within-site, and tree-within-plot levels.

These equations were fitted using height and DBH measurements of trees in the sample plot that were associated with the sample trees. The mixed-effects at the site- and plot-level were added to the predictions of tree height.

2.8.2   Branch foliage biomass estimation

Foliage biomass at the branch-level (Wfb) was predicted with a branch specific non-linear mixed-effects equation for black spruce (Eq. A3) and white spruce (Eq. A4). The mixed-

effects applied on the interaction between Gb and Cd, at the site-, plot nested in site and tree nested in plot and site level were added to the predictions.

(A3) $\quad Wfb = 0.3725Gb^{1.095} + 0.59Cd - (0.3056 + b_i + b_{j(i)} + b_{k(ij)})Gb * Cd + \varepsilon_{l(ijk)}$

(A4) $\quad Wfb = 0.3962Gb^{1.037} + 11.62Cd - (0.308 + b_i + b_{j(i)} + b_{k(ij)})Gb * Cd + \varepsilon_{l(ijk)}$

where Gb is branch basal area (cm^2); Cd is the relative crown depth that has a value of 0 at the top of the tree and 1 at crown base; the b are random parameters; $ijkl$ are the subscripts for the lth branch in tree k in plot j in site i; and ε represents the random error.

2.8.3 Crown radii estimation

To estimate crown radius, the length of all sample tree living branches (Bl) was estimated with a non-linear mixed-model. Models for each species were fitted separately and random effects at the site-, plot- and tree-level were added to the predictions to obtain tree-specific branch length. Equation A5 and equation A6 show the branch length model for black and white spruce, respectively, as reproduced from Power et al. (2012).

(A5) $\quad Bl = 8.9515Bd^{(0.6768 + b_i + b_{j(i)} + b_{k(ij)})} * Cd^{0.4605} * SI^{0.3401} + \varepsilon_{l(ijk)}$

(A6) $\quad Bl = 17.5727Bd^{(0.7561 + b_i + b_{j(i)} + b_{k(ij)})} * Cd^{0.3068} + \varepsilon_{l(ijk)}$

where Bl is the branch length (cm); Bd is branch basal diameter (cm); Cd is relative crown depth, which has a value of 0 at the top of the tree and 1 at crown base; SI is the site index (m); $ijkl$ are the subscripts for the l^{h} branch in tree k in plot j in site i; b are random effects parameters; and ε is the random error.

Following branch length estimation, we calculated the horizontal distance (Hl) between the tree bole and the tip of the living branch using the estimated Bl and the measured branch angle (θ) (Eq. A7).

(A7) $\qquad Hl = Bl * \sin \theta$

For each sample tree, crown radius (Cr) was calculated as the average of the four longest estimated horizontal branch lengths within each crown section. Height of each crown radius was defined as the height of the tip of the largest branch used to calculate the crown radius value.

2.8.4   Crown surface area estimation

The second method used to estimate the crown surface area used a crown radius equation for black spruce (Eq. A8) and white spruce (Eq. A9) that is integrated over the crown depth (Eq. A10), as reproduced from Power et al. (2012).

(A8) $\quad Cr_{ijkl} = \dfrac{Cd_{ijkl}}{0.7582 - 0.0191Cl_{ijk} + (0.5548 - 0.0216Cl_{ijk} - 0.0213SI + 0.000017SPH} +$

$\varepsilon_i + \varepsilon_{j(i)} + \varepsilon_{k(ij)} + \varepsilon_{l(ijk)}$

(A9) $\quad Cr_{ijkl} = \dfrac{Cd_{ijkl}}{-0.1257 - 0.0091Cl_{ijk} + (0.3467 - 0.0124Cl_{ijk} + 0.0159SI + 0.0002SPH} +$

$\varepsilon_i + \varepsilon_{j(i)} + \varepsilon_{k(ij)} + \varepsilon_{l(ijk)}$

(A10) $\quad Cs_{ijk} = 2\pi \int_{x=Cb}^{x=Ht} \overline{Cr}_{ijkl} \sqrt{1 + \left(\dfrac{dCr_{ijkl}}{dx_{ijk}}\right)^2} d(x_{ijk})$

where Cr is the crown radius (cm); Cd is the crown depth with a value of 0 at the top of the tree and 1 at crown base; Cl is tree crown depth (m); SPH is the stand density (stems per ha); x is the location where the radius is estimated between the crown base and the top of the tree; $ijkl$ are the subscripts for whorl l in tree k in plot j in site i; ε represents the error terms of the

model at the levels of site (ε_i), plot-within site ($\varepsilon_{j(i)}$), tree-within-plot ($\varepsilon_{k(ij)}$) and branch-within-tree ($\varepsilon_{l(ijk)}$); and all other variables were previously defined.

CHAPITRE III

DIFFERENCES IN PIPE MODEL RATIOS BETWEEN TWO SPRUCE SPECIES, WITHIN INDIVIDUALS AND ACROSS DIFFERENT GROWING CONDITIONS

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3.1   Résumé

Le modèle tubulaire (pipe model) suppose que chaque unité de feuillage de l'arbre est reliée par un tube à ses racines. Le tube en question servant à la fois à transporter la sève et à supporter la feuille. Le modèle tubulaire est une relation allométrique utilisée pour l'estimation de la biomasse foliaire par les modèles de distribution du carbone et les modèles basés sur la conduction hydraulique de l'arbre. Dans cet article, nous vérifions l'hypothèse selon laquelle l'épinette noire (*Picea mariana* (Mill.) B.S.P.) qui est plus tolérante à l'ombre que l'épinette blanche (*Picea glauca* (Moench)Voss), a un plus grand ratio de modèle tubulaire (i.e. biomasse foliaire divisée par la surface basale d'aubier) à l'échelle de la branche, de l'arbre et à différents endroits le long de la tige. À cette fin, 50 épinettes noires et 57 épinettes blanches ont été échantillonnées à différents endroits en Ontario et au Québec. À l'aide d'échantillons de branches localisés systématiquement dans la cime vivante de l'arbre, des modèles non linéaires mixtes du feuillage à l'échelle de la branche ont été développés pour chacune des espèces et utilisés pour estimer la biomasse foliaire de chaque arbre. La superficie d'aubier a été estimée à l'aide de disques prélevés le long de la tige des arbres échantillon. Des modèles non linéaires mixtes du ratio de modèle tubulaire ont été paramétrés à différents endroits le long de la tige. Le ratio de modèle tubulaire s'est avéré plus grand chez l'épinette noire que chez l'épinette blanche, et ce, pour des arbres de mêmes dimensions. Les conditions de croissance telles que la classe sociale de l'arbre et la compétition ont aussi affecté le ratio de modèle tubulaire. Les différences entre les espèces et l'effet différent des conditions de croissance pourraient être attribuables à une différence de tolérance à l'ombre. Cette caractéristique amenant des différences de longévité de feuillage, de taux de transpiration, de photosynthèse et des différences quant aux contraintes mécaniques et hydrauliques influençant l'allocation des ressources.

3.2   Abstract

The pipe model proposes that each foliage unit is linked to a pipe unit for transporting sap and that mechanically supports foliage. This model represents important allometric relationships that have been used for biomass estimation, carbon partitioning models, and tree hydraulic dynamics models. In this paper, we test the hypothesis that the more shade tolerant black spruce (*Picea mariana* (Mill.) B.S.P.) has a larger pipe model ratio (i.e., foliage biomass divided by sapwood area) at the tree level, branch level and at different locations along the stem than white spruce (*Picea glauca* (Moench)Voss). For this purpose, a total of 57 black spruce and 50 white spruce trees were destructively sampled at different locations in Québec and Ontario, Canada. Using samples of branches systematically located through each tree crown, nonlinear mixed-effects models of foliage biomass at the branch level were developed for each species, and used to reconstruct the foliage biomass for each tree. Sapwood area was estimated from stem disks at different locations along the stem. Nonlinear mixed-effects models of the pipe model ratio at tree level (i.e., using total foliage and mean sapwood area) and at variable locations along the stem (i.e, foliage biomass above a point and using sapwood area at that point) were parameterized.   We found that pipe model ratios were larger for black spruce than for white spruce given similar tree-sizes. Growth conditions reflecting social class and competition also affected the pipe model ratios. The differences between species and the changes with growth conditions are likely due to a combination of shade tolerance leading to differences in leaf longevity as well as photosynthesis and transpiration rates, and also due to hydraulic and mechanical constraints that determine tree resource allocations.

3.3   Introduction

The pipe model theory proposed by Shinozaki et al. (1964a) states that foliage mass and stem wood area are proportional. This theory has been since interpreted in terms of wood providing both mechanical support and water supply to the foliage. In order to efficiently deliver water and nutrients, an efficiently designed and predictable pattern of circulation must link the roots and the foliage (West et al. 1997). The transport of water through the sapwood to the leaves where it is used for photosynthesis highlights the strong relationships that exist among different tree components (Deckmyn et al. 2006). As a result, the pipe model is considered to be a physiologically-based allometric scaling law (West et al. 1997).

Based on pipe model theory, Shinozaki et al. (1964b) developed a model of total foliage biomass versus wood basal area at the base of the crown. Other researchers have further validated the pipe model theory by relating the sapwood cross sectional area at different locations in the stem to leaf area or foliage biomass (e.g., Albrektson, 1984; Grier and Waring, 1974; Waring et al., 1982; Whitehead, 1978). Further, pipe model theory has been used in many different applications, including biomass distribution used in carbon partitioning models (Mäkelä, 1997; Valentine and Mäkelä, 2005), estimation of foliage biomass (Bond-Lamberty et al. 2002), and examinations of hydraulic constraints of growth (Niklasand Spatz 2004). The pipe model ratio, defined as the foliage biomass from any vertical location on the stem to the tree apex relative to the sapwood cross sectional area at this location, has been shown to vary with location on the stem and with tree species (Waring et al. 1982, Dean and Long 1986, Kantola and Mäkelä 2004).

The majority of the explanations for the intra- and inter-species differences in pipe model ratios have been based on transpiration requirements of the foliage versus the transport capacity of the sapwood (e.g., Albrektson 1984, Berninger and Nikinmaa 1997, Mäkelä and Vanninen 2001). However, evidence that the sapwood area versus foliage biomass

relationship is not only driven by the need for sap conduction exists. Differences of sapwood conductance throughout the roots, stem and branches, as well as the strong dependence between conductance, the diameters of the conduits and the length of the tracheids indicates that the physiological basis of the pipe model is more complex than initially thought (Rennolls 1994, Pothier et al. 1989, Cruiziat et al. 2002).

According to these theories we could expect that growth conditions would influence the pipe model ratio. Berninger and Nikinmaa (1994) remarked that climate influences the pipe model ratio of Scots pine. Gilmore et al. (1996) reported geographical variations in the pipe model ratio. In another study, Vanninen et al. (1996) showed that site index influenced the pipe model of Scots pine while a study by Mäkelä and Vanninen (1998) showed that Scots pine trees of different tree social positions (i.e., crown classes, relative position in the canopy) had different pipe model ratios. However, studies on black spruce (*Picea mariana* (Mill.) B.S.P.; Robichaud and Methven, 1992) and on balsam fir (*Abies balsamea* (L.) Mill.; Gilmore et al., 1996) did not report significant relationships between the pipe model ratio and growth conditions.

The study and comparison of the pipe models of black and white spruces is particularly of interest since these species are similar with regards to many ecological and physiological characteristics, but differ substantially in others. These species share a similar geographical distribution that extends from the Atlantic coast at the east end of their distribution through Canada to the west coast of Alaska, US, at their western boundary. Also, morphologically, the two species appear quite similar (Marie-Victorin 1995). However, black spruce is considered to be shade tolerant while white spruce is considered to be less shade tolerant (Burns and Honkala 1990). Differences have also been noted with regards to the crown characteristics of the two species, white spruce having larger crowns than black spruce (Power et al. 2012). On stands of the same quality, white spruce is known to have a larger stem wood production than black spruce and to grow taller (Pothier and Savard 1998, Tiffault et al. 2003). Wood properties also differ between the two species. Black spruce has higher wood density and Young's modulus, a measure of the stiffness of a material, than white

spruce (Jessome 1977). Given the differences between the two species and the water conduction link between foliage biomass and sapwood, the pipe model might be expected to differ between species in spite of common geographical ranges and other characteristics. We expect that even if black spruce's wood has a higher density, the greater shade tolerance of black spruce will be reflected in a larger pipe model ratio and that this relationship will be observed across different growing conditions.

Because of the link between the pipe model and resource allocation, the main objective of this study was to explore the relationships between foliage biomass and sapwood area in black and white spruce trees. Since the pipe model can be considered at different hierarchical levels, we explored this relationship at the tree-level initially, and then also characterized the pipe model ratio along the stem within and below the base of the living crown. Also, at the branch level, we examined the relationship between foliage biomass and branch basal area and contrasted this between the species. For all these levels of analyses, we investigated changes in these relationships with changes in growth conditions found in different stands. The study will allow discrimination between the variations in the pipe model ratio that belong to species differences versus difference that belong to growth conditions.

3.4   Materials and methods

3.4.1   Data

The data set includes 57 black spruce and 50 white spruce trees. The white spruce trees were obtained from the Petawawa Research Forest in Ontario, Canada, whereas the black spruce trees were collected in Québec, Canada. Each site included several stands and one sample plot was established in each stand (Table 3.1). Sampling at the various sites took place during the growing season (May through September) from 2008 to 2010.

White spruce trees from Ontario were sampled from existing plantations that received spacing or thinning treatments; however, the last thinning was conducted in 1982 and growth should now be similar to that of natural white spruce-dominated stands. Sample trees were taken inside or from the periphery of existing permanent sample plots (PSPs) ranging in size from 0.03 to 0.08 ha. For all live trees ≥ 1.1 cm DBH in the PSP, species was recorded and the DBH was re-measured; heights of previously measured trees were also re-measured. To obtain a distribution of sample trees across tree size, trees were sampled by selecting one tree from each of small and large DBH classes and two trees from the medium DBH class, resulting in four trees per plot. Trees with damaged crowns were excluded as candidate sample trees. To evaluate stand age, the plantation age was adjusted to age at 1 m above ground, using estimates provided by Pothier and Savard (1998). The measures of all live trees located in each PSP were used to calculate the plot-level variables presented in Table 3.2.

Black spruce trees from Québec were selected from stands that naturally regenerated following clearcutting or stand-replacing fire. Stands of different ages, densities (i.e., trees per ha) and site indices were selected using Québec's forest stand maps. For each selected stand, a variable-radius plot with basal area factor of 1 m^2 ha^{-1} was established at a location previously determined on the forest map. Species was recorded and DBH was measured for all live trees ≥ 1.1 cm DBH. Height was measured for 20 to 90 trees across the DBH classes. As with white spruce, trees in the plot were divided into small, medium and large DBH classes, each class including the same number of trees. For each plot, one sample tree was selected from each DBH class resulting in three trees per plot. Age at 1 m above ground of three dominant black spruce trees with undamaged crowns was recorded. The mean age of the three dominant trees was used as stand age. The information from the variable-radius plot was used to calculate the plot-level variables (Table 3.2).

For all stands, selected sample trees were felled and total height and height to live crown were measured on trees after felling. Height to live crown was considered as the height of the lowest branch that presented green foliage and above which all the whorls included at least one living branch. The vertical position of each live branch along the main stem and branch

basal diameter was measured. Branch basal diameter and branch insertion angle were recorded for each living branch of the tree.

The crown of the felled trees was then divided into five sections of equal length. In each section, one sample branch was randomly selected for foliage biomass measurement. Sample branches were placed into paper bags and transported to the laboratory. After drying at room temperature for a few weeks, foliage was removed from each sample branch and oven-dried at 60 ^{0}C for 24 hours. After being dried, the foliage was weighed to the nearest 0.01g.

In the hours following the felling of the sample tree, 1 to 2 cm sections of the tree stem (hereafter called "disks") were collected along the stem (Fig. 3.1). For all sample trees, disks were collected at stump height (0.3 m), at crown base, at 1 m increments from the crown base to the top of the tree, and at several other positions between crown base and stump height (interval less than 2.5 m). Immediately after collecting the disks, sapwood was delimited from heartwood using the light transmission technique (Grier and Waring 1974). On the upper side of each disk, the diameter inside bark and heartwood diameter were measured on two perpendicular axes. Geometric means of these two diameter measures were used to calculate inside bark disk area, heartwood area, and sapwood area.

Total and heartwood volumes were calculated for each stem section delimited by two consecutive disks. First, the volume of the stump was calculated assuming a cylinder using the stump disk and the distance from the disk to the ground. Following Husch et al. (1982), the volume of the first stem section delimited by the stump disk and the next disk toward the tree apex was calculated assuming a frustum of neloid. All other section volumes were calculated assuming a paraboloid frustrum shape and Smalian's equation (Husch et al. 1982), with the exception of the topmost segment for which volume was calculated assuming a conical shape. The sapwood volume of the tree was calculated by subtracting the heartwood volume from the total volume of the tree. The sapwood volume of the tree was then normalized by dividing it through the length of the tree stem (i.e., tree height), giving a proxy of the mean sapwood surface area, hereafter termed just "mean sapwood area".

3.4.2   Calculations of plot- level variables

Sample data were compiled to obtain the plot-level variables used in the modeling (Table 3.2). First, unmeasured heights of trees in each plot were imputed using the models described in Power et al. (2012). Once all unmeasured heights were imputed, the dominant height (DH) for each plot was calculated by averaging the height of the 100 largest trees (by DBH) per hectare. Quadratic mean DBH (QDBH, cm), density (SPH, stems ha^{-1}), and basal area (G, m^2 ha^{-1}) were calculated for each plot using only the trees that comprised the main cohort of the stand. We excluded saplings that belonged to the regeneration cohort except for three stands of black spruce 20 to 30 years old, where the saplings were considered to be part of the main cohort. Site index (SI; dominant height at 50 years total age) for each plot was calculated using the DH, stand age and SI equations developed by Pothier and Savard (1998).

3.4.3   Branch-level foliage biomass modelling and imputation

Because foliage biomass at the branch level (Wfb) is known to vary with the branch basal area at the point of attachment to the main stem (Gb) and also with the relative position of the branch inside the crown (Cd) (Berninger and Nikinmaa 1994), a basic power function that included these two variables and their interaction was first tested:

$$(3.1) \quad Wfb_{ijkl} = \beta_1 Gb_{ijkr}^{\beta_2} + \beta_3 Cd_{ijkr} + \beta_4 Gb_{ijkr} Cd_{ijkr} + \varepsilon_i + \varepsilon_{j(i)} + \varepsilon_{k(ij)} + \varepsilon_{r(ijk)}$$

Where β_1 to β_4 are fixed-effects parameters; $ijkr$ are subscripts for branch r in tree k in plot j in site i; and ε represents the error terms of the model at the site (ε_i), plot within site ($\varepsilon_{j(i)}$), tree within plot ($\varepsilon_{k(ij)}$) and branch within tree ($\varepsilon_{r(ijk)}$) levels.

For this model, Cd was defined as having a value of 0 at the top of the tree and a value of 1 at the crown base. This model was parameterized using the nlme function of R, v.2.13.2 software (Pinheiro et al. 2010) and data pooled for both species. This mixed-effects model

included the random effects of site-, plot-, tree, and branch-level errors, thereby accounting for common correlations of plots within sites, trees within plots, and branches within trees, and heteroscedasticity due to the hierarchy within the sample data. The error terms at each level were assumed to follow normal distributions. Also, the level-1 errors (i.e., branch-level errors) were checked for homogeneity of variances using residual plots and for normality using normality plots. If heteroscedasticity of the level-1 errors was detected, a function to model the variance of the level-1 errors was added to the model (Pinheiro et al. 2010).

Once this base model was fitted (Eq. 3.1), the residuals combined over all levels were then plotted against the other plot- and tree-level explanatory variables that represented growth conditions (Table 3.2). The variables that showed relationships with the residuals were selected as candidate explanatory variables, and these were then added individually or in combination, in additive or multiplicative form to the base model. Likelihood ratio tests were performed using the augmented versus the base models to decide whether to retain or reject the additional explanatory variables using $\alpha=0.05$. The likelihood ratio test allows us to perform a hypothesis test on the fit of two models where one of the two models is a special case of the second. Models that included the same number of explanatory variables were then ranked using AIC and this was used in selecting the branch foliage biomass model for the pooled-species data.

To test for differences between species, the branch foliage biomass model for the pooled-species data was altered by using a species-specific dummy variable (*Dm* equal 0 for black spruce and 1 for white spruce) to alter each fixed-effects parameter. This method, compared to an analysis of variance, permitted the use of non-linear equations to compare the two species. This modified model was then fitted, again using the pooled-species data, and compared to the model without the species dummy variable using a likelihood ratio test ($\alpha=0.05$). Rejection indicated different branch foliage biomass models for the two species. When rejected, the model was simplified by testing alterations of each fixed-effect parameter. If one or more alterations were not significant, the alteration with the highest p-value was removed and the equation was refitted. Using this iterative process, a final species-specific

branch foliage biomass model was obtained. The branch foliage biomass versus branch basal area relationship was then examined using the final model. Predicted branch foliage biomasses versus branch basal areas for different crown depths were plotted and compared for the two species.

The selected branch foliage model, including the random-effects on the intercept as a predictor was then used to estimate the subject-specific foliage biomass for each branch within a tree. From this, total foliage biomass and foliage biomass above any vertical position on the tree were calculated and used in the subsequent pipe model ratio explorations.

3.4.4 Tree-level pipe model ratio models

The pipe model ratio at the tree level (Rt) was defined as total foliage biomass divided by the mean sapwood area. We chose to use the mean sapwood area, a variable that represents the sapwood area along the entire stem, to study the pipe model ratio at the tree level with varying growth conditions, rather than using a localized measure of sapwood area at DBH or crown base. First, Rt was plotted against the plot- and tree-level variables (Table 3.2) to select candidate explanatory variables. Then, each candidate variable was entered into a basic power function:

$$(3.2) \quad Rt_{ijk} = \beta_1 x^{\beta_2} + \varepsilon_i + \varepsilon_{j(i)} + \varepsilon_{k(ij)}$$

Where x is an explanatory variable at the plot- or tree-level; β_1 to β_2 are fixed-effect parameters; ijk are the subscripts for tree k in plot j in site i; and ε represents the error terms of the model at the site (ε_i), plot within site ($\varepsilon_{j(i)}$) and trees within plot ($\varepsilon_{k(ij)}$) levels.

Assumptions for random-effects errors of Eq. 3.2 were similar to those for the branch foliage biomass model, except that the level-1 errors are at the tree-level. Using the nlme function of R, v.2.13.2 software (Pinheiro et al. 2010) and data pooled for both species,

models using each candidate variable were fitted and the variable that produced the lowest model AIC was retained as the base model. Following the same process as for the branch-level foliage biomass model: i) additional explanatory variables were added to the base model and a model was selected; ii) this model was altered using the species-specific dummy variable and compared to the model without species to test species differences; and ii) the species-specific model was simplified, if possible. The final tree-level pipe ratio model was then used to graphically compare the pipe model ratio between the two species.

3.4.5 Disk-level pipe model ratio models

The pipe model ratio at the disk level (Rd) was defined as the cumulative foliage biomass between any position l on the stem and the apex of the tree divided by the sapwood area at position l (Fig. 3.1). Initially, the same modelling approach was used as for the pipe model ratio at the tree level. First, a basic power function was fitted using candidate plot- and tree-level explanatory variables (Table 3.2) and the pooled data. However, the random-effects included errors at the four levels, namely the site, plot, tree, and position within tree levels. Then, the model with the best single explanatory process was added as with the tree-level pipe model ratio.   From this process, a model was selected for the pooled-species data. The modelling approach allowed us to statistically test the effect of the variables evaluated on the pipe model ratio.

However, since the cumulative foliage biomass is the same for all positions below the live crown, a segmented model was fitted using the joint point at the base of the live crown. The segmented model was compared to the previously selected model using a likelihood ratio test ($\alpha = 0.05$).

Finally, again following the process used for the tree-level pipe model ratio, we altered all fixed-effects parameters using the species-specific dummy variable. A likelihood ratio test of this model to the model without the altered parameters was used to test for species

differences, and then simplified for a final model. The final model was used to examine any species differences in the disk-level pipe model ratios.

3.5   Results

3.5.1   Branch level foliage biomass

Using the model protocols as explained, no other candidate variables were added to the base branch foliage biomass model. The model with the alterations of all fixed-effects parameters using the species-specific dummy variable had significantly higher value of log-likelihood than the model without the alterations (likelihood ratio test, p-value<0.01). However, only one alteration of fixed-effects parameters was retained in the simplified species-specific model, as follows:

$$(3.3) \quad Wfb_{ijkr} = \beta_1 Gb_{ijkr}^{(\beta_2 + \beta_5 Dm)} + \beta_3 Cd_{ijkr} + \beta_4 Gb_{ijkr} Cd_{ijkr} + \varepsilon_i + \varepsilon_{j(i)} + \varepsilon_{k(ij)} + \varepsilon_{r(ijk)}$$

Where Dm is a dummy variable for species with a value of 0 for black spruce and 1 for white spruce; β_1 to β_5 are fixed-effects parameters; and all other terms are as previously defined for Eq 3.1.

Estimated parameters for Eq. 3.1 and 3.3 are given in Table 3.3. The log likelihood for the model without species (Eq. 3.1, log L= -2495) was lower than for the species-specific model (Eq. 3.3, logL=-2477). As expected based on the model with alterations of all fixed-effects parameters for species, the associated likelihood ratio test again indicated species differences (p-value<0.01). The root mean square errors (RMSE) calculated for the pooled errors diminished from 64.8g for Eq. 3.1 to 62.7g for Eq. 3.3.

Using the fitted species-specific model, black spruce branches support a larger amount of foliage biomass for a given branch basal area, and these differences also increase with increasing branch basal area (Fig. 3.2). For both species, the foliage biomass by unit of branch basal area diminishes from the top of the tree to the crown base except for the smaller branches (less than 5mm of diameter).

3.5.2   Tree-level pipe model ratio

The final model for the tree-level pipe model ratio included only DBH over height as a predictor variable (Eq. 3.4). The model with the alterations of all fixed-effects parameters using the species-specific dummy variable was significantly different from the model without the alterations (likelihood ratio test, p-value= <0.01). However, only the alteration for β_1 was retained in the simplified species-specific model (Eq. 3.5).

$$(3.4) \quad Rt_{ijk} = \beta_1 (\frac{D^{\beta_2}}{H}_{ijk}) + \varepsilon_i + \varepsilon_{j(i)} + \varepsilon_{k(ij)}$$

$$(3.5) \quad Rt_{ijk} = (\beta_1 + \beta_3 Dm)(\frac{D^{\beta_2}}{H}_{ijk}) + \varepsilon_i + \varepsilon_{j(i)} + \varepsilon_{k(ij)}$$

Where D/H is the ratio of DBH over height; Dm is a dummy variable for species with a value of 0 for black spruce and 1 for white spruce; β_1 to β_3 are fixed-effects parameters; and all other terms are as previously defined for Eq. 3.2.

Overall, the log-likelihood for the pooled species model (Eq. 3.4) was -773, whereas the species-specific model (Eq. 3.5) had a log-likelihood of -765 (likelihood ratio test p-value <0.01). Moreover, the root mean squared error (RMSE) for the pooled errors at all levels was 70.5 g/cm² for Eq. 3.4 versus 47.4 g/cm² for Eq. 3.5. Based on Figure 3.3, Rt is higher for black spruce than for white spruce given the same tree attributes. Moreover, Rt increases

faster with D/H for black spruce than for white spruce. Parameter estimates for Eq. 3.4 and 3.5 are given in Table 3.3.

3.5.3   Disk-level pipe model ratio

The model for the pipe model ratio at the disk level without distinctions for species and position above or below crown height included variables in multiplicative and additive forms as follows:

$$(3.6)\ Rd_{ijkl} = \beta_1 Hrel_{ijkl}^{\beta_2} Dens_{ij}^{\beta_3} + \beta_4 SPH_{ijk} + \varepsilon_i + \varepsilon_{j(i)} + \varepsilon_{k(ij)} + \varepsilon_{l(ijk)}$$

Where *Hrel* is the relative height of the disk on the stem (values of 0 at ground height and 1 at tree top); *SPH* is in stems per hectare; β_1 to β_4 are fixed-effects parameters; *ijkl* are the subscripts for the disk l in tree k in plot j in site i; and ε represents the error terms of the model at the site (ε_i), plot within site ($\varepsilon_{j(i)}$), trees within plot ($\varepsilon_{k(ij)}$) and disks within tree ($\varepsilon_{l(ijk)}$) levels.

This model gave better results based on the log-likelihood than any other model tested. However, using the same modelling protocol and the segmented model resulted in a different set of explanatory variables as follows:

$$(3.7)\ \begin{aligned} Rd_{ijkl} &= \beta_1 Sd_{ijkl}^{\beta_2} SPH_{ij}^{\beta_3} + \beta_4 DBH_{ijk} + \\ &\quad C(\beta_5 Cd_{ijkl}^{\beta_6} SPH_{ij}^{\beta_7} + \beta_8 DBH_{ijk}) + \varepsilon_i + \varepsilon_{j(i)} + \varepsilon_{k(ij)} + \varepsilon_{l(ijk)} \end{aligned}$$

Where *Sd* is the relative position of the disk below crown base with a value of 0 at the base of the tree and 1 at crown base; *C* is a dummy variable with a value of 0 for disks below crown base and 1 for disks over crown base; *Cd* is the relative position of the disk in the living crown with a value of 0 at crown base and 1 at the top of the tree; and all other terms are as previously defined for Eq. 3.6.

The segmented model (Eq. 3.7) had a slightly higher log likelihood value (logL= -6432) than did Eq. 3.6 (logL=-6461). Since these are not nested models, no likelihood ratio test was possible. Further, since the foliage biomass is the same for all points below the live crown, this model was considered more biologically tractable. As a result, we retained the segmented model and modified this using the species-specific dummy variables. Several alterations to fixed-effects parameters were retained in the species-specific segmented model as follows:

$$(3.8) \quad Rd_{ijkl} = (\beta_1 + \beta_5)Sd_{ijkl}^{(\beta_2 + \beta_6 Dm)}Dens_{ij}^{(\beta_3 + \beta_7 Dm)} + (\beta_4 + \beta_8 Dm)DBH_{ijk} + C(8a) + \varepsilon_i + \varepsilon_{j(i)} + \varepsilon_{k(ij)} + \varepsilon_{l(ijk)}$$

$$(3.8a) \quad \beta_1 Cd_{ijkl}^{(\beta_2 + \beta_4 Dm)}Dens_{ij}^{(\beta_3 + \beta_5 Dm)}$$

Where Dm is a dummy variable for species with a value of 0 for black spruce and 1 for white spruce; β_1 to β_8 are fixed-effects parameters; and all other terms are as defined for Eq. 3.6 and 3.7.

The species-specific model (Eq. 3.8, including 3.8a) resulted in an increase of the likelihood to -6317 from a value of -6432 for the segmented model (Eq. 3.7), and the likelihood ratio test (p-value < 0.01) indicated differences between black and white spruces. Also, the RMSE value was smaller for Eq. 3.8 (46.6) than for Eq. 3.7 (61.4) further indicating differences in Rd relationships between black and white spruces. Parameter estimates for Eqs. 3.6 to 3.8 (including 3.8a) are given in Table 3.3.

Using the species-specific segmented model, the pipe model ratio increases from the base of the tree to the base of the live crown for both species (Fig. 3.4). Also, an increase in DBH was related to an increase of the pipe model ratio, whereas an increase in stand density was associated with a reduction in the pipe model ratio. However, the Rt values were larger for black spruce than for white spruce, and the estimated parameter associated with stand density was nearly zero for white spruce. For the portion of the stem located above crown

base, the pipe model ratio slightly increases from crown base to the top of the tree for black spruce (Fig. 3.5). For white spruce, the ratio also slightly increases from crown base to mid crown for white spruce, but then rapidly increases from the mid-point of the crown to the top of the tree. Similar changes with DBH and with stand density can be observed for the segments above and below the live crown base.

3.6   Discussion

To our knowledge, this is the first paper comparing branch-level foliage biomass and the pipe model ratio of black and white spruces, two ecologically important tree species. Our results showed that black spruce has more foliage biomass given the same branch basal area as white spruce. Moreover, at both the tree and disk levels, black spruce maintains a higher pipe model ratio than white spruce. These differences were consistent across growth conditions. Why do these differences occur? We propose here that the differences between these two related species can be explained in terms of different adaptations of leaves to shading, and also crown form differences. These adaptations will be discussed in the context of hydraulic and mechanical support.

3.6.1   Shade tolerance differences

Black spruce is more shade tolerant than white spruce (Burns and Honkala 1990) resulting in a greater ability to regenerate and survive under lower light levels. Further, black spruce seedlings have higher stomatal conductance and higher specific leaf area showing better adaptation to shade than white spruce (Dang and Cheng 2004).

Shade tolerance as well as the light environment is known to affect the distribution of the foliage inside the living crown (Zeide and Pfeifer 1991, Mäkela and Vanninen 2001). Black spruce has been shown to have longer leaf longevity and higher photosynthetic

nitrogen-use efficiency in older needles than white spruce (Kayama et al. 2007). As a result, since needles can be retained longer under shade conditions, black spruce can support foliage deeper inside the living crown, partly explaining why branch foliage biomass is greater given the same branch basal area (Fig. 3.2).

Shade tolerance differences between black and white spruces also contribute to differences in pipe model ratios at tree and disk levels. Kaufmann and Troendle (1981) reported that the shade intolerant species lodgepole pine (*Pinus contorta* Dougl.) and aspen (*Populus tremuloides* Michx.) have smaller pipe model ratios than the shade tolerant species Engelmann spruce (*Picea engelmannii* Parry) and subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.). The authors hypothesized that this was due to smaller sapwood areas for the more shade tolerant species since these trees would be expected to have a larger proportion of shade leaves that require less water and transpire less. The same trend was observed by Waring et al. (1982) when they compared 10 Gymnopserm species varying in shade tolerance.

3.6.2 *Hydraulic support requirements*

The larger pipe model ratio for black spruce implies that this species maintains a larger amount of foliage biomass per unit of sapwood area than white spruce. These differences may be partly explained by their requirements for hydraulic support. We hypothesized that white spruce experiences stronger hydraulic stresses than black spruce. Of the sampled sites, the white spruce received the least amount of precipitation and had the highest temperatures (Table 3.1). Moreover, white spruce trees are often taller than black spruce given the same growing conditions, resulting in increased hydraulic limitations primarily due to gravitational force (Koch et al. 2004). A strategy to compensate for hydraulic stress is to increase the conductive area of the trunk and stock sap in the sapwood, a phenomenon observed for white spruce (Becker et al. 2000). Finally, Pepin et al. (2002) demonstrated a high sensitivity of black spruce to soil water deficits and attributed stomatal closure in black spruce to drying of the top soil layer, even though deeper layers were moist. This comportment may limit the

impacts of stress on the water potential in the xylem of black spruce and could possibly allow the trees to have a lower sapwood area resulting in a larger pipe model ratio.

Bond- Lamberty et al. (2002) found a larger proportion of sapwood in the stems of fast growing species. Our results of lower pipe model ratios for white versus black spruce are consistent with these findings. These observations are also consistent with the reported characteristics of these species, that is: i) white spruce grows faster than black spruce (Pothier and Savard 1998, Thiffault et al. 2003); and ii) black spruce is known to have a lower transpiration rate per unit of leaf area than other boreal tree species (Ewers et al. 2005).

Hydraulic support requirements may also be used to explain the diminution of the foliage biomass from the apex of the tree to crown base given a branch basal area. The loss of hydraulic conductivity over longer branch lengths, would contribute to a diminution of the foliage density from upper to lower branches (Protz et al 2000). The diminishing branch foliage biomass per unit branch basal area from tree apex to crown base may also be the result of larger branches closer to the crown base having a greater proportion of non-conductive tissues. As hypothesized by Berninger and Nikinmaa (1994), the initiation of heartwood in the branches follows the loss of foliage from the lower branches.

The sap conduction requirements can also explain the positive effect of the DBH over height ratio on the tree-level pipe model ratio. Stems with larger values of D/H have greater diameter growth for a given height than trees with smaller D/H values. This observation indicates that these trees have allocated more resources to diameter growth than to height growth. As a result of faster diameter growth, earlywood to latewood proportions are larger. Since earlywood has a higher hydraulic conductivity than latewood (Tyree and Zimmerman 2002), trees with larger proportions of earlywood in the sapwood will likely have less sapwood area resulting in a higher pipe model ratio. The same phenomenon may be used to explain the effect of the DBH and stand density on the pipe model ratio at disk level below crown base.

3.6.3   Mechanical support requirements

Mechanical support requirements are another factor contributing to the variation of branch biomass per unit branch basal area. White spruce has a wider crown than black spruce (Power et al. 2012), and, as a result, white spruce must produces branches with larger basal area to mechanically support longer branches. However, the increase in branch length does not necessary imply an increase in foliage biomass. Instead, more often there is a shift in the location of foliage biomass along the branch from the interior to the less shaded exterior of the branch (Baldwin and Peterson 1997). Thus white spruce has longer branches with a smaller amount of foliage. Moreover, since black spruce has denser wood and a larger Young's modulus than white spruce (Jessome 1977), black spruce branches may be mechanically able to support a larger amount of foliage biomass than white spruce for the same branch basal area. Collectively, these characteristics contribute to a larger amount of foliage biomass by branch basal area unit for black spruce.

At the tree and disk levels, the difference in the pipe model ratio between black and white spruces can also be explained by the need for mechanical support. As trees grow taller, the resistance at the tree base must correspondingly increase to support the stress induced by the increased weight and also the increased effects of wind and snow on the tree crown. Stem diameter is known to increase proportionally faster than stem height and this increase is related to the need for mechanical stability in response to wind and other forces (King 1981). According to pipe model theory, when the foliage related to a pipe unit is shed, the pipe remains in the stem but is not used for water conduction (Shinozaki et al. 1964b). These disused pipes become heartwood. However, there can be a delay in the conversion of sapwood to heartwood (Mäkelä and Valentine 2006). As a result, measures of sapwood area can include disused pipes. Given that white spruce is taller and has wider crowns than black spruce (Power et al. 2012), a faster diameter growth coupled with a delay in conversion of sapwood to heartwood may be another factor explaining the smaller values of the pipe model ratio for this species.

The rapid increase in the disk-level pipe model ratios from mid-crown to top of the tree in white spruce is likely the result of minimal foliage shedding and heartwood formation in the upper crown. Further, the delay in heartwood formation would also contribute to lower disk-level pipe model ratios below the crown mid-point. In terms of the differences between the two spruce species, the faster growth of white spruce over black spruce along with greater foliage shedding due to lower shade tolerance of white spruce may explain the differences in the pipe model ratios for this part of the tree crown.

3.6.4   *Originality and limitations of the study*

In this study, we conducted an in-depth analysis of the pipe model ratios for black and white spruces, two important tree species of North America. We acknowledge that data from other study sites will help overcome the small number of intensive sample sites and increase the robustness of the results obtained in our study. To our knowledge, this is the first paper on this topic, but the results are consistent with our understanding of the ecophysiology of these species.

3.7   Conclusions

This research contributes to the knowledge of the pipe model ratio for black and white spruce, two common and important species of the Boreal Forest of North America. Moreover, the study highlights differences between to phylogenetically close species in the relationship between two functionally linked compartments of the tree.   The differences between species and the changes with tree size and density are likely due to a combination of shade tolerance leading to differences in leaf longevity as well as photosynthesis and transpiration rates, and also due to hydraulic and mechanical constraints that determine tree resource allocations.   Further research to explore how pipe model influences resource

allocation at the whole tree level would help to better understand the differences in wood production between black and white spruces.

Table 3.1 Characteristics and locations of the sample sites

Sites	Petawawa, Ontario	Lac-St-Jean, Quebec	Témiscamingue, Quebec
Location	45^0 59'N, 77^0 25'W	49^0 00'N, 72^0 40'W	46^0 45'N, 78^0 20'W
Species	White spruce	Black spruce	Black spruce
Mean Annual Temperature (°C)	4.3	2.7	1.7
Mean Annual Precipitation (mm)	853	887	937
Number of plots	12	12	7
Age (years)	40-75	30-120	30-120
Density (stems ha^{-1})	130-2500	900-7000	1500-4500
Number of plots	12	12	7
Number of Sample Trees	56	36	21

Table 3.2 Summary statistics for plot, tree and branch level variables (50 white spruce trees in 12 plots, 57 black spruce trees in 19 plots)

Variable	Black spruce				White spruce			
	Min.	Mean	Max.	Std. Dev.	Min.	Mean	Max.	Std. Dev.
Branch basal area (mm^2), **Gb**	0.8	130.0	615.0	115.7	3.1	428.8	2124	393.1
Diameter at breast height (cm), **DBH**	5.4	14	26.8	5.6	10.8	27.7	42.2	7.5
Diameter at breast height / Total height, **D/H**	0.64	1.05	1.48	0.17	0.79	1.44	2.20	0.31
Total tree height (m), **Ht**	5.5	13.2	20.8	4.4	13.3	19.3	26.9	4.0
Dominant Height (m), **DH**	9.2	15.6	20.5	3.6	15.6	21.9	26.2	4.0
Stand age (age at 1m height),	20	70	120	28.4	43	61	71	13
Quadratic mean DBH (cm), **QDBH**	5.8	11.4	26.8	3.7	15.4	26.8	35.2	5.8
Stand basal area (m^2/ha), **G**	10.0	29.8	47	9.8	13.2	24.3	68.2	12.3
Site index (height in m at 50 years), **SI**	9.5	14.6	17.7	2.1	15.8	19.53	22.1	2.2
Stand density (stems ha^{-1}), **SPH**	921	3697	11263	2478	136	661	3657	852

Notes: NA = non-applicable; Min. = Minimum; Max. = Maximum; St. Dev. = Standard Deviation

Table 3.3 Parameter estimates for branch foliage biomass (Eq. 3.1 and 3.3), tree-level pipe model ratio (Eq. 3.4 and 3.5), and disk-level pipe model ratio (Eq. 3.6 to 3.8 including 3.8a)

| Model	β_1	β_2	β_3	β_4	β_5	β_6	β_7	β_8	σ^2site	σ^2plot	σ^2tree	$\sigma^2\varepsilon$	RMSE
					Parameter estimate P-Values					**Variance components**			
Eq. 3.1	0.695 <0.01	0.941 <0.01	3.828 0.298	-0.266 <0.01	NA	NA	NA	NA	0.0005	0.0479	31.074	1.077	54.8
Eq. 3.3	0.417 <0.01	1.08 <0.01	6.105 0.091	-0.351 <0.01	0.049 <0.01	NA	NA	NA	0.0644	<0.0001	5.8783	1.0901	52.7
Eq. 3.4	138.9 <0.01	0.551 <0.01	NA	NA	NA	NA	NA	NA	2998	185.2	NA	307.6	70.5
Eq. 3.5	166.2 <0.01	1.14 <0.01	-116.9 <0.001	NA	NA	NA	NA	NA	1246	177.9	NA	303.7	47.4
Eq. 3.6	91.784 <0.01	0.8263 <0.01	0.0406 0.0116	2.3559 <0.01	NA	NA	NA	NA	2114	302.8	298.2	146.5	55.5
Eq. 3.7	46.125 <0.01	0.5894 <0.01	0.069 0.005	2.1696 <0.01	112.38 <0.01	0.9729 <0.01	-0.061 0.20	-0.1204 0.46	1526	314.5	271.4	141.6	51.4
Eq. 3.8a	37.617 0.02	0.433 <0.01	-0.027 0.523	2.925 0.00	0.213 0.00	NA	NA	-NA	NA	NA	NA	NA	NA
Eq. 3.8	977.1 <0.05	0.363 0.00	-0.283 0.000	3.231 0.00	-905.6 <0.01	0.641 0.00	0.254 0.00	-2.354 0.00	503.1	155.5	214.3	123.9	46.6
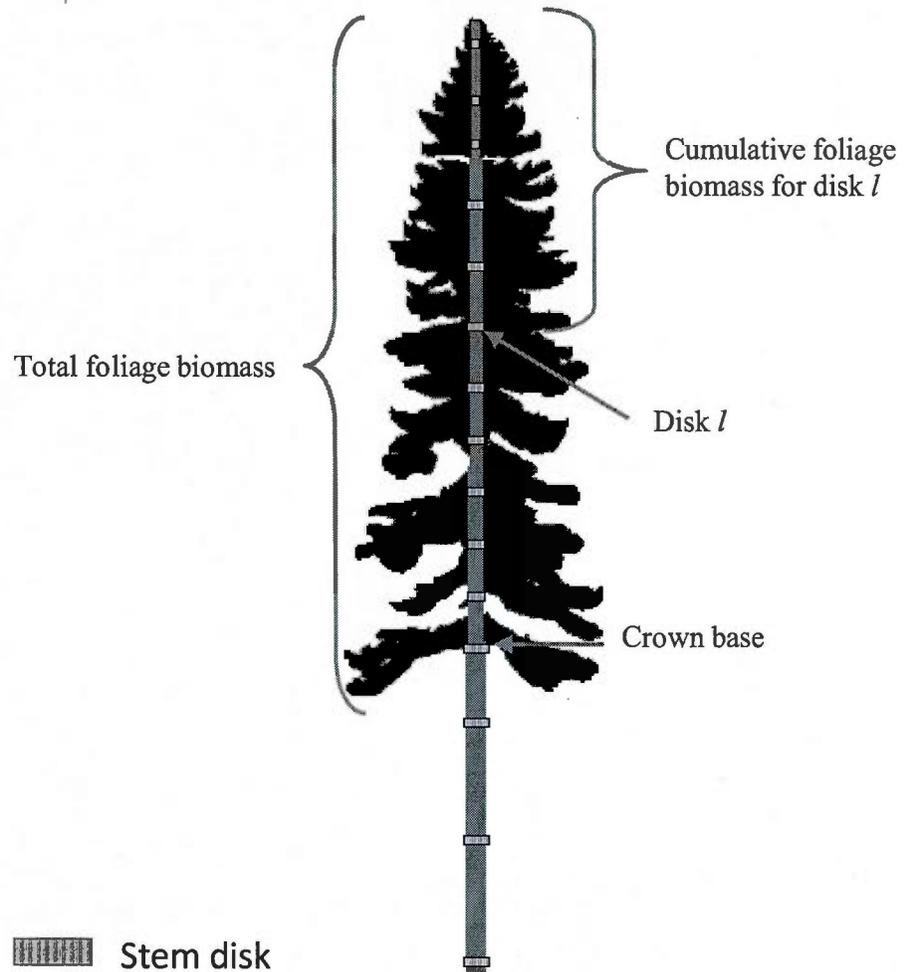
**Figure 3.1** Sample tree representations with stem disks, and total versus cumulative foliage biomass.
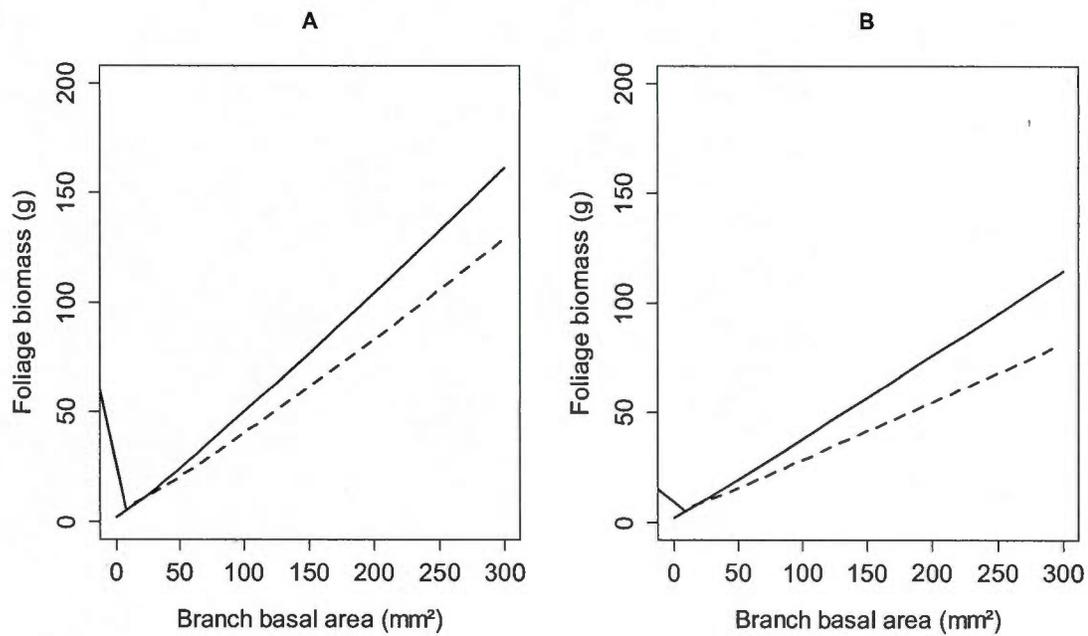
Figure 3.2 Black and white spruce foliage biomass branch basal area relationship for: A) Black spruce for relative depth of 0.33 (solid line) and 0.66 (dashed line); and B) White spruce for relative depth of 0.33 (solid line) and 0.66 (dashed line).
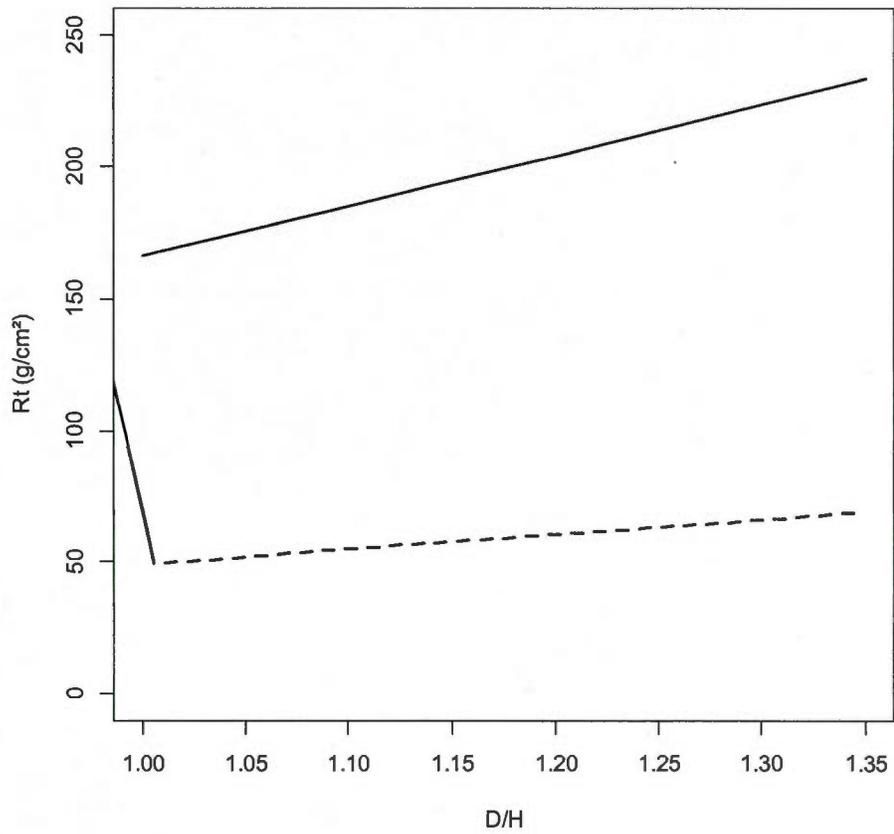
Figure 3.3 Tree level pipe model ratio (Rt) plotted against DBH over total height ratio (D/H) for black spruce (solid line) and white spruce (dashed line).
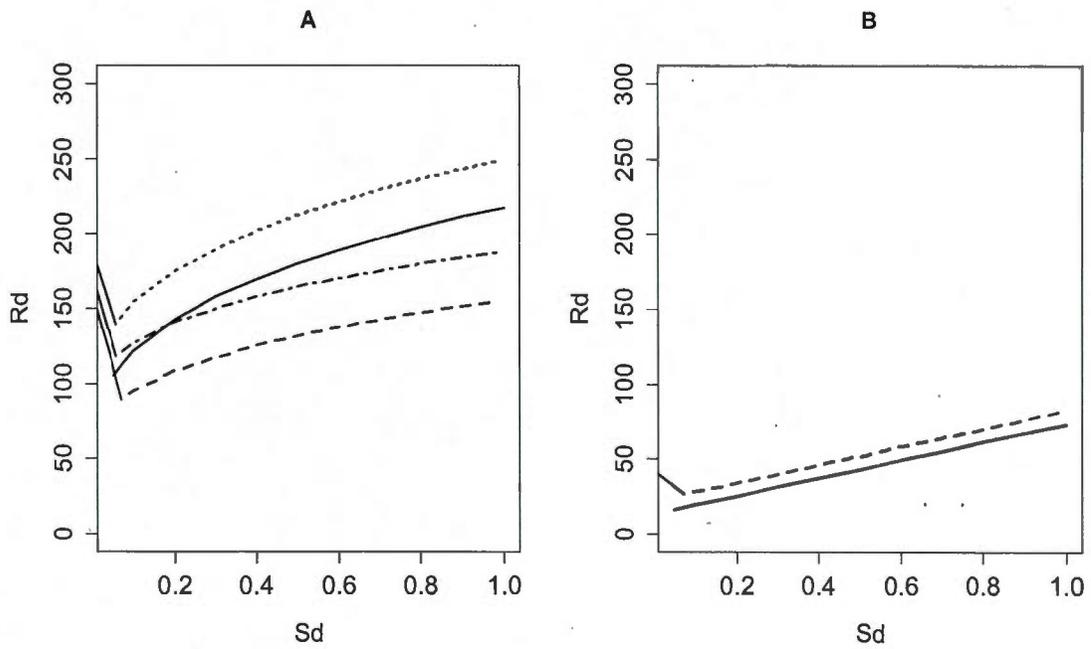
Figure 3.4 Pipe model ratio (Rd) plotted against relative position in the stem below crown base (Sd) for: A) Black spruce 500 stems/ha, DBH=15 (solid line) and DBH=25 (dotted line), 2500 stems/ha, DBH=15 (dashed) and DBH=25 (dashed and dotted line); and B) White spruce 500 and 2500 stems/ha, DBH=15 (solid line) and DBH=25 (dashed line).
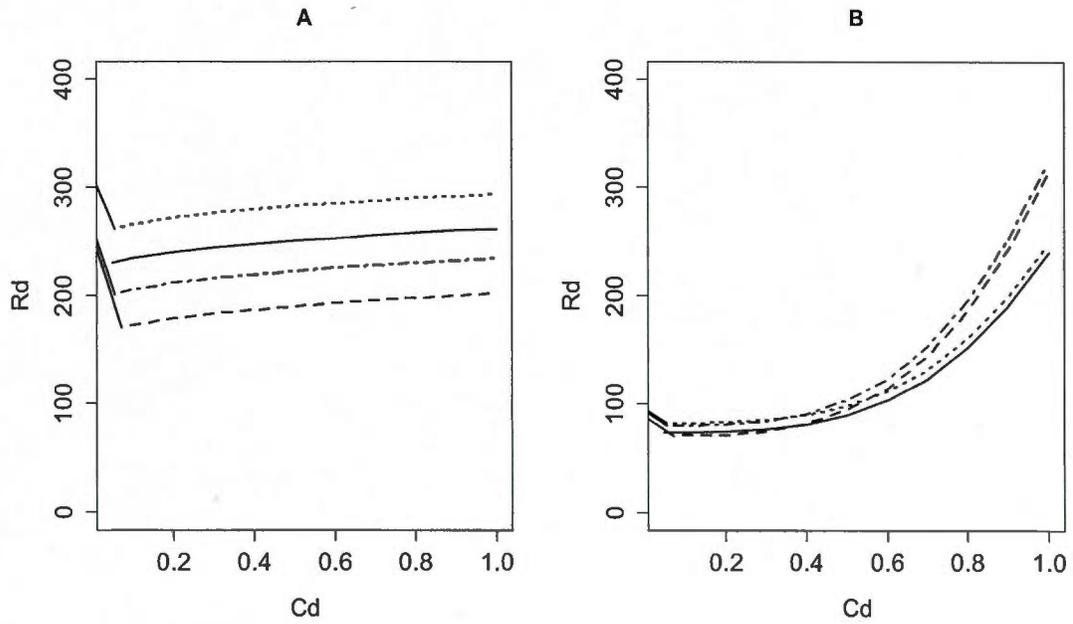
**Figure 3.5** Pipe model ratio (Rd) plotted against crown depth (Cd) for: A) Black spruce 500 stems/ha, DBH=15 (solid line) and DBH=25 (dotted line), 2500 stems/ha, DBH=15 (dashed line) and DBH=25 (dashed and dotted line); and B) White spruce 500 stems/ha, DBH=15 (solid line) and DBH=25 (dotted line), 2500 stems/ha, DBH=15 (dashed line) and DBH=25 (dashed and dotted line).

CHAPITRE IV
CONCLUSION GÉNÉRALE

L'étude de l'épinette noire et de l'épinette blanche a permis de relever de nombreuses différences dans les relations allométriques qui unissent les composantes de la biomasse aérienne de ces deux espèces. Cette étude est originale du fait que c'est, à notre connaissance, la première comparaison de l'allométrie de ces deux espèces et la première étude où l'effet de l'espèce sur l'allométrie est séparé de l'effet des conditions de croissance. Les différences observées nous portent à croire que les deux espèces se distinguent par une stratégie différente d'investissement des ressources dans leur biomasse aérienne. La thèse approfondit les connaissances sur la morphologie, les relations qui unissent les différentes parties de l'arbre et l'influence de l'environnement sur ces caractéristiques. Cette comparaison nous permet de voir comment deux espèces phylogéniquement proches, qui partagent la même distribution géographique et qui peuvent se retrouver sur les mêmes stations, s'adaptent différemment à leurs milieux de croissance.

4.1   Principaux résultats

Nous avons constaté que les différences de relations allométriques entre les deux espèces sont parfois grandement expliquées par des différences d'environnement de croissance. Lorsque les conditions de croissance sont prises en compte dans l'analyse des relations allométriques, certaines différences entre les espèces disparaissent signifiant ainsi que les différences observées entre les espèces peuvent être entièrement expliquées par des conditions de croissance différentes. Dans ces cas, les espèces ne présentent pas de différences intrinsèques. Parmi les conditions de croissance influençant les relations allométriques, la compétition pour l'espace et pour la lumière avec les autres arbres du peuplement forestier semble influencer grandement l'allométrie des deux espèces. Ainsi, la longueur et le profil de la cime vivante, la relation entre la surface de la cime vivante et la biomasse foliaire ainsi que la relation entre la surface d'aubier et la biomasse foliaire sont toutes influencées par la compétition, et ce, pour les deux espèces. En ce qui concerne la longueur de la cime vivante, les différences entre les espèces sont entièrement expliquées par les conditions de croissance.

Malgré la prise en compte de nombreux facteurs influençant la morphologie et les relations allométriques, de nombreuses différences entre les épinettes noires et les épinettes blanches demeurent. Ainsi, le profil de la cime de l'épinette blanche est plus large et affecté dans une plus grande mesure par la compétition que le profil de la cime de l'épinette noire. L'épinette noire maintient une plus grande quantité de feuillage et un feuillage plus dense que l'épinette blanche. De plus, l'épinette noire possède une plus grande quantité de biomasse foliaire par unité de surface d'aubier que l'épinette blanche.

On peut voir, dans cette démarcation entre les deux espèces, une différence de stratégie d'investissement des ressources. Ainsi, l'épinette noire, dû à sa cime plus étroite, investit moins dans ses branches que l'épinette blanche, ce faisant, elle alloue plus de ressources à son feuillage, maintenant ainsi une plus grande quantité de feuillage et un feuillage plus dense que l'épinette blanche. Cette stratégie est possible compte tenu de la plus grande tolérance à l'ombre de l'épinette noire dont le feuillage atteint plus rapidement la saturation lumineuse. Conséquemment, une cime large, permettant d'exposer pleinement à la lumière le feuillage, n'est possiblement pas nécessaire pour l'épinette noire. Cette différence de stratégie s'observe également dans la relation allométrique entre la biomasse foliaire et la superficie d'aubier. Le feuillage de l'épinette noire étant plus ombragé, il nécessite moins d'eau. Conséquemment un plus petit rapport entre la biomasse foliaire et la surface d'aubier est observé. L'épinette blanche, ayant une cime plus large, doit également investir plus de ressources dans son tronc afin de répondre aux exigences de support mécanique, justifiant ainsi partiellement son plus petit rapport biomasse foliaire/superficie d'aubier.

Lors de l'analyse de l'influence des conditions de croissance sur les relations allométriques, il est arrivé qu'aucune différence n'ait été trouvée entre les épinettes noires et les épinettes blanches lorsque les conditions de croissance étaient prises en considération. Ceci est notamment le cas pour la longueur de la cime vivante et pour la distribution verticale du feuillage. Ce résultat signifie, dans ce cas, que les différences entre les espèces étaient

entièrement expliquées par leur environnement de croissance et que la stratégie de croissance entre les deux espèces était similaire.

4.2 Limites de la thèse

Comme pour toute étude, certaines limites s'appliquent à nos conclusions. Notre échantillonnage, bien que couvrant plusieurs combinaisons d'âges, de densités et de qualités de site, ne reflète sans doute pas l'ensemble des conditions de croissance observées pour les deux espèces. De plus, la variation géographique des sites aurait pu être améliorée, la majorité des sites étant concentrés au sud-est de la distribution des espèces. Comme il est connu que des variations génétiques existent à l'intérieur de larges populations comme celles de l'épinette noire et de l'épinette blanche et que certains traits fonctionnels changent avec la latitude (e.g. forme de la cime), on peut croire que ces variations pourraient affecter les résultats de l'étude. Cependant, les effets aléatoires attribués aux sites à l'intérieur de nos régressions étaient habituellement faibles. On peut donc supposer que l'effet de la localisation géographique était plutôt faible ou qu'elle était capturée par d'autres variables caractérisant l'arbre ou le peuplement.

Il faut également rappeler que le portrait des relations allométriques présenté dans cette étude est incomplet puisqu'il ne concerne que les parties de l'arbre situées au dessus du niveau du sol. Un portrait global des différences de relations allométriques entre l'épinette noire et l'épinette blanche devrait, dans le futur, analyser les liens entre le système racinaire de l'arbre et ses parties aériennes. L'analyse de la partie racinaire permettrait de vérifier si une réelle différence de productivité existe entre les deux espèces ou si les différences rapportées relèvent plutôt d'une différence d'allocation des ressources. Malheureusement, compte tenu de la difficulté à observer le système racinaire des arbres, particulièrement dans le cas d'arbres matures, les données sur cette partie de l'arbre sont rarement disponibles.

4.3 Applications pratiques

Plusieurs applications pratiques des résultats de la thèse peuvent être envisagées. D'abord, la caractérisation de la morphologie de la cime des deux espèces pourrait avoir une incidence sur l'application des traitements sylvicoles. Par exemple, pour l'épinette blanche, ayant une largeur de cime plus grande que l'épinette noire, la densité optimale de son peuplement devrait être inférieure à celle de l'épinette noire. Les relations allométriques explorées pourront être intégrées dans des modèles de croissance à bases fonctionnelles (e.g. CROBAS, DRYADE, SILVA, etc.). L'utilisation de ces modèles devient de plus en plus pertinente dans le contexte des changements climatiques et de l'estimation des effets de nouveaux traitements sylvicoles. À titre d'exemple, la biomasse foliaire, considérée comme le moteur de croissance de l'arbre dans plusieurs modèles à bases fonctionnelles, variera avec la densité du peuplement. Il est donc possible d'obtenir des estimations de croissance des arbres en faisant varier la densité du peuplement, simulant ainsi des éclaircies effectuées à différentes intensités, les traitements d'éclaircies ayant un impact sur les dimensions de la cime vivante et par le fait même sur la quantité de biomasse foliaire. L'étude des relations allométriques permet également de mieux comprendre et de comparer les patrons d'allocation des ressources entre les espèces et leurs milieux de croissance. L'analyse des patrons d'allocation permettra de mieux comprendre comment les espèces se distinguent par rapport aux relations qu'elles entretiennent avec leur milieu de croissance.

RÉFÉRENCES

Albrektson, A. 1984. «Sapwood Basal Area and Needle Mass of Scots Pine (*Pinus-Sylvestris* L) Trees in Central Sweden». *Forestry*, vol. 57, no. 1, p. 35-43.

Alemdag, I.S. 1982. «Above-Ground Dry-Matter of Jack Pine, Black Spruce, White Spruce and Balsam Fir Trees at 2 Localities in Ontario». *The Forestry Chronical.* Vol. 58, no. 1, p. 26-30.

Alves, L. F., et F. A. M. Santos. 2002. «Tree allometry and crown shape of four tree species in Atlantic rain forest, south-east Brazil». *Journal of Tropical Ecology*, vol. 18, no. 2, p. 245-260.

Akaike, H. 1973. «Information theory as an extension of the maximum likelihood principle». In*: Second International Symposium on Information Theory. Edited by* B.N. Petrov and F. Csaki. p. 267-281. Akademiai Kiado, Budapest.

Antos, J. A., R. Parish et G. D. Nigh. 2010. «Effects of neighbours on crown length of Abies lasiocarpa and Picea engelmannii in two old-growth stands in British Columbia». *Canadian Journal of Forest Research-Revue Canadienne de Recherche Forestière*, vol. 40, no. 4, p. 638-647.

Assmann, E. 1970. *The principles of Forest Yield Study.* Oxford, U.K.: Pergamon Press.

Baldwin, V.C, Jr., et K. D. Peterson. 1997. «Predicting the crown shape of loblolly pine trees». *Canadian Journal of Forest Research-Revue Canadienne de Recherche Forestière*, vol. 27, no. 1, p. 102-107.

Becker, P., F. C. Meinzer et S. D. Wullschleger. 2000. «Hydraulic limitation of tree height: A critique». *Functional Ecology*, vol. 14, no. 1, p. 4-11.

Beckingham, J.D., et J.H. Archibald (1996). *Field Guide to Ecosites of Northern Alberta*. Edmonton, Canadian Forest Service, Northern Forestry Centre.

Beuchat, C. A., J. Kuikka, J. H. Brown, B. J. Enquist et G. B. West. 1997. «Allometric scaling laws in biology [3] (multiple letters)». *Science*, vol. 278, no. 5337, p. 371-373.

Berninger, F., et E. Nikinmaa. 1994. «Foliage area - sapwood area relationships of Scots pine (*Pinus-sylvestris*) trees in different climates». *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestière*, vol. 24, no. 11, p. 2263-2268.

Berninger, F., et E. Nikinmaa. 1994. «Implication of varying pipemodel relationships on Scots Pine growth in different climates». *Functional Ecology*, vol. 11, p.146-156.

Biging, G.S., and Dobbertin, M. 1992. «A comparison of distance-dependent competition measures for height and basal area growth of individual conifer trees». *Forest Science*, vol. 38, no. 3, p. 695-720.

Bond-Lamberty, B., C. Wang et S. T. Gower. 2002. «Aboveground and belowground biomass and sapwood area allometric equations for six boreal tree species of northern Manitoba». *Canadian Journal of Forest Research-Revue Canadienne de Recherche Forestière*, vol. 32, no. 8, p. 1441-1450.

Burns, R.M., et B.H. Honkala. 1990. *Silvics of North America: 1. Conifers; 2. Hardwoods*. Coll. «Agriculture Handbook». Washington D.C.: U.S. Department of Agriculture, Forest Service.

Butos, C., R. Beauregard, M. Mohammad et H. E. Hernandez. 2008. «Structural performance of finger-jointed black spruce lumber with different joint configurations». *Forest Product Journal*, vol. 53, no. 9, p.72-76.

Canadian Forest Service. 2005. *The State of Canada's Forests 2004-2005: The boreal forest*. [online]. Available from http://cfs.nrcan.gc.ca/pubwarehouse/pdfs/25648.pdf [accessed 29 July 2011].

Cauboue, M., et D. Malenfant (1988). *Exigences écologiques des épinettes (PICEA), des pins (PINUS) et des mélèzes (LARIX) plantés au Québec. Le reboisement au Québec*. Gouvernement du Québec. Québec.

Cannell, M. G. R. 1985. «Dry matter partitioning in tree crops». In *Attributes of Trees as Crop Plants,* M. G. R. Cannell et J.E. Jackson, p. 160-193. U.K.: Institute of Terestrial Ecology.

Cannell, M.G.R., R. Milne, L.J. Sheppard et M.H. Unsworth. 1987. «Radiation interception and productivity of willow». *Journal of Applied Ecology,* vol. 24, p. 261-278.

Clyde, M. A., et S. J. Titus. 1987. «Radial and longitudinal variation in stem diameter increment of lodgepole pine, white spruce, and black spruce - species and crown class-differences». *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere,* vol. 17, no. 10, p. 1223-1227.

Cruiziat, P., H. Cochard and T. Améglio. 2002. «Hydraulic architecture of trees: main concepts and results». *Annals of Forest Science,* vol. 7, p. 723-752.

Dang, Q. L. and Cheng, S. 2004. «Effects of soil temperature on ecophysiological traits in seedlings of four boreal tree species». *Forest Ecology and Management,* vol. 194, p. 379-387.

Daniels, R.F., Burkhart, H.E., and Classon, T.R. 1986. «A comparison of competition measures for predicting growth of loblolly pine trees». *Canadian Journal of Forest Research-Revue Canadienne de Recherche Forestière,* vol. 16, no. 6, p. 1230-1237.

Davies, O., et A. Pommerening. 2008. «The contribution of structural indices to the modelling of Sitka spruce (*Picea sitchensis*) and birch (Betula spp.) crowns». *Forest Ecology and Management,* vol. 256, no. 1-2, p. 68-77.

Dean, T. J., et J. N. Long. 1986. «Variation in sapwood area-leaf area relations within two stands of lodgepole pine». *Forest Science,* vol. 32, no. 3-2, p. 749-758.

Deleuze, C., J. C. Herve, F. Colin et L. Ribeyrolles. 1996. «Modelling crown shape of Picea abies: Spacing effects». *Canadian Journal of Forest Research-Revue Canadienne de Recherche Forestière,* vol. 26, no. 11, p. 1957-1966.

Deckmyn, G., S.P. Evans and T.J. Randle. 2006. «Refined pipe theory for mechanistic modelling of wood development». *Tree Physiology,* vol. 26 p. 703-717.

Ducey, M. J. 2009. «Predicting crown size and shape from simple stand variables». *Journal of sustainable forestry,* vol. 28, no. 1-2, p. 5-21.

Duursma, R.H., et A. Mäkelä. 2007. «Summary models for light interception and light-use efficiency of non-homogeneous canopies». *Tree Physiology*, vol. 27, p. 859-870.

Ellsworth, D. S., et P. B. Reich. 1993. «Canopy structure and vertical patterns of photosynthesis and related leaf traits in a deciduous forest». *Oecologia*, vol. 96, no. 2, p. 169-178.

Enquist, B. J., G. B. West, E. L. Charnov et J. H. Brown. 1999. «Allometric scaling of production and life-history variation in vascular plants». *Nature*, vol. 401, no. 6756, p. 907-911.

Ewers, B.E., S.T. Gower, B. Bond-Lamberty and C.K. Wang. 2005. «Effects of stand age and tree species on canopy transpiration and average stomatal conductance of boreal forest». *Plant, Cell & Environment*, vol. 28, p. 660-678.

Farnsworth, K.D., et P.R. Van Gardingen. 1995. «Allometric analysis of Sitka spruce branches: mechanical versus hydraulic design principles». *Trees*, vol. 10, p. 1-12.

Garber, S. M., et D. A. Maguire. 2005. «The response of vertical foliage distribution to spacing and species composition in mixed conifer stands in central Oregon». *Forest Ecology and Management*, vol. 211, no. 3, p. 341-355.

Gillespie, A. R., H. L. Allen et J. M. Vose. 1994. «Amount and Vertical-Distribution of Foliage of Young Loblolly-Pine Trees as Affected by Canopy Position and Silvicultural Treatment». *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestière*, vol. 24, no. 7, p. 1337-1344.

Gilmore, D. W., et R. S. Seymour. 1997. «Crown architecture of Abies balsamea from four canopy positions». *Tree Physiology*, vol. 17, no. 2, p. 71-80.

Gilmore, D. W., R. S. Seymour et D. A. Maguire. 1996. «Foliage-sapwood area relationships for Abies balsamea in central Maine, U.S.A.». *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestière*, vol. 26, p. 2071-2079.

Goudiaby, V., S. Brais, F. Berninger et R. Schneider. 2012. «Vertical patterns in specific volume increment along stems of dominant jack pine (*Pinus banksiana*) and black spruce (*Picea mariana*) after thinning». *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestière*, vol. 42, p. 733-748.

Grier, C. C., et Waring, R. H. 1974. «Conifer foliage mass related to sapwood ». *Forest Science*, vol. 20, no. 3, p. 205-206.

Grossnickle, Steven C. 2000. *Ecophysiology of Northern Spruce Species the Performance of Planted Seedlings*: Ottawa National Research Council of Canada.

Hann, D.W. 1999. «An adjustable predictor of crown profile for stand-grown Douglas-fir trees». *Forest Science,* vol. 45, no. 2 p. 217-225.

Harper, G. J. 2008. «Quantifying branch, crown and bole development in *Populus tremuloides* Mich. from north-eastern British Columbia». *Forest Ecology and Management,* vol. 255, p. 2286-2296.

Hegyi, F. 1974. «A simulation model for managing jack pine stands». *In Growth Models for Tree and Stand Simulation. Edited by* J. Fries. Royal College of Forestry. p.74-90. Stockholm, Sweden.

Horn, H.S. . 1976. *The adaptive geometry of trees*. Princeton Princeton University Press.

Husch, B., C.I. Miller et T.W. Beers. 1982. *Forest Mensuration*, 3rd. Malabar, Florida: Krieger publishing company.

Jessome, A.P. (1977). *Résistance et propriété connexe des bois indigènes au Canada*. Forintek Canada.

Kantola, A., et A. Makela. 2004. «Crown development in Norway spruce [Picea abies (L.) Karst.]». *Trees-Structure and Function,* vol. 18, no. 4, p. 408-421.

Kaufmann, M.R. and C.A. Troendle. 1981. «The relationship of leaf area and foliage biomass to sapwood conducting area in four subalpine forest tree species». *Forest Science,* vol. 27, p. 477-482.

Kayama, Masazumi, Satoshi Kitaoka, Wenjie Wang, Dongsu Choi et Takayoshi Koike. 2007. «Needle longevity, photosynthetic rate and nitrogen concentration of eight spruce taxa planted in northern Japan». *Tree Physiology,* vol. 27, p. 1585-1593.

King, D. A. 2005. «Linking tree form, allocation and growth with an allometrically explicit model». *Ecological Modelling,* vol. 185, no. 1, p. 77-91.

King, D. A., 1981. «Tree dimensions: maximizing the rate of height growth in dense stands». *Oecologia* vol. 51, p. 351-356.

Koch, G. W., S. C. Stillet, G. M. Jennings et S. D. Davis. 2004. «The limits to tree height». *Nature,* vol. 428, no. 6985, p. 851-854.

Kneeshaw, D. D., R. K. Kobe, D. K. Coates et C. Messier. 2006. «Sapling size influences shade tolerance ranking amoung southern boreal tree species». *Journal of Ecology*, vol. 94, no. 2, p. 471-480.

Lamhamedi, M. S., et P. Y. Bernier. 1994. «Ecophysiology and field performance of black spruce (*Picea mariana*) - a review». *Annales Des Sciences Forestieres*, vol. 51, no. 6, p. 529-551.

Landsberg, J. J., et S.T. Gower. 1997. *Applications of physiological ecology to forest management*. Academis press, Londre.

Landsberg, M. S., et P. Y. Bernier. 1994. « A generalised model of forest productivity using simplified concepts of radiation-use efficiency, carbon balance and partitioning». *Forest Ecology and Management*, vol. 95, p. 209-228.

Larsen, James Arthur. 1980. *The Boreal Ecosystem*: New York ; Toronto Academic Press.

Maguire, D. A., et D. W. Hann. 1990. «Constructing models for direct prediction of 5-year crown recession in southwestern Oregon Douglas-fir». *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestière*, vol. 20, no. 7, p. 1044-1052.

Maguire, D. A., et W. S. Bennett. 1996. «Patterns in vertical distribution of foliage in young coastal Douglas-fir». *Canadian Journal of Forest Research-Revue Canadienne de Recherche Forestière*, vol. 26, no. 11, p. 1991-2005.

Mäkelä, A. 1997. «A carbon balance model of growth and self-pruning in trees based on structural relationships». *Forest Science*, vol. 43, no. 1, p. 7-24.

Mäkelä, A., et A. Albrektson. 1992. «An analysis of the relationship between foliage biomass and crown surface in *Pinus sylvestris* in sweden.». *Scandinavian Journal of Forest Research*, vol. 7, p. 297-307.

Makela, A., et P. Vanninen. 2001. «Vertical structure of Scots pine crowns in different age and size classes». *Trees-Structure and Function*, vol. 15, no. 7, p. 385-392.

Mäkelä, A., et P. Vanninen. 1998. «Impacts of size and competition on tree form and distribution of aboveground biomass in Scots pine». *Canadian Journal of Forest Research-Revue Canadienne de Recherche Forestière*, vol. 28, no. 2, p. 216-227.

Mäkelä, A. and H.T. Valentine. 2006. «Crown ratio influences allometric scaling in trees». *Ecology*, vol. 87, p. 2967-2972.

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Man, R., et V. J. Lieffers. 1997. «Seasonal photosynthetic responses to light and temperature in white spruce (*Picea glauca*) seedlings planted under an aspen (*Populus tremuloides*) canopy and in the open». *Tree Physiology*, vol. 17, no 7, p. 437-444.

Marfo, J., et Q. L. Dang. 2009. «Interactive effects of carbon dioxide concentration and light on the morphological and biomass characteristics of black spruce and white spruce seedlings». *Botany*, vol. 87, no. 1, p. 67-77.

Marie-Victorin, F. 1995. *Flore Laurentienne*, 3ième édition. Boucherville, Qc: Gaëtan Morin Éditeur Ltée.

McMahon, T. A. 1973. «Size and shape in biology». *Science*, vol. 179, no. 4079, p. 1201-1204.

McMahon, T. A., et R. E. Kronauer. 1976. «Tree structures: deducing the principle of mechanical design». *Journal of Theoretical Biology*, vol. 59, no. 2, p. 443-466.

Messier, C., R. Doucet, J. C. Ruel, Y. Claveau, K. Colin et M. J. Lechowicz. 1999. «Functional ecology of advance regeneration in relation to light in boreal forests». *Canadian Journal of Forest Research-Revue Canadienne de Recherche Forestière*, vol. 29, p. 812-823.

Mitchell, Kenneth J. 1975. «Dynamics and simulated yield of Douglas-fir.». *Forest Science Monograph*, vol. 17.

Mizoue, N., et T. Masutani. 2003. «Image analysis measure of crown condition, foliage biomass and stem growth relationships of *Chamaecyparis obtusa*». *Forest Ecology and Management*, vol. 172, no. 1, p. 79-88.

Nepal, S. K., G. L. Somers et S. B. Caudill. 1996. «A stochastic frontier model for fitting tree crown shape in loblolly pine (*Pinus taeda* L.)». *Journal of Agricultural, Biological, and Environmental Statistics*, vol. 1, no. 3, p. 336-353.

Niklas, Karl J. 1994. «Plant allometry : the scaling of form and process». Chicago: University of Chicago Press.

Niklas, K. J., et H. C. Spatz. 2004. «Growth and hydraulic (not mechanical) constraints govern the scaling of tree height and mass». *Proceedings of the National Academy of Sciences of the United States of America*, vol. 101, no. 44, p. 15661-15663.

O'Brien, S. T., S. P. Hubbell, P. Spiro, R. Condit et R. B. Foster. 1995. «Diameter, height, crown, and age relationships in eight neotropical tree species». *Ecology*, vol. 76, no. 6, p. 1926-1939.

Oker-Blom, P., et S. Kellomaki. 1983. «Effect of grouping of foliage on the within-stand and within-crown light regime - comparison of random and grouping canopy models». *Agricultural Meteorology*, vol. 28, no. 2, p. 143-155.

Oker-Blom, P., T. Pukkala et T. Kuuluvainen. 1989. «Relationship between radiation interception and photosynthesis in forest canopies - effect of stand structure and latitude». *Ecological Modelling*, vol. 49, no. 1-2, p. 73-87.

Oker-Blom, P. et S. Kellomäki. 1983. «Effect of grouping of foliage on the within-stand and within-crown light regime: comparison of random and grouping canopy models». *Agricultural Meteorology*, vol. 28, p. 143-155.

Oliver, Chadwick Dearing. 1990. *Forest Stand Dynamics*: New York ; Montréal McGraw-Hill.

Pepin, S., A.P. Plamondon and A. Britel. 2002. «Water relations of black spruce trees on a peatland during wet and dry years». *Wetlands*, vol. 22, p. 225-233.

Perron, J. Y. 1985. *Tarif de cubage général, volume marchand brut.* Québec, Direction des inventaires forestiers. Ministère des ressources naturelles de la faune et des parcs. Gouvernement du Québec.

Pinheiro, J.C., Bates, D.M., DebRoy, S., Sarkar, D., et The R Core Team. 2010 Nlme: Linear and nonlinear mixed effects models. R package version 3.1-103. Available online at www.rproject.org.

Pinheiro, J.C., et D.M. Bates. 2000. *Mixed Effects Models in S and S-Plus.* . Coll. «Statistics and Computing». New-York: Springer-Verlag.

Popma, J., et F. Bongers. 1988. «The effect of canopy gaps on growth and morphology of seedlings of rain forest species». Oecologia, vol. 75, p. 625-632.

Porte, A., A. Bosc, I. Champion et D. Loustau. 2000. «Estimating the foliage area of Maritime pine (*Pinus pinaster* Ait.) branches and crowns with application to modelling the foliage area distribution in the crown». *Annals of Forest Science*, vol. 57, no. 1, p. 73-86.

Pothier, D., H. A. Margolis, J. Poliquin et R. H. Waring. 1989. «Relation between the anatomy and the permeability of jake pine sapwood trough stand development». *Canadian Journal of Forest Research-Revue Canadienne de la recherche Forestière*, vol. 19, p. 1564-1570.

Pothier, D., et F. Savard. 1998. *Actualisation des tables de production pour les principales espèces forestières du Québec*. Québec: Ministère des ressources naturelles et de la faune du Québec.

Power, H., V. LeMay, F. Berninger, D. F. Sattler et D. D. Kneeshaw. 2012. «Differences in crown characteristics between black (*Picea mariana*) and white spruce (*Picea glauca*)». *Canadian Journal of Forest Research-Revue Canadienne de Recherche Forestière*, vol. 42, no. 9, p. 1733-1743.

Protz, C.G., U. Silins and V.J. Lieffers. 2000. «Reduction in branch sapwood hydraulic permeability as a factor limiting survival of lower branches of lodgepole pine». *Canadian Journal of Forest Research-Revue Canadienne de Recherche Forestière*, vol. 30, p. 1088-1095.

Putz, F. E., G. G. Parker et J.H. Archibald. 1984. «Mechanical abrasion and intercrown spacing». *American Midland Naturalist*, vol. 112, p. 24-28.

Rennolls, K. 1994. «Pipe-model theory of stem profile development». *Forest Ecology and Management*, vol. 69, p. 41-55.

Robichaud, E., et I. Methven. 1992. «The applicability of the pipe model theory for the prediction of foliage biomass in trees from natural, untreated black spruce stands.». *Canadian Journal of Forest Research-Revue Canadienne de Recherche Forestière*, vol. 22, p. 1118-1123.

Saito, S., T. Sato, Y. Kominami, D. Nagamatsu, S. Kuramoto, T. Sakai, R. Tabuchi et A. Sakai. 2004. «Modeling the vertical foliage distribution of an individual *Castanopsis cuspidata* (Thunb.) Schottky, a dominant broad-leaved tree in Japanese warm-temperate forest». *Trees-Structure and Function*, vol. 18, no. 4, p. 486-491.

Sattler, D. F., et V. Lemay. 2011. «A system of nonlinear simultaneous equations for crown length and crown radius for the forest dynamics model SORTIE-ND». *Canadian Journal of Forest Research-Revue Canadienne de Recherche Forestière*, vol. 41, no. 8, p. 1567-1576.

Schmidt-Nielsen, K. 1984. *Scaling Why is Animal Size soImportant?* Cambridge: Cambridge university press.

Schneider, R., M. Fortin, C. H. Ung, D.E. Swift et S. Y. Zhang. 2011. «Modeling jack pine (*Pinus banksiana*) foliage density distribution». *Forest Science*, vol. 57, no. 3, p. 180-188.

Shinozaki, K., K. Yoda, K. Hozumi et T. Kira. 1964a. «Aquantitative analysis of plant form - The pipe model theory 1. Basic analyses.». *JapaneseJournal of ecology*, vol. 14, no. 3, p. 97-104.

Shinozaki, K. 1964b. «A quantitative analysis of of plant form - Thepipe model theory. II. Further evidence of the theory and its application in forest ecology». *Japanese journal of ecology*, vol. 14, no. 4, p. 133-139.

Sorrensen-Cothern, K. A., E. D. Ford et D. G. Sprugel. 1993. «A model of competition incorporating plasticity through modular foliage and crown development». *Ecological Monographs*, vol. 63, no. 3, p. 277-304.

Sprugel, D. G. 1983. «Correcting for bias in log-transformed allometric equations». *Ecology*, vol. 64, no. 1, p. 209-210.

Sutton, R.F. (1969). *Silvics of White Spruce [Picea glauca (Moench) Voss]*. Ottawa, Department of fisheries and forestry - Canada..

Thiffault, Nelson, Vincent Roy, Guy Prégent, Guillaume Cyr, Robert Jobidon et Jean Ménétrier. 2003. «La sylviculture des plantations résineuses au Québec». *Le Naturaliste Canadien*, vol. 127, no. 1, p. 63-80.

Thorpe, H.C., R. Astrup et K.D. Coates. 2010. «Competition and tree crowns: A neighborhood analysis of three boreal three species». *Forest Ecology and Management*, vol. 259, p. 1586-1596.

Tyree, M.T., et M.H. Zimmermann. 2002. *Xylem Structure and the Ascent of Sap*, second. Coll. «Springer Series in Wood Science». Berlin: Springer.

Ung, C.H., P. Bernier et X.J. Guo. 2008. «Canadian national biomass equations: new parameter estimates that include British Columbia Data». *Canadian Journal of Forest Research-Revue Canadienne de Recherche Forestière*, vol. 38, p. 1123-1132.

Valentine, H. T., A. R. Ludlow et G. M. Furnival. 1994. «Modeling crown rise in even-aged stands of Sitka spruce or loblolly pine». *Forest Ecology and Management*, vol. 69, no. 1-3, p. 189-197.

Valentine, H. T., et A. Mäkelä. 2005. «Bridging process-based and empirical approaches to modeling tree growth». *Tree Physiology*, vol. 25, no. 7, p. 769-779.

Vanninen, P., H. Ylitalo, R. Sievanen et A. Makela. 1996. «Effects of age and site quality on the distribution of biomass in Scots pine (*Pinus sylvestris* L)». *Trees-Structure and Function*, vol. 10, no. 4, p. 231-238.

Vincent, A.B. (1965). *Black Spruce, A Review of its Silvics, Ecology and Silviculture*. Department of Forestry. Otawa, Department of Forestry Canada.

Von Gadow, K., et G. Hui. 1999. *Modelling Forest Development*. Dordrecht: Kluwer academic publishers.

Wang, Y.P., P.G. Jarvis et M.L. Benson. 1990. «Two dimensional needle-area density distribution within the crowns of *Pinus radiata*. ». *Forest Ecology and Management*, vol. 32, p. 217-237.

Waring, R. H., P.E. Schroeder et R. Oren. 1982. «Application of the pipe model theory to predict canopy leaf area». *Canadian Journal of Forest Research-Revue Canadienne de Recherche Forestière*, vol. 12, p. 556-560.

Weiskittel, A. R., D. W. Hann, J. A. Kershaw Jr et J.K. Vanclay. 2011. *Forest Growth and Yield Modeling*. West Sussex, UK.: Wiley-Blackwell.

Weiskittel, A. R., J. A. Kershaw Jr., P. V. Hofmeyer et R. S. Seymour. 2009. «Species differences in total and vertical distribution of branch- and tree-level leaf area for five primary conifer species in Maine, USA. » *Forest Ecology and Management*, vol. 258, p.1695-1703.

West, G. B., J. H. Brown et B. J. Enquist. 1997. «A general model for the origin of allometric scaling laws in biology». *Science*, vol. 276, no. 5309, p. 122-126.

Whitehead, D. 1978. «The estimation of foliage area from sapwood basal area in Scots pine». *Forestry*, vol. 51, p. 137-149.

Wiemann, M. C. et G. B. Wiliamson. 1989. «Wood specific gravity gradients in tropical dry and montane rain forest trees». *American Journal of Botany*, vol. 76, no. 6, p. 924-928.

Wright, I. J. et al. 2004. «The worldwide leaf economics spectrum». *Nature,* vol. 428, p. 821-827.

Xu, M. G., et T. B. Harrington. 1998. «Foliage biomass distribution of loblolly pine as affected by tree dominance, crown sire, and stand characteristics». *Canadian Journal of Forest Research-Revue Canadienne de Recherche Forestière,* vol. 28, no. 6, p. 887-892.

Zeide, B., et P. Pfeifer. 1991. «A method for estimation of fractal dimension of tree crowns». *Forest Science,* vol. 37, no. 5, p. 1253-1265.