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LISTE DES SYMBOLES

A	a	Species-specific coefficients for DBH estimate
	ACAC	Année de croissance après coupe
	AEA	Année étude d'arbre
	A_{max}	Light-saturated rate of net photosynthesis ($\mu\text{mol m}^{-2} \text{s}^{-1}$; $\mu\text{mol kg}^{-1} \text{s}^{-1}$)
	a_n	Specific leaf area, in chapter 4 ($\text{m}^2 \text{kg}^{-1}$)
	a_q	Parameter related to self-pruning
	AR(1)	First-order autoregressive covariance structure
	Aut	Autumn
	$AWHC_{\text{mass/mass}}$	Mass based Available Water Holding Capacity (g g^{-1})
	$AWHC_{\text{vol/vol}}$	Volume based Available Water Holding Capacity ($\text{cm}^3 \text{cm}^{-3}$)
	a_o	Decrease of photosynthesis per unit crown length (m^{-1})
B	b	Species-specific coefficients for DBH estimate
	BD_w	Branchwood mass density (kg m^{-3})
C	c_b	Ratio of crown radius to crown length
	C_{max}	Maximum crown coverage
	c_t	Ratio of transport root length to stem length
D	$D_{1.3}^{9+}$	Average diameter at breast height for all stems ≥ 9 cm (cm)
	DBH	Diameter at breast height – 1.30 m of stem height (cm)
	DBH_{dom}	Dominant diameter at breast height – 1.30 m of stem height (cm)
	D_{br}	Branch diameter (mm)
	DHP	Diamètre à hauteur de poitrine (cm)
	ds_0, db_0, dt_0	Specific sapwood area turnover rate per unit relative pruning (yr^{-1})
	ds_1, db_1, dt_1	Specific sapwood area turnover rate in case of pruning (yr^{-1})

	D_{sp}	Stump diameter (cm)
	DW	Dry weight (kg)
F	F	Fisher value
	FC_{mass}	Field capacity (g)
	fe	Bark factor
	FD_w	Foliage mass density of the crown ($kg\ m^{-3}$)
	F_v	Fractal volume of tree crown (m^3)
G	$G_{1.3}$	Stand basal area at breast height ($m^2\ ha^{-1}$)
	G_a	Stand basal area after thinning - Residual ($m^2\ ha^{-1}$)
	GE	Growth efficiency ($m^3\ kg^{-1}\ yr^{-1}$)
	G_h	Basal area removed by thinning ($m^2\ ha^{-1}$)
	G_i	Initial basal area - before thinning ($m^2\ ha^{-1}$)
	$g_{1.3}$	Tree basal area at breast height ($cm^2\ tree^{-1}$)
	G_r	Relative basal area removed (%)
H	H_b	Crown radius (m)
	H_c	Crown length (m)
	H_{dom}	Dominant tree height (m)
	H_s	Length of the bare stem (m) = Height of crown base (m)
	H_t	Transport root radius (m)
	H_{br}	Branch relative depth into crown
	H_{cr}	Crown section height (m)
	H_{sp}	Stump height (cm)
	H_{tr}	Total tree height (m)
	H_{ts}	Height of the stem section (m)
I	i_{DBH}	Tree diameter increment at breast height ($cm\ yr^{-1}$)
	i_G	Annual stand basal area increment ($m^2\ ha^{-1}\ yr^{-1}$)
	i_g	Annual cross-sectional stem area at breast height ($cm^2\ tree^{-1}\ yr^{-1}$)

	i_{gub}	Cross-sectional stem area at 1.3 m increment under bark ($\text{cm}^2 \text{ yr}^{-1}$)
	$g_{1.3ub}$	Cross-sectional stem area at 1.3 m under bark (cm^2)
	i_{Htr}	Tree height increment (m yr^{-1})
	i_{Va}	Annual stand volume increment ($\text{dm}^3 \text{ ha}^{-1} \text{ yr}^{-1}$)
	i_{Vtr}	Annual stemwood volume increment ($\text{dm}^3 \text{ tree}^{-1} \text{ yr}^{-1}$)
	i_{Vn-5b}	5-year average total stemwood volume increment before thinning ($\text{dm}^3 \text{ tree}^{-1} \text{ yr}^{-1}$)
K	K	Extinction coefficient
L	L	Leaf area index
	L_{br}	Branch length (cm)
	LCP	Photosynthetic light compensation point ($\mu\text{mol m}^{-2} \text{ s}^{-1}$; $\mu\text{mol kg}^{-1} \text{ s}^{-1}$)
M	M	Total specific mortality rate (yr^{-1})
N	N	Number of replications (plots or individuals)
	N_a	Stand density after thinning (tree ha^{-1})
	n.a.	Not available
	N_h	Stem density harvested during thinning (tree ha^{-1})
	N_i	Initial stand density (before thinning) (tree ha^{-1})
	n.r.	No random effect in the regression model
P	p	Probability at 0.05
	P_0	Maximum rate of canopy photosynthesis per unit area ($\text{kg C m}^2 \text{ yr}^{-1}$)
	PAR	Photosynthetic active radiation ($\mu\text{mol m}^{-2} \text{ s}^{-1}$)
	PPFD	Photosynthetic photon flux density ($\mu\text{mol m}^{-2} \text{ s}^{-1}$)
	PWP_{mass}	Permanent wilting point (g)

Q	Q_{10}	Temperature response coefficient of respiration
R	r_1	Specific maintenance respiration rate of foliage + fine roots
	r_2	Specific maintenance respiration rate of wood
	R_d	Diurnal respiration of needles ($\mu\text{mol m}^{-2} \text{s}^{-1}$; $\mu\text{mol kg}^{-1} \text{s}^{-1}$)
	REG	Regression procedure in sas software
S	S	Cambium surface (m^2)
	SE	Standard Error
	s_f	Specific senescence rate of foliage (yr^{-1})
	SI_{50}	Site index (height in metre at age 50)
	SLA	Specific Leaf Area, in chapter 2 ($\text{m}^2 \text{kg}^{-1}$)
	SP(POW)	Spatial power covariance structure
	s_r	Specific senescence rate of fine roots (yr^{-1})
	Sum	Summer
	SVI	Specific Volume of stemwood Increment ($\text{cm}^3 \text{cm}^{-2} \text{yr}^{-1}$)
	SVI_{5b}	Average SVI of 5-year period preceding thinning ($\text{cm}^3 \text{cm}^{-2} \text{yr}^{-1}$)
	SWC	Gravimetric soil Water Content
	SWC_{depth}	Available soil Water Content (cm)
	S-Y_M	Season-Year of tree harvesting and Measurements
	S-Y_T	Season-Year of Thinning
	S_{3y}	Stemwood biomass increment of the last three years after thinning (kg)
T	t	Student value
	T	Time of day
V	V_n	Stemwood volume, for the year n ($\text{dm}^3 \text{yr}^{-1}$)
	V_r	Total stem volume ($\text{dm}^3 \text{tree}^{-1}$)
	V_a	Total stand volume after thinning ($\text{m}^3 \text{ha}^{-1}$)
	V_h	Total stand volume removed by thinning ($\text{m}^3 \text{ha}^{-1}$)

	V_i	Total stand volume before thinning ($\text{dm}^3 \text{ tree}^{-1}$)
	VIF	Variance Inflation Factor
	VPD	Vapour Pressure Difference ($\mu\text{mol H}_2\text{O m}^{-2} \text{ s}^{-1}$)
W	W_b	Sapwood weight of the branches (kg)
	W_{BW}	Total tree branchwood dry weight (kg tree^{-1})
	W_{bw}	Branchwood dry weight of crown section (kg)
	W_{F}	Total tree foliage dry weight (kg)
	W_{f}	Foliage dry weight of crown section (kg)
	Win	Winter
	W_r	Tree fin root dry weight (kg)
	W_s	Sapwood weight of the stem (kg)
	W_t	Sapwood weight of the transport roots (kg)
Y	Y	Carbon use efficiency ($\text{kg C kg}^{-1} \text{ DW}$)
	yr	Year
	Yr_AT	Year after thinning
Z	2z	“Fractal dimension” of foliage in crown
0 - 9	1a	Dépôts de till
	4gs	Dépôts glaciolacustres de texture grossière
	4ga	Dépôts glaciolacustres de texture fine - argile
$\alpha - \omega$	α	Apparent quantum yield ($\mu\text{mol m}^{-2} \text{ s}^{-1}$ ou $\mu\text{mol kg}^{-1} \text{ s}^{-1}$)
	α_b	Sapwood area: foliage weight ratio in branches ($\text{m}^2 \text{ kg}^{-1}$)
	α_r	Fine root: foliage weight ratio
	α_s	Sapwood area: foliage weight ratio in stem ($\text{m}^2 \text{ kg}^{-1}$)
	α_t	Sapwood area: foliage weight ratio in transport roots ($\text{m}^2 \text{ kg}^{-1}$)
	$\beta_1 \rightarrow \beta_4$	Coefficients of the regression models, in chapter 3
	$\beta_1 \rightarrow \beta_3$	Parameters for crown height estimation, in chapter 4

μ	Overall mean of the regression models
ε_{bp}	Error term of the regression models
γ_{bp}	Random effect of the regression model associated with block
δ	Parameter for quadratic and arithmetic DBH relationship
ε	Quantum efficiency (kg C MJ^{-1})
ξ	“Surface area density” of foliage ($\text{kg m}^{-2.5}$)
ρ_s	Stemwood density (kg m^{-3})
ρ_b	Branchwood density (kg m^{-3})
ρ_t	Transport root density (kg m^{-3})
σ_1	Parameter for DBH variance and DBH relationship
σ_2	Parameter for DBH variance and DBH relationship
ϕ'_b	Form factor of stemwood in branches
ϕ_c	Form factor of stemwood in stem within crown
ϕ_s	Form factor of stemwood in stem below crown
$\phi_{s,tot}$	Parameter for stem volume and basal area \times stem height
ϕ'_t	Form factor of stemwood in transport roots
ψ_s	Form factor of senescent sapwood in stem below crown
ψ_c	Form factor of senescent sapwood in stem inside crown
ψ'_b	Form factor of senescent sapwood in branches
ψ'_t	Form factor of senescent sapwood in transport roots

RÉSUMÉ GÉNÉRAL

En raison de la difficulté d'approvisionnement en bois de qualité que traverse le Québec, l'éclaircie commerciale a été préconisée comme un moyen sylvicole d'accroître le potentiel de croissance des espèces d'intérêt commercial. L'effet de l'éclaircie commerciale a été étudié chez le pin gris (*Pinus banksiana* Lamb.) et chez l'épinette noire (*Picea mariana* (Mill.) BSP). Notre hypothèse générale était que le pin gris, qui est intolérant à l'ombre, répondrait rapidement et intensément à l'éclaircie alors que l'épinette noire, modérément tolérante à l'ombre, répondrait plus faiblement.

La thèse a été réalisée en Abitibi-Témiscamingue et aborde la réponse écophysologique des deux essences à l'ouverture du couvert dans un contexte d'éclaircie commerciale à travers trois études prenant place à des échelles spatiales et temporelles différentes. Dans le cadre des deux premières études, des dispositifs expérimentaux distincts ont été mis en place pour chacune des deux essences. Dans chaque dispositif, un traitement témoin (sans intervention) et deux traitements d'éclaircie - des réductions relatives de surface terrière (G_r) de 0,3 et 0,4 pour le pin gris, de 0,4 et 0,5 pour l'épinette noire (chapitre II) et de 0,4 et 0,5 pour les deux espèces (chapitre III), ont été assignées aléatoirement à des parcelles expérimentales dans deux blocs expérimentaux pour chacune des deux espèces (chapitre II) et dans cinq blocs expérimentaux pour le pin gris et quatre pour l'épinette noire (chapitre III).

La première étude s'intéresse à la réponse des aiguilles et étudie la photosynthèse des deux essences sur une base journalière en même temps que les paramètres de la photosynthèse. La deuxième étude porte sur une période d'un à six ans après éclaircie et aborde la réponse des tiges individuelles mise en lumière à partir d'analyses de tiges effectuées sur 30 individus de pin gris et 24 d'épinette noire. Nous nous sommes intéressés à la distribution de croissance le long de la tige, aux modifications de structure de cime et à l'efficacité de croissance. Alors que les deux premières études utilisent une approche expérimentale, la troisième repose sur le modèle CroBas, un modèle de bilan de C, que nous avons paramétrisé pour chacune des deux essences en utilisant les données récoltées dans le cadre des deux premières études et des données provenant de la littérature. Le modèle simule la réponse des peuplements pour une période allant jusqu'à 20 ans après éclaircie.

À l'échelle spatiale de l'aiguille, la concentration en N et la surface foliaire spécifique n'ont pas varié significativement à la suite de l'éclaircie aussi bien chez le pin gris que chez l'épinette noire. À l'échelle temporelle de la seconde, l'efficacité photosynthétique (α), la respiration diurne (R_d), la photosynthèse au point de compensation (LCP) et le taux de photosynthèse nette à lumière saturante (A_{max}) n'ont également pas réagi significativement à l'éclaircie chez les deux espèces. À l'échelle journalière et pour les aiguilles âgées d'un an, la photosynthèse a connu une augmentation significative à l'image de la lumière chez le pin gris, ce qui n'a pas été le cas chez l'épinette noire. La réponse positive observée chez le pin

gris a été liée à l'augmentation de la lumière après éclaircie, les réserves hydriques du sol étant demeurées inchangées.

À l'échelle de l'individu et de l'année et sur une période de 6 ans, la réponse des arbres a été évaluée en fonction de la surface terrière prélevée relative [surface terrière prélevée / surface terrière initiale) $\times 100$]. En l'absence d'éclaircie, l'accroissement en volume spécifique de bois ou SVI (rapport de l'accroissement annuel de la tige sur la surface cambiale) a été de 0,75 et 0,76 $\text{cm}^3 \text{cm}^{-2} \text{an}^{-1}$ (1,30 m du sol) respectivement chez le pin gris et chez l'épinette noire. Toutefois, on a noté des accroissements significatifs en SVI deux et trois ans après éclaircie respectivement chez le pin gris et chez l'épinette noire. À 6 ans après éclaircie, les SVI ont été chez le pin gris et chez l'épinette noire, respectivement de 1.77 $\text{cm}^3 \text{cm}^{-2} \text{an}^{-1}$ et de 1.10 $\text{cm}^3 \text{cm}^{-2} \text{an}^{-1}$ (1,30 m du sol) pour la plus forte intensité d'éclaircie (réduction de surface terrière de 47,87 %). L'accroissement annuel absolu en volume de tige a été significatif dès les troisième et quatrième années après éclaircie respectivement chez le pin gris et chez l'épinette noire. L'accroissement en SVI a débuté en bas de la tige et s'est propagé en hauteur par la suite chez le pin gris alors que l'épinette noire a montré une réponse uniforme le long de la tige. L'efficacité de croissance (rapport de l'accroissement en biomasse de tige sur la biomasse foliaire) et la biomasse foliaire à mi-couronne ont significativement augmenté après éclaircie chez le pin gris et expliquent sa réponse positive alors que l'épinette noire a eu un choc d'éclaircie (réduction de SVI) les première et deuxième années après traitement. La réponse positive qui a suivi a été liée à une plus forte productivité associée à une allométrie inchangée.

Les courbes de simulations de hauteur et de DHP obtenues à l'aide du modèle CroBas ont montré un bon ajustement à celles de Pothier et Savard (1998). Les accroissements en DHP, hauteur et volume ont également montré un bon ajustement aux accroissements issus de nos données expérimentales six ans après éclaircie aussi bien chez le pin gris que chez l'épinette noire avec généralement des précisions de prédiction de plus de 80 % et des biais relativement faibles (0,01 – 0,03). À partir de valeurs initiales de volume de peuplement et de surface terrière respectivement de 347 $\text{m}^3 \text{ha}^{-1}$ et de 37 $\text{m}^2 \text{ha}^{-1}$ chez le pin gris et de 320 $\text{m}^3 \text{ha}^{-1}$ et 48 $\text{m}^2 \text{ha}^{-1}$ chez l'épinette noire, nous avons obtenu des accroissements respectifs 20 ans après éclaircie de 38 et 32 % chez le pin gris et de 25 et 20 % chez l'épinette noire et ce, pour la plus forte intensité d'éclaircie ($41 \% \leq G_r \leq 66 \%$; moyenne = 47,87 %). Toutefois, aucun effet compensatoire, à savoir une intensité d'éclaircie qui permette d'atteindre des valeurs de volume et de surface terrière d'avant traitement, n'a été noté chez les deux espèces.

La meilleure réponse à l'éclaircie du pin gris lui confère un potentiel de production ligneuse plus intéressant pour l'industrie forestière alors que l'épinette noire apparaît plus intéressante si l'objectif est de produire des tiges dont la réponse a tendance à maintenir un défilement constant.

Mots clés : Accroissement de la tige, éclaircie commerciale, modèle de bilan de carbone, photosynthèse, *Picea mariana* (Mill.) BSP, *Pinus banksiana* Lamb.

CHAPITRE I

INTRODUCTION GÉNÉRALE

1.1 Contexte général de l'étude et les enjeux mondiaux de la forêt

En 2010, la surface occupée par les forêts était de 4,03 milliards d'hectares, environ 30 % de la surface du globe terrestre, ce qui représente des réserves totales en bois estimées à près de 434 milliards de m³ (FAO, 2011). Entre 1990 et 2005, et du fait des besoins accrus, l'exploitation forestière a entraîné une réduction des forêts naturelles à l'échelle du globe de 16 millions d'hectares (West, 2006) correspondant à la coupe d'une superficie globale de 8,3 millions d'hectares par an pour un volume de 2,8 millions de m³ par an (année 2005) (FAO, 2011). Il est impossible de dissocier l'évolution des besoins en produits de bois d'une part d'avec la démographie mondiale galopante (Mather, 1992 ; FAO, 2011 ; Puettmann *et al.*, 2008) et d'autre part d'avec la croissance économique rapide (Puettmann *et al.*, 2008 ; FAO, 2011).

Initialement consécutive à l'avancée économique de l'Europe et de l'Amérique du Nord, la demande mondiale en bois est en perpétuelle progression surtout avec l'essor des pays à économie émergente comme le Brésil, la Chine, l'Inde et l'Afrique du Sud (Banque Mondiale, 2008). Dans le cas de la Chine par exemple, la demande en bois a connu une croissance de 40 millions de m³ à près de 150 millions de m³ entre 1997 et 2005 (Banque Mondiale, 2009). On prévoit que cette demande de la Chine va doubler au cours des 10 prochaines années. À l'échelle mondiale, la consommation en bois en 2006, incluant le bois pour l'énergie, le bois rond industriel et le bois de sciage, s'élevait à près de 3 508 millions de m³ (FAO, 2011). Afin de répondre adéquatement à cette demande en bois,

il devient dès lors urgent de trouver des stratégies sylvicoles permettant d'accroître la productivité des forêts.

1.2 Crise forestière, tendance lourde en aménagement et transformation

De façon générale, l'intensification de la sylviculture au cours des siècles a été conditionnée par les problèmes récurrents qu'a connus l'humanité relativement à la difficulté d'approvisionnement en bois à la suite d'une surexploitation (Puettmann *et al.*, 2008). L'industrialisation ayant débuté en Europe, les problèmes d'approvisionnement en bois y sont apparus en premier par rapport au reste du monde, ce qui est à l'origine de l'émergence d'une sylviculture ayant eu pour but l'augmentation de la productivité des peuplements forestiers. Par rapport à l'Europe, la sylviculture est relativement récente en Amérique du Nord spécialement au Canada, en raison de l'importance des surfaces forestières et de la plus grande disponibilité naturelle en bois, de sorte que les difficultés d'approvisionnement en bois y sont apparues plus tardivement qu'en Europe.

Au Québec, la difficulté d'approvisionnement en bois de qualité que traverse l'industrie forestière est documentée par la Commission d'étude sur la gestion de la forêt publique québécoise à travers un rapport de consultation produit en 2004 (Coulombe *et al.*, 2004) et qui a conclu à une surexploitation de la forêt du fait de la capacité de transformation du bois plus grande que la quantité des ressources ligneuses disponibles. En raison d'une préférence de l'industrie portant sur les résineux, la réduction de l'approvisionnement en bois de qualité s'est traduite par une tendance à la baisse du diamètre moyen des tiges récoltées du groupe sapin, épinette noire, pin gris et mélèze (SEPM) de 19 cm en 1977, à 16 cm en 2002 (Coulombe *et al.*, 2004). La Commission d'étude sur la gestion de la forêt publique a préconisé une réduction de la possibilité forestière du groupe SEPM de 20 % sur l'horizon 2008-2013 (Coulombe *et al.*, 2004), entraînant du coup la fermeture de plusieurs papetières. Cette mesure a durement touché l'Abitibi-Témiscamingue dont la forêt constitue l'une des assises économiques de la région. Toutefois, avant même que l'on entre dans cette phase de difficulté que traverse le secteur forestier, la région souhaitait déjà en 1997 mettre en place des stratégies d'aménagement forestier qui se prêtaient à des objectifs de rendement accru.

Pour cela, l'industrie forestière régionale de l'Abitibi-Témiscamingue, le ministère des Ressources naturelles et l'UQAT collaborent au suivi d'un réseau expérimental des éclaircies commerciales de l'Abitibi. L'objectif de ce réseau est de parfaire les prescriptions sylvicoles en évaluant l'effet de différentes intensités d'éclaircie et c'est aussi l'objectif de nos recherches.

1.3 L'éclaircie sylvicole

L'éclaircie est une pratique sylvicole consistant à réduire la densité des peuplements forestiers dans le but de minimiser la compétition pour la lumière, l'eau et les nutriments du sol, ce qui stimule, selon des délais variables, la croissance des individus résiduels (Hale, 2001). En fonction du DHP des individus prélevés lors de l'éclaircie, on oppose souvent l'éclaircie précommerciale qui prélève des tiges non commerciales, à l'éclaircie commerciale qui elle, prélève des diamètres de dimension commerciale, dont la rentabilité financière permettrait de couvrir certains coûts de récolte (Jørgensen, 2009). Lors de la coupe finale ou des éclaircies subséquentes, la valeur marchande des tiges récoltées, à la suite d'une éclaircie précommerciale ou commerciale, se voit théoriquement augmentée. Si l'éclaircie affecte l'étage, on parlera 1) d'éclaircie par le haut consistant à prélever des individus dominants ou codominants afin de favoriser les individus les plus vigoureux de même classe de dominance (Dunster et Dunster, 1996) ou, 2) d'éclaircie par le bas visant à prélever les individus de plus petits diamètres, déformés ou certains codominants entrant en compétition avec les individus à préserver (Dunster et Dunster, 1996). Si l'éclaircie porte sur les arbres à favoriser ou à supprimer, on parlera 1) d'éclaircie sélective qui vise particulièrement la libération la plus efficace des individus d'élite par la coupe des individus les plus gênants (Dunster et Dunster, 1996), ou 2) d'éclaircie sanitaire. Si l'éclaircie est basée sur la technique, on parlera par exemple d'éclaircie systématique en ligne consistant à prélever des lignes d'arbres complètes à intervalles réguliers intercalées de lignes d'arbres laissées intactes. L'intérêt de l'éclaircie est qu'elle est plus attractive visuellement qu'une coupe totale et mieux acceptée socialement pour les raisons suivantes : elle assure le maintien de la continuité de la forêt, génère des peuplements dont les individus ont des diamètres plus importants et des cimes plus longues et favorise l'augmentation de la pénétration de la lumière à travers le couvert (Kimmins, 1997).

1.4 Historique mondial et canadien de la recherche sur l'éclaircie

Utilisée actuellement à des fins d'augmentation de la productivité pour des raisons économiques, l'éclaircie est une coupe partielle qui a connu une évolution dans la terminologie utilisée de même que dans les concepts pratiques. Pour ce qui est de la terminologie, il existe en effet une pléthore de termes utilisés et qui définissait les traitements sylvicoles ayant eu pour objectif d'aménager les forêts tout en assurant l'intégrité du couvert forestier. Pommerening et Murphy (2004) ont recensé à travers une revue de littérature l'emploi courant de 24 termes plus ou moins synonymes. Il y a aussi des situations confuses où des coupes partielles très différentes comme celles appliquées aux peuplements équiennes et inéquiennes sont désignées sous l'unique terme général et assez peu explicite de « coupe sélective » (O'Hara, 2002). En ce qui concerne les concepts pratiques, l'éclaircie n'avait pas pour objectif à ses débuts de rentabiliser économiquement les tiges coupées lors de la première éclaircie. En effet, l'éclaircie visait à réduire la densité du peuplement en coupant les tiges de mauvaise qualité afin de permettre une meilleure croissance des individus résiduels. L'objectif de rentabiliser une première coupe d'éclaircie (éclaircie commerciale) n'est apparu que plus tard. En prenant en compte ces considérations liées à la confusion entre les termes utilisés à ses débuts et les objectifs de la coupe, des traitements sylvicoles basés sur la coupe d'arbres et qui auraient pu être des précurseurs de l'éclaircie pourraient remonter aux environs des années 1800 en Europe (Zeide, 2001).

À ses débuts en Amérique du Nord, l'éclaircie était désignée telle quelle sans distinction entre éclaircies précommerciale et commerciale (Miller *et al.*, 2004 cité par Lugo *et al.*, 2006 ; Anonyme, 1938). Ainsi, lorsque nous ferons référence à l'éclaircie dans la section suivante, celle-ci ne fera pas la différence entre les éclaircies précommerciale et commerciale. L'éclaircie est apparue d'abord en 1912 aux États-Unis principalement pour l'aménagement des forêts de sapin Douglas de la côte pacifique (Miller *et al.*, 2004 cité par Lugo *et al.*, 2006). Ensuite, les différentes étapes qui marquent les débuts de l'éclaircie au Canada (Anonyme, 1938), sont données ci-après. C'est à 1918 que remontent les plus anciens dispositifs du Canada, établis notamment en Ontario à Petawawa. Les dispositifs, qui étaient initialement des sites de démonstration d'éclaircie se sont par la suite propagés sur l'ensemble du Canada : Québec (1922-1925), Nouvelle-Écosse (1928), Nouveau-Brunswick

(1928-1936), Saskatchewan (date inconnue) et Colombie-Britannique (date inconnue). Le point commun entre tous ces dispositifs d'éclaircie à l'échelle du Canada était que la variable d'intérêt était l'accroissement annuel total en volume de bois (Anonyme, 1938). De plus, il n'existait pas à cette époque une approche rigoureuse scientifique et uniforme d'évaluation de l'effet de l'éclaircie. C'est ainsi que la première éclaircie historiquement menée au Québec (1922-1925) ne comportait pas de traitement témoin. En Saskatchewan, les parcelles n'ont été mesurées ni avant ni après l'éclaircie, et l'effet de cette dernière était évalué par une simple appréciation visuelle. L'expérience menée en Colombie-Britannique apparaît historiquement comme la première qui améliorait l'approche scientifique en étudiant différentes intensités d'éclaircie et la qualité du bois du peuplement résiduel (Anonyme, 1938).

1.5 Importance économique du pin gris et de l'épinette noire

Deux des espèces d'importance commerciale de la forêt boréale de l'Est canadien sont le pin gris (*Pinus banksiana* Lamb.) et l'épinette noire (*Picea mariana* Mill. (B.S.P.)). Le pin gris présente une bonne résistance à la carie et au pourrissement (Lanouette *et al.*, 1998) et il est utilisé comme bois de construction, pâte à papier, poteaux et pieux servant de murs de soutènement (connus sous le nom de palplanches) (Sims *et al.*, 1990). L'épinette noire quant à elle sert comme bois de sciage (Sims *et al.*, 1990) et est l'espèce qui produit les fibres les plus longues et les plus denses, augmentant ainsi considérablement la résistance du papier. Les peuplements de pin gris et d'épinette noire sont aussi assez abondants. Par exemple, à l'échelle du Canada, le pin gris représente à lui seul près de 20,4 % du volume sur pied des espèces appartenant au groupe des bois tendres (Lanouette *et al.*, 1998). Bien qu'on n'ait pas trouvé l'équivalent en volume à l'échelle du Canada pour l'épinette noire, celle-ci reste l'espèce la plus commune couvrant environ 150 millions de km² (Canada's NFI, 2010). Le pin gris et l'épinette noire sont aussi les deux espèces qui font l'objet au Québec d'efforts de reboisement les plus importants. Ainsi, en 2001, 21 millions de plants de pin gris, soit environ 18 % de tous les plants reboisés, ont été plantés au Québec (Plourde et Krause, 2004).

1.6 Cadre conceptuel de l'étude

Lorsqu'un peuplement atteint une densité maximale, son accroissement en volume se stabilise même si l'on fait varier par la suite la densité du peuplement (Skovsgaard et Vanclay, 2008). Quand une éclaircie est menée à ce stade de développement de peuplement où la compétition est maximale, il se produit immédiatement une réduction de l'indice de surface foliaire (LAI) (Bréda *et al.*, 1995 ; Stoneman *et al.*, 1997) couplée à une augmentation de la disponibilité en lumière (Stiell, 1980), en eau (Bréda *et al.*, 1995 ; Aussenac et Granier, 1988 ; Haberland et Wilde, 1961) et en nutriments (Haberland et Wilde, 1961). Il en résulte pour les tiges individuelles un accroissement en DHP (Finzi et Canham, 2000 ; Pelletier et Pitt, 2008), en volume (Lavigne, 1988) et en biomasse ligneuse (Brix, 1983 ; Baldwin *et al.*, 2000). L'éclaircie apparaît alors comme une redistribution d'une même quantité de ressources au profit d'un nombre restreint d'individus résiduels entraînant pour ces derniers une croissance accrue. À l'échelle du peuplement, une éclaircie forte entraîne une réduction en production de volume total de bois (Mäkinen et Isomäki, 2004 ; Skovsgaard et Vanclay, 2008), mais la production en volume marchand pourrait augmenter dans le cas d'une éclaircie faible à modérée (Mäkinen et Isomäki, 2004).

Les mécanismes qui pourraient être à l'origine des accroissements observés après éclaircie peuvent être de deux ordres :

- a- un accroissement de la capacité des arbres à faire la photosynthèse ;
- b- une modification du patron d'allocation du carbone entre les feuilles, branches, tige et racines de l'arbre (Chapin, 1991 ; Plauborg, 2004) de sorte que le rapport de l'accroissement de la tige sur celui du feuillage connu encore sous le terme d'efficacité de croissance a été proposé comme un moyen d'évaluer la vigueur des individus (Waring *et al.*, 1980). Selon Brix (1983) et Poudroux *et al.* (2001), l'éclaircie entraîne une augmentation de l'efficacité de croissance contrairement à ce qu'a rapporté Lavigne (1988) ;
- c- un accroissement de la disponibilité des ressources (lumière, eau et nutriments du sol).

Par ailleurs, l'augmentation de la croissance en réponse à l'éclaircie ou à un changement des conditions environnementales n'est pas uniforme le long de la tige (Peltola *et al.*, 2002 ; Bouriaud *et al.*, 2005). Trois hypothèses ont été avancées : la première repose sur la densité du feuillage qui peut varier en hauteur et influencer différemment la croissance des différentes sections de tiges (Forward et Nolan, 1961). La seconde stipule que l'augmentation de la biomasse foliaire après éclaircie est un poids additionnel à supporter par l'arbre qui doit changer le défilement de sa tige (Stiell, 1960) pour assurer sa stabilité mécanique. La troisième hypothèse est que les forces dues au vent sont toujours plus importantes après l'ouverture des peuplements entraînant chez l'arbre une modification de la distribution de croissance qui tendrait à rendre constant ces forces le long de la tige, c'est la théorie désignée sous le terme de « constant stress hypothesis » (Dean et Long, 1986).

1.7 Comportement du pin gris et l'épinette noire par rapport à l'éclaircie commerciale

Plusieurs essais d'éclaircie ont déjà été réalisés dans des peuplements de pin gris (Weetman, 1971 ; Krause *et al.*, 1982) et d'épinette noire (Krause *et al.*, 1982 ; Timmer, 1984 ; Fleming *et al.*, 2005). Chez le pin gris, l'augmentation de la lumière entraîne un accroissement en surface foliaire (et en volume de cime) qui favorise une meilleure interception de la lumière et une augmentation de la photosynthèse et de la productivité nette individuelle (Harrington et Edwards, 1999). Newton et Jolliffe (1998) voient en cela une plasticité phénotypique relativement aux conditions environnementales changeantes. L'utilisation efficace de la lumière serait importante en cas d'une éclaircie faible, mais déclinerait dans le cas d'une éclaircie très forte, du fait que l'intensité lumineuse dépasse le seuil qui entraîne chez l'arbre un taux maximum de photosynthèse nette. Chez l'épinette noire, la réponse à l'éclaircie se traduit par une augmentation de l'allocation des ressources destinées à la production de surface foliaire et à la croissance secondaire (DHP) perceptibles quatre ans après le traitement (Weetman, 1971). Ces résultats confirment l'idée selon laquelle le pin gris, une espèce intolérante à l'ombre, répondrait facilement aux traitements sylvicoles alors que l'épinette noire, présentant une tolérance intermédiaire à l'ombre (Sims *et al.*, 1990), répondrait faiblement aux stimuli externes.

Ainsi, même si des réponses positives à l'éclaircie ont été rapportées chez le pin gris et chez l'épinette noire, des zones d'ombre relatives aux mécanismes qui sous-tendent la réponse persistent. Il s'agit des mécanismes physiologiques, de la forme de la cime et de l'efficacité du feuillage ainsi que du fonctionnement cambial qui va réguler la formation de bois le long de la tige. L'objectif est alors d'étudier chez ces deux espèces l'effet de l'éclaircie sur leurs mécanismes physiologiques, de croissance et d'allocation de biomasse. Nous posons comme hypothèse générale que le pin gris, étant donné sa plus faible tolérance à l'ombre que l'épinette noire, devrait répondre à l'ouverture du couvert plus rapidement et plus fortement.

La vérification de l'hypothèse générale de l'étude se fera à travers une démarche qui s'articulera autour de quatre chapitres. Le premier chapitre sera une revue de littérature sur l'éclaircie. Le second chapitre abordera les réponses de photosynthèse et de respiration à la suite de l'éclaircie selon une échelle spatiale de l'aiguille et deux échelles temporelles suivantes : 1) la seconde et 2) la journée. Le troisième chapitre s'intéressera à la réponse à l'éclaircie pour ce qui est de l'accroissement en volume de la tige et en biomasse des branches et du feuillage, en même temps que les modifications au niveau de l'efficacité de croissance. La combinaison des résultats des chapitres II et III se fera à travers un modèle de bilan de carbone que nous proposerons dans le chapitre IV. Ce quatrième chapitre générera des données de simulation dont l'échelle spatiale du calcul sera l'individu et le peuplement, et celle temporelle sera l'année, et l'information originale fournie sera relative aux modifications d'allocation de carbone au niveau de la tige qui surviennent après l'éclaircie. Dans les sections suivantes, nous énoncerons les hypothèses spécifiques de chacun des chapitres de la thèse tout en fournissant les aspects détaillés de la façon dont seront menées les différentes études.

1.7.1 Chapitre II : Effets de l'éclaircie sur la photosynthèse du pin gris (*Pinus banksiana* Lamb.) et de l'épinette noire (*Picea mariana* (P. Mill.) en forêts boréales de l'est

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Malgré les différentes études écophysiological menées sur le pin gris et sur l'épinette noire (Stewart *et al.*, 1995 ; Sullivan *et al.*, 1997 ; Noland *et al.*, 2001 ; Robinson *et al.*, 2001 ; Hangs *et al.*, 2002), peu ont porté sur des individus adultes. Une généralisation des résultats obtenus sur de jeunes individus à des individus adultes est toujours problématique. En effet, il a été démontré que la conductance stomatale et son effet régulateur sur les échanges gazeux (photosynthèse et respiration), indépendamment des facteurs environnementaux, augmentait avec l'âge chez l'épinette noire (Stewart *et al.*, 1995 ; Sullivan *et al.*, 1997) et chez le pin gris (Sullivan *et al.*, 1997). Notre objectif est alors d'étudier les modifications des paramètres de la photosynthèse et de la respiration à l'échelle spatiale de l'aiguille et temporelle de la seconde et de la journée sur des individus adultes de pin gris et d'épinette noire soumis à différentes intensités d'éclaircie commerciale. De telles échelles d'étude sont justifiées par le fait qu'elles rendent mieux compte de la différence fonctionnelle entre les différents âges d'aiguilles. L'originalité de l'étude repose sur les mesures de photosynthèse dans des contextes d'éclaircie commerciale, puisque de telles mesures n'ont pas été signalées dans la littérature.

Il a été montré que les espèces intolérantes à l'ombre répondaient mieux à l'augmentation de la lumière que les espèces plus tolérantes (Wright *et al.*, 1998). Ainsi, notre hypothèse est que l'augmentation de la lumière après éclaircie entraînera une augmentation de la photosynthèse du pin gris qui est une espèce intolérante à l'ombre (Sims *et al.*, 1990) alors que l'épinette noire, modérément tolérante à l'ombre (Sims *et al.*, 1990), devrait répondre de façon plus faible.

Nos expérimentations seront conduites 2 à 3 ans après éclaircie dans des peuplements purs (au moins 75 % de la surface terrière selon l'espèce) de pin gris et d'épinette noire. Des densités relatives de 0,5 (éclaircie modérée) et 0,4 (éclaircie forte) seront ciblées pour l'épinette noire et 0,4 (éclaircie modérée) et 0,3 (éclaircie forte) pour le pin gris (Grenier *et al.*, 2001). Dans chacun des deux blocs d'étude, six individus seront choisis, soit deux individus dans chacune des 3 parcelles expérimentales du bloc représentant une intensité d'éclaircie donnée. Sur chaque individu, seront été identifiés trois rameaux portant des aiguilles de l'année et des aiguilles d'un an. Les mesures d'échange gazeux seront conduites à l'aide d'un analyseur de gaz à infrarouge (LI-COR 6400, LI-COR Inc., Lincoln, NE). Un premier type d'expérience consistera à mener des courbes de réponse de la photosynthèse à la lumière. Un deuxième type d'expérience portera sur la mesure de la photosynthèse du lever au coucher du soleil à des intervalles de 2 à 3 heures. Des mesures complémentaires comme la concentration en N des aiguilles et la surface foliaire spécifique (SLA) seront également menées. Les températures de l'air et du sol de même que la réserve hydrique du sol seront mesurées et ensuite leurs effets sur les paramètres de la photosynthèse déterminés.

Le traitement des données portera d'abord sur l'ajustement des courbes de réponse de photosynthèse à une fonction de Mitscherlich (Potvin *et al.*, 1990). Cela permettra de déterminer les paramètres de la photosynthèse suivants : le taux de photosynthèse nette à lumière saturante (A_{max}), l'efficacité photosynthétique (α), la photosynthèse au point de compensation (LCP) et la respiration diurne (R_d). Des analyses de régression seront ensuite appliquées à chacune des deux classes d'âges d'aiguilles dont la photosynthèse est exprimée par unité de surface et de masse 1) à l'échelle de la seconde : A_{max} , LCP, α et R_d , et 2) à l'échelle de la journée : la lumière atteignant les aiguilles mesurées et la photosynthèse. Le SLA et la concentration en N seront mesurés à l'échelle de l'aiguille. Pour tenir compte des différences de surfaces terrières initiales et prélevées entre les parcelles d'étude, la variable explicative constituée par l'intensité de l'éclaircie sera évaluée en surface terrière prélevée relative (surface terrière prélevée / surface terrière initiale) \times 100).

1.7.2 Chapitre III : Distribution verticale de l'accroissement en volume spécifique le long de la tige d'individus dominants de pin gris (*Pinus banksiana* Lamb.) et d'épinette noire (*Picea mariana* (Mill.) B.S.P.) en réponse à l'éclaircie

Venceslas Goudiaby, Suzanne Brais, Frank Berninger et Yvon Grenier

Ce chapitre avait été soumis au Canadian Journal of Forest Research. Nous avons été invités à le resoumettre après correction. C'est la version révisée que nous présentons dans la thèse. Cette version sera resoumise.

L'éclaircie entraîne chez le pin gris et chez l'épinette noire une augmentation du diamètre à hauteur de poitrine (Weetman, 1968, 1971 ; Vincent, 2009). Son effet sur les modifications de la distribution de la croissance le long de la tige n'est pas connu surtout dans un contexte d'éclaircie commerciale. L'objectif de l'étude est alors d'évaluer l'effet de l'éclaircie sur la croissance en volume de la tige ainsi que sur la distribution de la croissance le long de cette dernière et de les lier à l'efficacité de croissance, qui est le rapport de l'accroissement de la tige sur la surface foliaire. L'hypothèse est que le pin gris et l'épinette noire répondront à l'éclaircie par une augmentation en diamètre de leurs tiges, mais nous nous attendons à ce que l'épinette noire ait une croissance moindre en raison de sa nature conservatrice. La croissance en réponse à l'éclaircie, si l'on s'en tient aux compartiments aériens, est un phénomène complexe dont les priorités d'allocation peuvent varier entre les compartiments des branches, de la tige et du feuillage par rapport à la quantité de bois formée au cours d'une saison de croissance (Weiner, 2004). Des variations d'allocation de biomasse au sein du même compartiment sont aussi possibles. L'échelle d'étude permettant de cerner cette variabilité inter et intracompartiment, et que nous avons adoptée, est celle de l'individu et de l'année sur une période de six ans, cette dernière correspondant au délai maximum après éclaircie dont nous disposons dans nos dispositifs expérimentaux.

Le dispositif expérimental sera constitué de 5 sites (blocs) de pin gris et de 4 d'épinette noire. Des densités relatives de 0,5 (éclaircie modérée) et de 0,4 (éclaircie forte) seront ciblées pour chacune des deux espèces (Grenier *et al.*, 2001). Sur chaque arbre, le DHP, la longueur totale de l'arbre, la longueur de la tige hors cime et celle de la cime vivante seront mesurés sur 30 individus de pin gris et sur 24 d'épinette noire. La longueur, le diamètre basal et la hauteur sur le tronc de chaque branche seront mesurés et les biomasses foliaire et ligneuse de chaque branche estimées par régression grâce aux biomasses foliaires et ligneuses initialement

déterminées au laboratoire. La biomasse foliaire totale de l'arbre sera obtenue par la somme de la biomasse foliaire de chaque branche constitutive de l'arbre. Des disques de tige seront ensuite prélevés aux hauteurs suivantes : 0 m ; 0,30 m ; 0,60 m ; 1 m ; 1,30 m et à tous les mètres consécutifs jusqu'au sommet de l'arbre. L'analyse de tige sera ensuite faite au laboratoire par la mesure de la largeur des cernes de croissance et l'estimation des accroissements annuels en volume de bois à l'aide de WinDendro™ et de WinStem™ (Regent Instruments Inc., Quebec City, QC, Canada).

En ce qui concerne les analyses statistiques, les variables réponses suivantes seront testées : l'accroissement annuel total en volume de bois, l'accroissement en volume spécifique de bois, la biomasse foliaire totale de l'arbre, la densité foliaire et de branches de la cime de l'arbre et l'efficacité de croissance. Du fait des surfaces terrières initiales et des surfaces terrières prélevées différentes entre les sites, des analyses de régression seront effectuées à la place d'ANOVA. Pour cela, la surface terrière prélevée relative sera utilisée comme variable explicative. Afin de comparer les croissances entre des tiges issues de traitements d'éclaircie dont le diamètre des individus est différent d'une part et pour lier la croissance de la tige à la physiologie d'autre part, l'accroissement annuel en volume de tige sera rapporté à la surface cambiale (accroissement en volume spécifique).

1.7.3 Chapitre IV : Effets de l'éclaircie sur la croissance du pin gris (*Pinus banksiana* Lamb.) et de l'épinette noire (*Picea mariana* (Mill.) B.S.P.) – Résultats de simulations utilisant CroBas

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Plusieurs facteurs de l'environnement sont responsables de la croissance observée après éclaircie et les mécanismes de réponse des arbres ne sont pas strictement restreints à la physiologie ou à la dendrométrie, mais font appel à la combinaison des deux en plus des relations allométriques et fonctionnelles. À ce jour, le principe de l'allocation hiérarchique du carbone entre les compartiments des arbres (Lacointe, 2000) de même que des modèles combinant la relation tubulaire ou « pipe model » (Shinozaki *et al.*, 1964) et l'équilibre fonctionnel entre les compartiments aériens et sous-terrains de l'arbre ont émergé comme des approches utiles pour analyser la réponse des arbres aux variations de disponibilité en ressources. Notre objectif est alors d'adapter chez le pin gris et chez l'épinette noire un modèle structurel et fonctionnel de bilan de carbone du nom de CroBas développé initialement chez le pin sylvestre (Mäkelä, 1997) et adapté par la suite au sapin dont un module additionnel (Raulier, 2006) permet de quantifier et de prédire la croissance des diamètres commerciaux en fonction des intensités d'éclaircie.

Le modèle CroBas repose sur la division de l'arbre en cinq compartiments fonctionnels : les feuilles, la tige, les branches, les racines structurantes et les racines fines. Les feuilles assurent la fixation du carbone par photosynthèse, la tige et les branches constituent la charpente de l'arbre, les racines structurantes assurent l'ancrage de l'arbre au sol et les racines fines sont responsables du prélèvement des nutriments et de l'eau du sol. Le modèle CroBas repose sur trois principes : 1) un rapport constant entre la biomasse foliaire et la surface de la section transversale de l'aubier à la base de la cime (modèle tubulaire ou « pipe model » - Shinozaki, 1964), 2) un équilibre fonctionnel (Brouwer, 1962) qui implique

un rapport constant entre les racines fines et la biomasse foliaire, et 3) un rapport existant entre la surface foliaire et la surface latérale de la cime (dimension fractale de la cime – relation dimensionnelle). Le modèle présente un pas de temps annuel et une échelle spatiale individuelle. Le nombre d'individus à l'hectare permet cependant de ramener les variables à l'échelle du peuplement. Enfin, CroBas ne nécessite que la hauteur totale de l'arbre, la longueur de la cime et le nombre de tiges à l'hectare pour faire des simulations.

Le fonctionnement de CroBas repose sur le calcul du bilan de carbone (gain de carbone – perte de carbone). Le bilan de carbone est ensuite associé à des patrons d'allocation de biomasse au niveau des différents compartiments de l'arbre. Dans la section qui suit, nous montrerons comment ces différents paramètres sont interconnectés. La première démarche est de déterminer la biomasse des compartiments fonctionnels de l'arbre qui présentent une forme géométrique évidente (branches, tige, racines structurantes) en utilisant des équations de volume prenant en compte la surface transversale de l'aubier du compartiment concerné, sa longueur et un facteur de forme (relation structurelle). La surface transversale de l'aubier des branches, de la tige et des racines structurantes est estimée à partir de la biomasse foliaire et du modèle tubulaire. La biomasse foliaire est calculée à partir de la longueur de la cime et du rapport entre la surface latérale de la cime et la surface foliaire de l'arbre (dimension fractale). La biomasse des racines fines est estimée à partir de la biomasse foliaire en se servant du rapport de Brouwer (1962).

Le gain de carbone par photosynthèse est calculé à partir de la surface foliaire du peuplement et du taux de photosynthèse maximum. La perte de carbone est représentée par la somme de 1) la respiration d'entretien des compartiments de l'arbre et 2) la respiration de croissance des mêmes compartiments. La productivité nette est obtenue par la différence entre la photosynthèse et la respiration. Le taux de sénescence de chaque compartiment de l'arbre est ensuite intégré dans les calculs de bilan de carbone de sorte à maintenir les relations structurelles entre les compartiments de l'arbre.

Les résultats du second et du troisième chapitre, en plus des données provenant de la littérature, permettront de définir les paramètres du modèle. Pour valider le modèle, les

diamètres et les hauteurs simulés seront comparés à leurs homologues issus des tables de volume de Pothier et Savard (1998) sur l'horizon 0-120 ans. Pour améliorer l'ajustement à nos données empiriques, le modèle sera ensuite calibré en jouant sur les coefficients d'allocation de la biomasse et sur la dimension fractale. Ensuite, des scénarios d'éclaircie du chapitre III seront conduits et les DHP et surface terrière simulés seront comparés avec ceux à partir des données empiriques du chapitre III. L'allocation de carbone au niveau de la tige sera calculée, ce qui permettra de tirer des interprétations fonctionnelles à la base des réponses à l'éclaircie du pin gris et de l'épinette noire et c'est ce qui représente la contribution originale de ce quatrième chapitre.

CHAPITRE II

EFFECTS OF THINNING ON JACK PINE (*PINUS BANKSIANA* LAMB.) AND BLACK SPRUCE (*PICEA MARIANA* (MILL.) B.S.P.) PHOTOSYNTHESIS IN THE EASTERN BOREAL FORESTS OF CANADA¹

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2.1 Résumé

La réduction du diamètre marchand moyen récolté des espèces d'intérêt commercial de la forêt boréale de l'est du Canada a entraîné une difficulté de l'approvisionnement en bois de qualité destiné à l'industrie forestière. L'éclaircie commerciale est alors proposée comme une solution adéquate pour pallier ce déficit. Toutefois, les réponses physiologiques qui sous-tendent la réponse des espèces à l'éclaircie ne sont pas bien connues. Les effets de l'éclaircie commerciale sur la photosynthèse ont alors été évalués chez le pin gris (*Pinus banksiana* Lamb.) et chez l'épinette noire (*Picea mariana* (Mill.) B.S.P.). Deux dispositifs expérimentaux comportant chacun deux blocs complets randomisés ont été appliqués à chacune des deux espèces. Chaque bloc comprend une parcelle témoin non éclaircie et deux autres parcelles dont les intensités relatives sont de 0,4 (éclaircie modérée) et 0,3 (éclaircie forte) chez le pin gris et de 0,5 (éclaircie modérée) et 0,4 (éclaircie forte) chez l'épinette noire. Des courbes de réponse à la lumière de la photosynthèse de même que des cinétiques journalières de photosynthèse ont été menées sur des aiguilles de l'année et sur celles âgées d'un an provenant de 3 rameaux choisis chez deux individus par parcelle expérimentale. L'éclaircie a été évaluée en surface terrière prélevée relative $[(\text{surface terrière prélevée} / \text{surface terrière initiale}) \times 100]$ et son effet est testé sur la photosynthèse deux ans après traitement. La réserve en eau du sol, les températures de l'air et du sol et la concentration en azote des aiguilles n'ont pas été affectées par l'éclaircie chez les deux espèces. Toutefois, la disponibilité en lumière a été d'autant plus importante que l'intensité du prélèvement de surface terrière a été plus forte. Ceci pourrait expliquer la relation significative et positive entre l'intensité de l'éclaircie et la photosynthèse à l'échelle de la journée chez les aiguilles de pin gris âgées d'un an. La photosynthèse de l'épinette noire n'a pas varié à la suite de l'augmentation de la lumière. Le taux de photosynthèse nette à lumière saturante (A_{\max}), l'efficacité photosynthétique (α), le point de compensation (LCP) et la respiration diurne (R_d) n'ont pas varié chez les deux espèces. Les réponses à l'éclaircie du pin gris et de l'épinette noire devraient être interprétées à la lumière de leur autécologie.

2.2 Abstract

A decrease in the average diameter of commercially harvested tree species in the Eastern boreal forest of Canada has led to a decrease in availability of quality wood for the forest industry. Commercial thinning has been proposed as a means to increase stem diameter growth. However, little is known about physiological responses underlying species responses to thinning. Effects of commercial thinning on photosynthesis were assessed for jack pine (*Pinus banksiana* Lamb.) and black spruce (*Picea mariana* (Mill.) B.S.P.). Two experimental designs with two randomized blocks each were applied to each species. In each block one control plot and two other plots with a relative intensity of 0.4 (moderate thinning) and 0.3 (intensive thinning) for jack pine and 0.5 (moderate thinning) and 0.4 (intensive thinning) for black spruce were assigned. Photosynthetic light response curves and diurnal patterns of photosynthesis were carried out on current-year and one-year-old needles coming from 3 shoots selected on two individuals per experimental plot. Thinning is assessed in terms of relative basal area removed $[(\text{basal area removed}/\text{initial basal area}) \times 100]$ and its effect is tested on photosynthesis two years after thinning. Soil water content, air and soil temperatures, and needle N concentration were not affected by thinning for either species. However, light availability increased with basal area removed and could explain the significant positive relationship between thinning intensity and diurnal course of photosynthesis for one-year-old needles of jack pine. Black spruce photosynthesis did not respond to increases in light. Light-saturated rate of net photosynthesis (A_{max}), photosynthetic efficiency (α), light compensation point (LCP), and diurnal respiration (R_d) did not vary with thinning for either of the species. Jack pine and black spruce behaviours to thinning should be interpreted in light of species autecology.

2.3 Introduction

Jack pine (*Pinus banksiana* Lamb.) and black spruce (*Picea mariana* (Mill.) B.S.P.) are two tree species common in the eastern Canadian boreal forests that are of great commercial value. The thinning of mature stands of these species has proven to be an effective means to increase individual stem biomass and diameter growth (Weetman 1971, Barbour et al. 1994, Newton and Jolliffe 2003). The objective of thinning in forestry is usually to accelerate individual tree growth by reducing competition for light (Hale 2003), soil nutrients, and water (Latham and Tappeiner 2002). However, the physiological processes underlying these responses remain unclear for mature jack pine and black spruce, as photosynthesis measurements from mature thinned stands have yet to be reported for these two species. While competition and photosynthesis responses to light (Ter-Mikaelian et al. 1999), nitrogen, and water (Robinson et al. 2001) were tested on jack pine seedlings, these results can hardly be transferred to mature trees because, as demonstrated in a comprehensive review, gas exchange parameters significantly change with ontogeny (Thomas and Winner 2002).

Greater light availability as a result of thinning has been shown to induce changes in foliage physiology (Tang et al. 1999) and to increase light-saturated net photosynthesis (A_{max}), and dark respiration (R_d) rates, as well as the photosynthetic light compensation point (LCP) (Loach 1967, Pothier and Prévost 2002). However, the capability to respond to increased light availability depends on the shade tolerance of the tree species (Wright et al. 1998). Rates of photosynthesis, light-saturated net photosynthesis, apparent quantum yield (α), and dark respiration, as well as the photosynthetic light compensation point tend to be greater for shade-intolerant species than for shade-tolerant ones (Bazzaz 1979). In response to increased light availability, shade-intolerant species have demonstrated greater photosynthetic plasticity and were likely to reach A_{max} at higher light intensities (Bazzaz 1979, Loach 1967, Pothier and Prévost 2002).

Regardless of their shade tolerance, increasing light availability may lead to a very irregular response in leaf respiration because it increases in some species and decreases in others

(Loach 1967). Increased light interception at the tree scale (Tang et al. 1999) following thinning can lead to higher stomatal conductance and transpiration. Therefore, response to thinning is a combination of water loss by evapotranspiration and C uptake by photosynthesis, owing to the stomata being the dual pathway for water loss and C uptake. However, stand transpiration in boreal forest stands does not strongly change in response to thinning because understory vegetation (Vesala et al. 2005) compensates for reduced foliage area. Increases in tree growth after thinning in such conditions would likely be a consequence of photosynthesis increase at the expense of water loss.

The aims of this study were to assess changes in tree photosynthesis induced by thinning of pure, even-aged black spruce and mature jack pine stands and to relate those changes to measurements of light and water availability. Our hypotheses were that (1) for jack pine, an early successional and shade intolerant species, the photosynthetic response to thinning corresponds to a decrease in the competition for light, water, and nutrients; and that (2) black spruce, although likewise sensitive to light, water, and nutrients, has less photosynthetic responsiveness because of its greater shade tolerance (Hom and Oechel 1983). Moreover, it has been shown that black spruce has little ability to take advantage of favourable conditions (Groot and Hökkä 2000).

2.4 Materials and Methods

2.4.1 Study site

The study was carried out in Abitibi-Témiscamingue, a region situated in the boreal shield of northwestern Quebec (Rowe 1972). Black spruce, white spruce (*Picea glauca* Moench. Voss.), jack pine, and balsam fir (*Abies balsamea* (L.) Mill.) are all common species of this ecological zone (Rowe 1972). The jack pine experiment [block 1 (48°32'45" N and 77°49'04" W); block 2 (48°32'21" N and 77°49'21" W)] was located in the Township of Landrienne in an 82-year-old natural jack pine stand. The topography is relatively flat and the elevation approximately 352 m. The average daily temperature is 1.1°C with an average

minimum of -22.9°C in February and an average maximum of 23.1°C in July. Total annual average precipitation is 920 mm with a maximum monthly average of 107.5 mm falling in July (Environment Canada 2009). Soils, classified as orthic podzols, evolved from a well-drained, glaciolacustrine sandy loam surface deposit (AAFC 1998). The black spruce study was set in two different locations (Township of Bacon or block 1: $49^{\circ}24'31''$ N and $78^{\circ}39'42''$ W; Township of Rainboth or block 2: $49^{\circ}22'16''$ N and $78^{\circ}31'37''$ W). The topography is also relatively flat and the elevation approximately 300 m. The average daily temperature is 0.8°C with an average minimum of -24.3°C in January and an average maximum of 23.3°C in July (Environment Canada 2009). Total annual average precipitation is 857 mm with a maximum monthly average of 113.2 mm falling in September. The soils are developed on poorly drained clay to sandy clayey loam glaciolacustrine deposits and are classified as gleyed luvisols (AAFC 1998).

2.4.2 Experimental design

Jack pine and black spruce experiments were separately conducted as completely randomized block designs with two blocks and three treatments each. Thinning was done from below in 0.5 ha experimental units in the summer of 2002 for jack pine and in 4 ha experimental units for black spruce in the winter of 2003. Relative densities of 0.5 (moderate thinning) and 0.4 (intensive thinning) were targeted for black spruce and 0.4 (moderate thinning) and 0.3 (intensive thinning) for jack pine using density management diagrams (Grenier et al. 2001, Grenier and Harvey 2004). Two to four 200 m² permanent plots were sampled in each experimental unit before and after treatment for basal area estimation (Tab. 2.1).

Table 2.1 Site information and stand characteristics two years after thinning of jack pine and black spruce stands

Block	Age (year)	Basal area (m ² ha ⁻¹)								
		Control			Moderate			Intensive		
		Before thinning	After thinning	Percent removed	Before thinning	After thinning	Percent removed	Before thinning	After thinning	Percent removed
Jack pine										
Block 1	82	22.30	22.30	0	19.70	17.90	9.14	18.50	14.10	23.78
Block 2	81	26.80	26.80	0	23.60	20.60	12.71	23.00	14.10	38.70
Black spruce										
Block 1	72	43.84	43.84	0	32.07	22.56	29.66	42.51	29.07	31.62
Block 2	77	50.05	50.05	0	34.56	26.70	22.75	39.72	20.45	48.51

2.4.3 Gas exchange measurements

For each species, photosynthesis measurements were conducted in one 200 m² permanent plot per block—treatment combination for a total of 6 plots per species. In each plot, the two dominant trees closest to the experimental plot centre were retained. Because tree photosynthesis response to thinning has been shown to occur in the lower crown (Tang et al. 1999), measurements were conducted in the lower third of the crown, i.e., 1.5 m above the crown base, which is accessible with ladders and platforms. Three shoots per tree were sampled for measurements at opposing directions around the outer crown, closer to the tips of the branches, where light exposure is maximized. Measurements were conducted on current-year and one-year-old needles on each shoot for a total number of 24 measured shoots (irrespective to needle age or thinning treatment applied) per species. Measurements for diurnal course of photosynthesis and for light response curves were conducted on different occasions and on different shoots. Measurements were respectively conducted with a conifer LI-6400-05 and a broad-leaf LI-6400 3 × 6 chamber units. The broad-leaf LI-6400 3 × 6 chamber unit was used for light response measurements because there is no conifer chamber equipped with a red-blue 6400-02B light source. Using broad-leaf chamber to measure conifers does not alter measurement accuracy because gas exchange measurement is proportional to surface area of needle enclosed in the chamber. Measurements are prior conducted with default value of surface area, and then the measured values of gas exchange are recomputed later using accurate surface area of sample needles determined in the laboratory. The number of needles enclosed in the chamber was on average 19 and 65, corresponding to surface areas of 6.0 cm² and 4.1 cm², respectively for jack pine and black spruce. At the end of the measurements, the needles were carefully detached from the collected shoots and sent to the laboratory for nitrogen concentration, surface area, and weight characterization.

2.4.3.1 Photosynthetic light response curve

Measurements were conducted in July 2005, between 09:00 and 12:00 hours, when photosynthetic rates were at their highest. A LI-6400 was equipped with a red-blue 6400-02B light source. Prior to measurements, the CO₂ mixer and light source were calibrated. Temperature and relative humidity in the chamber were set close to ambient air values. Photosynthesis was measured after needles were first equilibrated with light saturation (2000 $\mu\text{mol m}^{-2} \text{s}^{-1}$); then, photon irradiances were gradually decreased to 1500, 500, 200, 100, 50, and 0 $\mu\text{mol m}^{-2} \text{s}^{-1}$. The lower window of the chamber unit was covered so that the light in the 3 \times 6 chamber unit exclusively came from the light source, without any interference from ambient light. This allowed us to determine the exact amount of light that reached the needles enclosed in the chamber—a quantity that happened to correspond with the range of irradiances targeted during the photosynthetic light response survey. The Mitscherlich nonlinear function (Potvin et al. 1990) was used to fit photosynthetic light response curves:

$$A = A_{\max}[1 - e^{-\alpha(\text{PPFD} - \text{LCP})}] \quad 2.1$$

where A represents net photosynthetic CO₂ assimilation, A_{max} is the light saturated rate of net photosynthesis, α corresponds to the initial slope of the curve (photosynthetic efficiency or apparent quantum yield), PPFD refers to the incident photosynthetic photon flux density, and LCP is the x-intercept of the curves and refers to the photosynthetic light compensation point. The Mitscherlich nonlinear function was fitted to the data because, as all the parameters of the function refer to physiological processes, the function fits the data better than quadratic models. As such, fitting a function to data has become the standard means of light curve fitting in physiological ecology (Peek et al. 2002, Heschel et al. 2004). Dark respiration (R_d) does not appear in the equation but was directly measured on trees as the rate of CO₂ evolution at zero incident photosynthetic photon flux density.

2.4.3.2 Diurnal course of photosynthesis

Diurnal course of photosynthesis measurements were conducted in 2004 for jack pine and in 2005 for black spruce under natural light conditions with an automatic 6400-05 conifer chamber mounted on the LI-6400. Transpiration and assimilation rates provided by the LI-6400 were based on the computation of the concentration differences between reference and sample infrared gas analyzers (IRGA). Sample and reference IRGAs were matched at the beginning of the measurements and every 30 minutes afterwards. Chamber temperature and relative humidity were set close to ambient values, and the chamber was clamped onto the shoot. Data were logged when, over a time period of 20 seconds, fluctuation in photosynthesis were lower than $0.1 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ and when variations of conductance were lower than $0.05 \text{ mol H}_2\text{O m}^{-2} \text{ s}^{-1}$.

For jack pine, instantaneous photosynthesis was measured with the LI-6400 approximately every two hours. The first and last measurements of the day were done before sunrise and after sunset, respectively. The PPFD was concurrently measured with a LI-190SA external quantum sensor (LI-COR Biosciences, Lincoln, Nebraska) mounted on the LI-6400. For black spruce, time limitation and distance between blocks did not allow us to conduct a full diurnal survey and measurements were approximately taken every three hours. In all, 8 measurements were conducted throughout the day for jack pine and 6 for black spruce. In addition, as it was impossible to measure all trees in a single day, measurements were taken for each species over a period of 6 days.

2.4.4 Specific leaf area and nutrient status of the needles

At the end of the survey, measured needles were removed, placed in plastic bags, refrigerated in a cooler, and transferred to the laboratory. Needles were scanned and surface areas were measured using the software Winseedle 5.0 (Regent Instruments Inc., Quebec City, QC, Canada). Needles were then weighted (Sartorius, BP 210) to the nearest 0.1 mg after drying in a ventilated oven at 65°C for 48 hours. Specific leaf area (SLA) was determined from the

ratio of projected needle surface area to needle dry mass. Gas exchange values initially measured on an area basis were then expressed on a mass basis by dividing them by their corresponding SLA.

Sampled needles were oven dried (65°C for 48 h) and ground to 2 mm with a Wiley Mill equipped with stainless steel cutters and a sieve. After subjecting the samples to another drying process, 0.5 g of the sample was digested for 90 min with 10 ml of H₂SO₄-H₂O₂-Se at 380°C (Parkinson and Allen 1975). Total N was determined using an FIA (Tecator Flow Injection Analyzer).

2.4.5 Environmental parameter measurements

2.4.5.1 Soil water status

Environmental parameters were measured two growing seasons after thinning, i.e., in 2004 for jack pine and in 2005 for black spruce. Soil was sampled with an auger in each experimental plot from surface soil to 70 cm depth at every 10 cm, for a total of seven soil samples per experimental plot. Gravimetric soil water content (SWC) was calculated for each of the 7 soil samples after weighting and drying (105°C). Field capacity (FC_{mass}; g) was measured on undisturbed soil samples at a tension value of 10 kPa according to Cassel and Nielsen (1986). Permanent wilting point (PWP_{mass}; g) was estimated on sieved (2 mm) samples at a tension value of -1500 kPa using the same procedure. Available water holding capacity (AWHC_{mass/mass}; g g⁻¹) was computed as the difference between water retained at field capacity and permanent wilting point. Finally, AWHC_{mass/mass} was expressed on a volume basis (AWHC_{vol/vol}; cm³ cm⁻³) by multiplying it by the sample's bulk density.

Available soil water content on the day of the measurements (Cassel and Nielsen 1986) was reported as depth (SWC_{depth}; cm) of the water as if it was accumulated in a layer and was computed as follows:

$$SWC_{\text{depth}} = [(AWHC_{\text{vol/vol}}) \times (\text{unit area} \times \text{length})] / (\text{unit area}) \quad 2.2$$

where the unit area represents the cross-sectional area of the auger and where length refers to the 70 cm soil depth.

2.4.5.2 Air and soil temperatures

Air temperature and relative humidity were continuously measured in each experimental plot using an automated weather station consisting of a data logger (CR10, Campbell Scientific Ltd., Leicestershire, United Kingdom) and a temperature and a relative air humidity probe (MP300, Campbell) mounted 2 m above ground level and close to the middle of the experimental plot. The measurement intervals for the air temperature and the relative air humidity sensors were set according to manufacturer's recommendations and the data average recording interval to 5 min; the data were then averaged for each hour of the months of July and August.

Soil temperature was measured close to the middle of each experimental plot, in the vicinity of the measured trees, using two soil temperature probes (Hobo 4 Channel External Data Logger), one located in the forest floor and the other one in the mineral layer, at around 5 cm depth within each layer. The temperature probes continuously measured at a time step of one minute and the data were averaged for each hour of the months of July and August.

2.4.6 Statistical analyses

Statistical analyses were performed using SAS software package (SAS Institute version 9.1, Cary, North Carolina, 2002). Photosynthetic light response curves were obtained by plotting photosynthesis against PPFD for each needle age at the tree level. The Mitscherlich nonlinear

function was fitted to light response and A_{max} , α , LCP, and R_d were derived from the NLIN procedure.

Because of differences in the initial basal area between experimental units and blocks, and because of variations in the basal area that was removed during treatment, a regression approach was preferred over a means comparison between treatments. Dependant variables were explained in terms of relative basal area removed [(basal area removed / initial basal area) \times 100]. A mixed linear model analysis, allowing for random and nested effects, was used in order to benefit from each observation (tree level) while taking into account the non-independence of nested effects (trees nested within experimental plot, and plot nested within block). Statistical analyses were separately conducted on current-year and one-year-old needles. Shoot values ($N = 3$) were averaged for each tree, removing in this way the shoot effect from the models. The following general model was used to test the effect of the relative basal area removed on diurnal photosynthesis.

$$Y_{bpti} = \beta_0 + \beta_1 G_{rbp} + \beta_2 T_{bpti} + \beta_3 G_{rbp} T_{bpti} + \beta_4 T_{bpti}^2 + \mu_b + \varepsilon_{bpti} \quad 2.3$$

where Y_{bpti} represents the dependent variable ($b =$ block, $p =$ plot, and $t =$ tree) for the i^{th} measurement, β_0 the intercept, β_1 the regression coefficient of the relative basal area removed (G_{rbp}), β_2 the regression coefficient for time of day (T_{bpti}), β_3 the regression coefficient of the interaction between relative basal area removed and time of day ($G_{rbp} T_{bpti}$), β_4 the regression coefficient of the quadratic effect of time (T_{bpti}^2), μ_b the random effect for block, and ε_{bpti} the error term. As photosynthesis measurements were repeated over time, and owing to the variation that had occurred, in some case, in the time elapse between two consecutive measurements, we used a REPEATED statement applied to time (T_{bpti}) with a SP(POW) covariance structure for unequally spaced data. We used Kenward-Roger (KR) approximation method of degree of freedom (Kenward and Roger 1997) because it is the

most appropriate for models with random effect and repeated statement (Saavedra and Douglass 2002).

For A_{\max} , α , LCP, R_d , N, soil water content, and soil and air temperatures, basal area removed was the only explanatory variable included in the model. A visual analysis of residuals was conducted and variables were transformed (square root), when necessary, in order to improve residuals normality and to eliminate any trend between residuals and predicted values. Fixed effects were considered significant at $p < 0.05$ based on type 3 test of fixed effects.

2.5 Results

2.5.1 Evaluation of the thinning treatment

Thinning removed 11 % and 26 % of initial basal area in the moderate treatment and 31 % and 40 % in the intensive treatment, for jack pine and black spruce, respectively (Tab. 2.1). For both species, no significant differences in initial basal area and relative basal area removed were found between experimental plots of the same thinning treatment.

2.5.2 Environmental factors

Average soil water contents of jack pine (17.7 mm) and black spruce (41.3 mm) stands were not affected by relative basal area removed during the course of measurements. On a diurnal time scale, minimum air temperature occurred early in the morning and maximum air temperature between 14:00 and 16:00 hours (Fig. 2.1). Mean minimum and maximum air temperatures during the measurement period were respectively, 9.7°C and 28.3°C for jack pine and 11.7°C and 31.1°C for black spruce plots. Relative air humidity displayed higher values in the morning for both jack pine and black spruce and remained lower for the rest of the day. Average soil temperatures in the forest floor and in the mineral layer were respectively, 15.7°C and 14.3°C for jack pine and 14.1°C and 12.7°C for black spruce.

Relative basal area removed had no significant effect, for either species, on mean minimum and maximum air temperatures, relative air humidity, and soil temperature. Soil temperatures in the forest floor and mineral layer were generally around 10-15°C in the morning and reached a maximum of approximately 15°C between 14:00 and 16:00 hours.

PPFD showed a significant quadratic relationship with time for both species (Fig. 2.1), with the highest values observed between noon and 14:00 hours. For jack pine, PPFD did not significantly vary with relative basal area removed in the vicinity of current-year needles (Tab. 2.2), while it significantly increased in the vicinity of one-year-old needles (Tab. 2.2). For black spruce (Tab. 2.2), relative basal area removed significantly increased PPFD in the vicinity of both current-year and one-year-old needles. No significant interactions were found between basal area removed and time for either species.

2.5.3 Gas exchange

2.5.3.1 Photosynthetic light response and derived parameters

The Mitscherlich nonlinear function used to fit jack pine and black spruce photosynthetic light response data explained over 90 % of the variance of the data (individual tree curves not shown) on a mass as well as on an area basis (Fig. 2.2). Observed values of A_{\max} , α , LCP, and R_d in control stands (on a needle surface area basis) were respectively, 8.07, 0.028, 17.70, and $-0.20 \mu\text{mol m}^{-2} \text{s}^{-1}$ for jack pine and 3.65, 0.027, 13.47, and $-0.35 \mu\text{mol m}^{-2} \text{s}^{-1}$ for black spruce. Relative basal area removed had no significant effect on jack pine or black spruce current-year or one-year-old needle A_{\max} , α , LCP, and R_d , whether expressed on a needle surface area or on a mass basis (Tab 2.3).

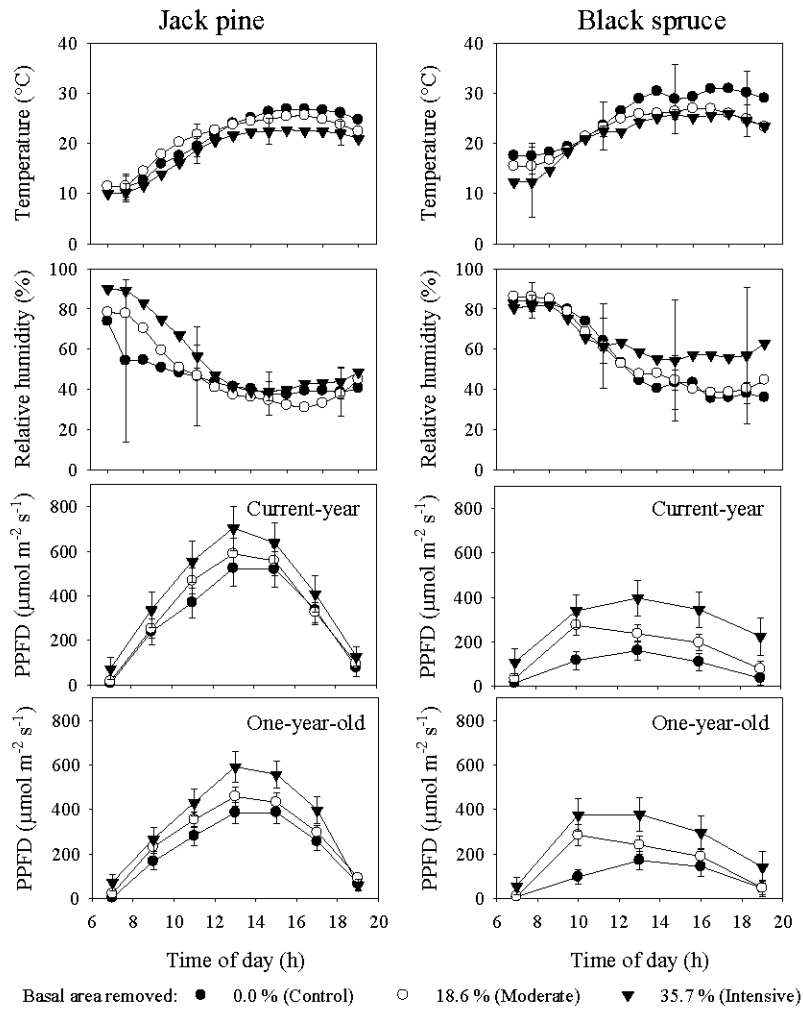


Figure 2.1 Diurnal course of air temperature and relative humidity per plot with the same thinning treatment and photosynthetic photon flux density for current-year and one-year-old needles for jack pine and black spruce two years after thinning treatment. Error bars represent standard errors.

Table 2.2 Effects of relative basal area removed on diurnal course of photosynthetic photon flux density in the vicinity of current-year and one-year-old needles of jack pine and black spruce two years following thinning

Jack pine						
	Current-year needles			One-year-old needles		
	Den DF	F value	p > F	Den DF	F value	p > F
G _r	3.2	1.19	0.438	3.2	0.41	0.040
T	88.8	38.92	< 0.001	81.2	30.11	< 0.001
G _r × T	80.1	0.01	0.273	79.8	0.02	0.05
T ²	83.4	80.35	< 0.001	82.2	71.24	< 0.001
Black spruce						
	Current-year needles			One-year-old needles		
	Den DF	F value	p > F	Den DF	F value	p > F
Gr	4.7	0.38	0.057	3.6	2.40	0.050
T	141.2	14.44	< 0.001	82.5	23.86	< 0.001
Gr × T	80.3	0.27	0.542	81.6	0.00	0.948
T ²	85.4	17.75	< 0.001	86.1	21.16	< 0.001

Note: G_r: relative basal area removed, PPFD: photosynthetic photon flux density, Den DF: denominator degree of freedom, T: time of day, T²: quadratic effect of time of day, p: probability at 0.05. Numerator degree of freedom is 1 for jack pine and black spruce. For jack pine: N = 96, measurements were taken 8 times a day. For black spruce: N = 72, measurements were taken 6 times a day (one missing shoot). For one-year-old needles in both species: homoscedasticity of residuals was obtained using square root transformation of PPFD.

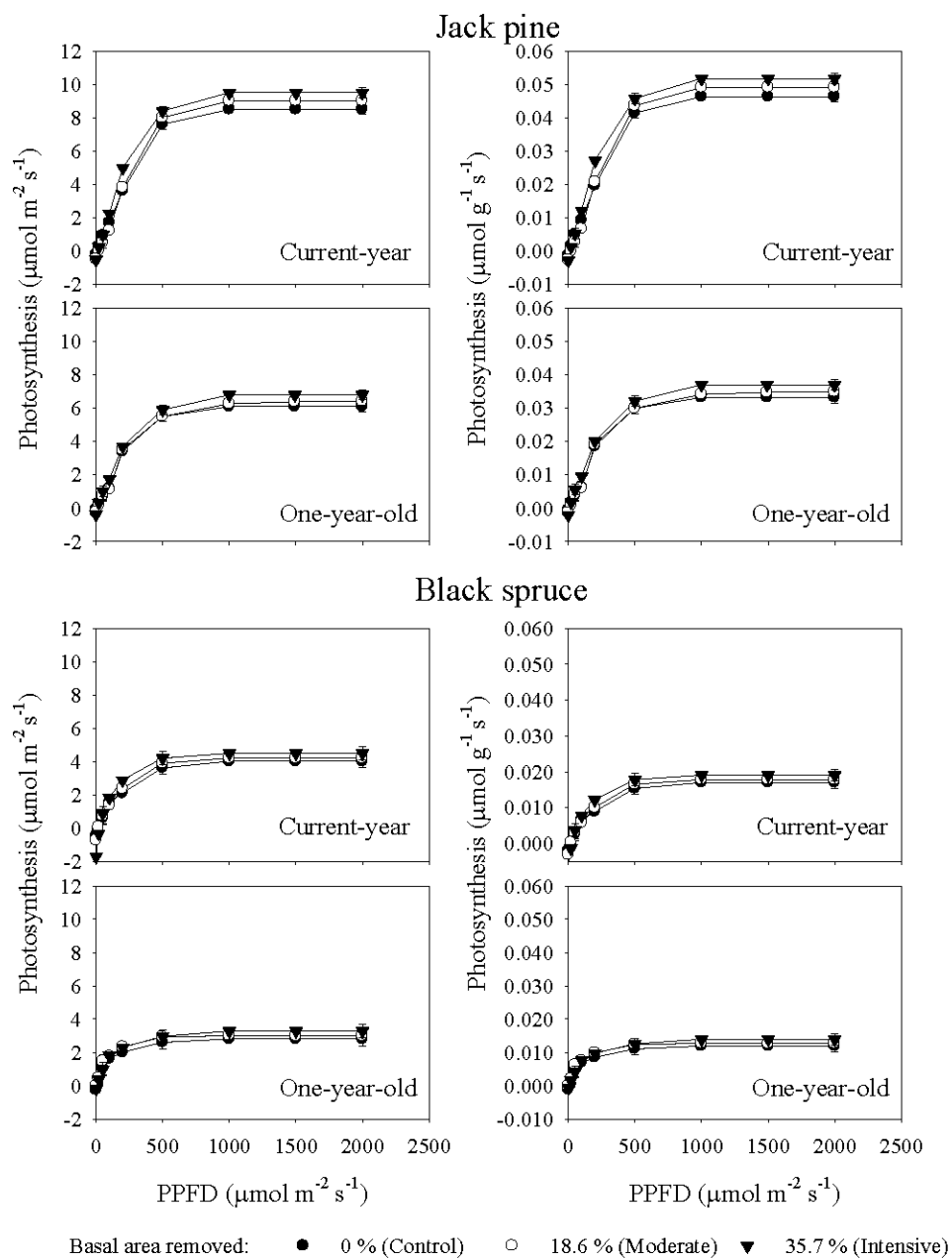


Figure 2.2 Photosynthetic light response curves based on predicted values of models expressed on a needle surface area and a mass basis for jack pine and black spruce in the vicinity of current-year and one-year-old needles. Error bars represent standard errors.

Table 2.3 Effects of relative basal area removed (G_r) on current-year and one-year-old needles photosynthetic parameters (surface area and mass basis) of jack pine and black spruce two years following thinning. Type 1 test of fixed effects

Jack pine						
	Surface area basis			Mass basis		
	Den DF	F	p > F	Den DF	F	p > F
Current-year needles						
A_{max}	6	0.59	0.473	6	3.27	0.120
LCP	6	0.13	0.734	6	0.01	0.932
α	6	1.85	0.223	6	1.85	0.223
R_d	6	0.84	0.396	6	0.99	0.358
One-year-old needles						
A_{max}	6	0.00	0.953	6	0.48	0.518
LCP	6	0.01	0.911	6	0.02	0.889
α	6	0.22	0.658	6	0.22	0.658
R_d	6	0.00	0.992	6	0.00	0.994
Black spruce						
	Surface area basis			Mass basis		
	Den DF	F	p > F	Den DF	F	p > F
Current-year needles						
A_{max}	5	0.59	0.470	5	1.02	0.353
LCP	5	1.06	0.344	5	1.87	0.220
α	5	1.05	0.344	5	5.46	0.058
R_d	5	1.51	0.265	5	2.11	0.197
One-year-old needles						
A_{max}	5	0.13	0.734	5	0.00	0.985
LCP	5	0.46	0.526	5	0.69	0.443
α	5	0.05	0.832	5	0.05	0.833
R_d	5	0.66	0.454	5	0.95	0.375

Note: A_{max} : light-saturated rate of net photosynthesis, LCP: light compensation point, α : apparent quantum yield, R_d : diurnal respiration, Den DF: denominator degree of freedom, F: Fisher value, and p: probability at 0.05. For jack pine and black spruce, numerator degree of freedom is 1.

For jack pine $N = 12$ and for black spruce $N = 11$ (one missing value).

2.5.3.2 Pattern of diurnal course of photosynthesis

Irrespective of the thinning treatment and species, values of diurnal course of photosynthesis were low in the morning, reached a maximum in the middle of the day, and declined

thereafter to their lowest values observed at the end of the day, when light availability became very low (Fig. 2.3).

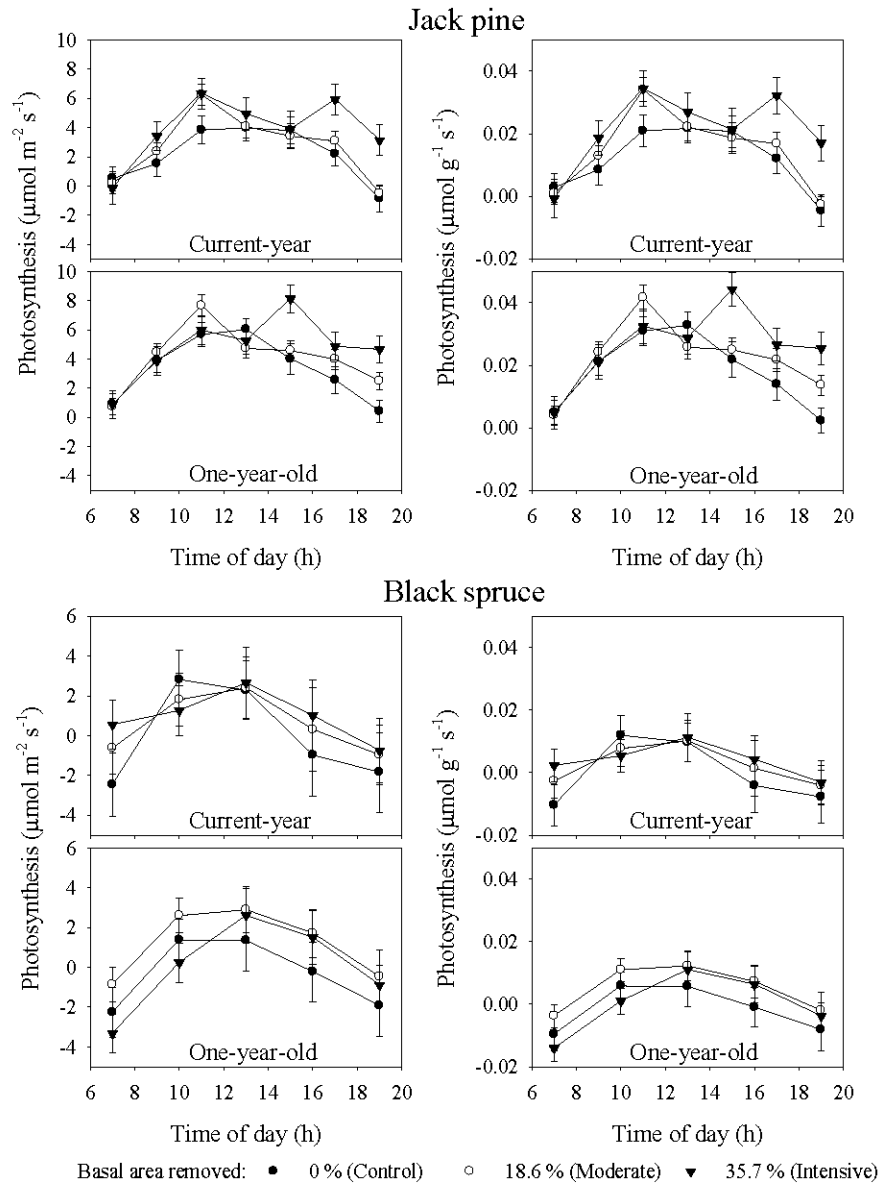


Figure 2.3 Diurnal course of needle photosynthesis based on predicted values of models for jack pine current-year and one-year-old needles and black spruce current-year and one-year-old needles on a needle surface area and a mass basis two years after thinning treatment. Error bars represent standard errors.

Photosynthesis of current-year needles of jack pine in control plots increased from 6:00 until 11:00 hours and then decreased until sunset. The quadratic effect of time on photosynthesis was highly significant. No significant effect of basal area removed was observed for the photosynthesis of current-year needles. The relationship between time and photosynthesis for one-year-old needles followed significant linear and quadratic relationships (Tab. 2.4, Fig. 2.3). Photosynthesis of one-year-old needles expressed on a surface area or on a mass basis significantly increased with basal area removed (Tab. 2.4, Fig. 2.3). Jack pine models for diurnal course of photosynthesis expressed on a needle surface area or on a mass basis explained respectively, 88 % and 97 % of diurnal course of photosynthesis for one-year-old needles.

For black spruce current-year and one-year-old needles, a significant quadratic relationship was observed between photosynthesis, and time with highest values observed between 12:00 and 14:00 hours. Basal area removed had no effect on black spruce current-year and one-year-old needles.

Table 2.4 Effects of relative basal area removed on diurnal course of photosynthesis for current-year and one-year-old needles (surface area and mass basis) of jack pine and black spruce two years following thinning

Jack pine						
	Surface area basis			Mass basis		
	Den DF	F	p > F	Den DF	F	p > F
Current-year needles						
G _r	2.7	0.38	0.590	2.8	0.34	0.689
T	69.1	156.90	< 0.001	70.6	192.32	< 0.001
G _r × T	61.4	1.37	0.093	62.0	0.85	0.059
T ²	66.9	96.3	< 0.001	67.3	116.51	< 0.001
One-year-old needles						
G _r	4.9	21.57	< 0.001	5.1	35.61	< 0.001
T	83.5	233.56	< 0.001	83.5	309.99	< 0.001
G _r × T	84.2	0.13	0.007	85.3	0.51	0.005
T ²	80.8	97.50	< 0.001	81.7	99.33	< 0.001
Black spruce						
	Surface area basis			Mass basis		
	Den DF	F	p > F	Den DF	F	p > F
Current-year needles						
G _r	5.3	0.02	0.377	4.3	0.09	0.463
T	99.0	8.58	0.047	98.3	8.79	0.004
G _r × T	80.3	0.72	0.388	80.7	0.77	0.402
T ²	85.4	10.61	0.002	86.2	11.62	0.002
One-year-old needles						
G _r	6.1	0.05	1.188	6.3	0.05	1.384
T	96.3	33.44	< 0.001	97.1	35.54	< 0.001
G _r × T	85.1	0.08	0.718	86.2	0.16	0.683
T ²	85.4	24.87	< 0.001	85.8	28.25	< 0.001

Note: for jack pine and black spruce: numerator degree of freedom is 1, G_r: relative basal area removed, T: time of day, T²: quadratic effect of time of day, F: Fisher value, and p: probability at 0.05.

For jack pine: N = 96, measurements were taken 8 times a day.

For black spruce: N = 72, measurements were taken 6 times a day (one missing shoot).

Homoscedasticity of residuals was obtained using square root transformation of photosynthesis.

All significant variables have positive relationships, except T², which has a negative relationship.

2.5.4 Specific leaf area and nutrient status of the needles

For the jack pine control treatment, SLA was 6.41 and 5.71 m² kg⁻¹ for current-year and one-year-old needles, respectively. For black spruce, SLA was 4.79 and 4.08 m² kg⁻¹ for current-year and one-year-old needles, respectively. No significant relationship was found between SLA and relative basal area removed for either species.

Needle nitrogen concentrations were 0.97 % and 0.76 % for jack pine current-year and one-year-old needles, respectively. For black spruce, needle nitrogen concentrations were 0.76 % and 0.73 % for current-year and one-year-old needles, respectively. For both species, relative basal area removed did not have any effect on needle N concentrations and no significant interaction between relative basal area removed and needle age was found.

2.6 Discussion

Thinning is a common silvicultural practice, which aims to enhance tree growth by decreasing between-tree competition for light, nutrients, and water (Aussenac 2000). We hypothesized that jack pine response to thinning would be related to a decrease in competition for light, water, and nutrients, while black spruce would be less responsive in terms of photosynthetic activity. During the course of measurements, we found no relationships between relative basal area removed and soil water availability, soil temperature, or N availability expressed by N foliar concentration for both species. In these experiments, slash as well as non-merchantable stems were left on the ground and presumably contributed to reduce soil water evaporation and to creating a possible buffer against changes in soil temperature.

However, the observed increase in light availability after thinning may have played a role in the increase in diurnal course of photosynthesis of one-year-old jack pine needles despite the fact that measured trees were dominant and not as likely to be light limited as the trees removed by thinning operations. Comparing thinned and unthinned loblolly pine

(*Pinus taeda* L.) stands, Tang et al. (2003) found that light availability was the only significant variable predicting needle level photosynthesis rates after thinning, while Wang et al. (1995) also identified nitrogen concentration of leaves as contributing factors allowing white birch (*Betula papyrifera* Marsh.) to increase its photosynthesis following thinning. Both studies were conducted on very young stands (less than 16-year-old).

Observed photosynthetic parameters were within the range of those previously reported for jack pine (Sullivan et al. 1997) and black spruce (Rayment and Jarvis 1999, Johnsen et al. 2003). The increase in light availability observed for both species did not lead to any increase in photosynthetic efficiency, as shown by the lack of changes in photosynthetic parameters. No comparable studies relating gas exchange, mainly photosynthesis and respiration, to thinning for mature trees were found in the literature. However, an increase in α in response to light increase was reported for herbaceous species (Peri et al. 2005). The lack of changes in needle α , A_{\max} , LCP, and R_d following an increase of PPFD indicates that jack pine and black spruce do not actively adjust their physiology after thinning to enhance their efficiency in light utilization.

Generally α and A_{\max} are positively correlated with nitrogen and negatively with SLA (Wang et al. 1995). Considering the lack of response to thinning of foliar N concentrations and SLA, the positive response in diurnal course of photosynthesis observed for jack pine one-year-old needles can only be explained by longer periods of higher irradiation. This was not the case for black spruce, characterized by a low-light photosynthesis saturation capability, with the effect that following stand opening, observed values of photosynthesis were in the same range as those observed in the control stands.

Midday decreases in photosynthesis, such as the one observed for jack pine on current-year needles, result from a combination of high temperature and dry air (mostly occurring in the middle of the day) leading to an increasing vapour pressure difference (VPD) that partially closes stomata. Such a decrease in photosynthesis is referred to as midday stomatal closure and has been described for Norway spruce (Zweifel et al. 2002) and jack pine

(Baldocchi et al. 1997). Sullivan et al. (1997) have shown that for mature jack pine and black spruce, CO_2 assimilation is stomatally limited and that environmental factors altering conductance (e.g., VPD) have a strong influence on CO_2 fluxes. Contrary to jack pine, black spruce did not show any midday stomatal depression, which is consistent with the fact that jack pine usually has greater stomatal sensitivity to VPD than black spruce (Dang et al. 1997).

Although we cannot statistically compare jack pine with black spruce, differences in photosynthetic parameters and responses to an increase in light availability merit an interpretation in the context of differing autecologies. Higher values of A_{max} , α , LCP, and R_d observed for jack pine compared to black spruce are consistent with their respective successional and shade tolerance status (Bazzaz 1979). Jack pine is a fast growing, shade-intolerant, early successional species, while black spruce is mid to late successional and moderately shade tolerant (Sims et al. 1990). It has also been shown that shade-intolerant species can respond to increases in light at higher ranges of light availability, while shade tolerant species cannot adapt easily (Wright et al. 1998).

Measurements were taken two years following treatments and, as trees have a capacity for acclimation to changing environments, long-term photosynthetic response to thinning may be different from what we reported. Photosynthesis is known to be significantly affected by time of day or season of measurement (Yang et al. 2002) as well as temperature. Therefore, observed photosynthetic parameters provided in our experiment can hardly be taken to apply to other periods.

Our objective was to provide insight into photosynthetic parameters, diurnal course of photosynthesis, nitrogen concentration, and light availability shifts after thinning at the needle scale of individual trees as well as soil water availability at the plot scale. However, differences among needles may have been skewed due to low tree replications, and the vertical nitrogen and photosynthesis gradient within the crown—factors that had not been accounted for in our experiment. Therefore, the possibility to generalize our results to whole

trees is somewhat limited. As is well known, photosynthetic parameters are distributed along a bottom up and lateral gradient, a phenomenon that is closely linked to light availability at the relative location of the corresponding needles (Schoettle and Smith 1999). Consequently, any attempt to scale up from needle to individual, without taking these previous considerations into account would be biased.

2.7 Conclusion

This study provides new insight into jack pine and black spruce photosynthesis and their responses to changes in resource availability induced by stand opening following thinning. Little information of this kind is currently available in the literature owing to the difficulties inherent in measuring mature trees. Linking ecophysiology to silviculture is a challenge, as short-term and small-scale measurements need to be related to longer term and larger scale processes. Our study is potentially useful for forest practitioners, as our investigation of photosynthesis, which is a proxy of tree growth, may help explain how thinning affects tree growth. Results from our study are already being successfully used in a carbon balance algorithm for process based C model parameterization (Goudiaby et al. in preparation).

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CHAPITRE III

VERTICAL PATTERNS IN SPECIFIC VOLUME INCREMENT ALONG THE STEM OF DOMINANT JACK PINE (*PINUS BANKSIANA* LAMB.) AND BLACK SPRUCE (*PICEA MARIANA* (MILL.) B.S.P.) IN RESPONSE TO THINNING¹

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¹ Soumis à Canadian Journal of Forest Research.

3.1 Résumé

Bien que plusieurs études aient fait état de la croissance du diamètre à hauteur de poitrine des arbres en réponse à l'éclaircie, des zones d'ombre demeurent encore quant au patron de distribution de croissance le long de la tige. Notre objectif à travers cette étude était de quantifier la distribution de croissance le long de la tige en réponse à l'éclaircie chez deux espèces d'intérêt commercial, à savoir le pin gris (*Pinus banksiana* Lamb.) et l'épinette noire (*Picea mariana* (Mill.) B.S.P.). Les accroissements annuels en volume totaux (i_{vt}) et spécifiques de bois (SVI, rapport de l'accroissement annuel en volume de tige sur la surface cambiale) le long de la tige, ont été étudiés un à six ans après éclaircie. Nous avons également étudié six ans après éclaircie l'efficacité de croissance (GE, rapport entre les biomasses de la tige et foliaire), les biomasses foliaires (W_F) et de branches (W_{BW}), la longueur de la cime vivante (L_{cv}), le rapport de cime vivante (LCR, rapport de la longueur de cime vivante sur la hauteur totale de l'arbre), la densité de masse foliaire (FD_w , rapport de la masse foliaire sur le volume de la cime), la densité de masse de branches (BD_w , rapport de la biomasse de branches sur le volume de la cime). L'éclaircie a entraîné chez le pin gris un accroissement significatif et continu en SVI et en i_{vt} respectivement la seconde et la troisième année après éclaircie. La réponse du SVI est partie de la base de la tige, puis s'est propagée en hauteur avec le temps. L'accroissement en volume du pin gris a été lié à l'augmentation en GE. La distribution de croissance le long de la tige, sous le contrôle de l'activité cambiale, a été liée à la nécessité d'augmenter le défilement pour des raisons de stabilité mécanique due à l'accroissement en W_F à mi-hauteur de cime. En ce qui concerne l'épinette noire, l'éclaircie a entraîné une réduction immédiate en SVI en raison d'un choc d'éclaircie. Nous avons noté un accroissement en SVI et en i_{vt} respectivement la troisième et la quatrième année après éclaircie alors que GE, W_F , et FD_w sont restés inchangés. De plus, on a eu une distribution uniforme en SVI le long de la tige. Pour les deux espèces, l'éclaircie n'a pas eu d'effet sur W_{BW} , L_{cv} , et LCR. En conclusion, l'intensité de la réponse à l'éclaircie du pin gris a été supérieure à celle de l'épinette noire, ce qui est en accord avec leur autécologie.

3.2 Abstract

Although many studies have focused on diameter at breast height response to thinning, little is known about growth distribution along the stem. Our objective was to quantify growth distribution along the stem after thinning for two species of commercial interest in Eastern Canada, jack pine (*Pinus banksiana* Lamb.) and black spruce (*Picea mariana* (Mill.) B.S.P.). Annual stemwood volume increment (i_{Vtr}), and annual specific volume increment (SVI, annual stemwood volume increment to cambial surface ratio), were examined one to six years following thinning. We also examined six years following thinning growth efficiency (GE, stemwood biomass to foliage biomass ratio), total tree foliage (W_F), and branchwood (W_{BW}) biomass, live crown length (L_{cr}), live crown ratio (LCR, live crown length to tree height ratio), foliage mass density (FD_w , foliage biomass to crown volume ratio), and branchwood mass density (BD_w , branchwood biomass to crown volume ratio). Thinning led jack pine to a significant and sustained increase in SVI and in i_{Vtr} the second and the third year after thinning, respectively. SVI increased at the base of the stem, spreading upward with time. For jack pine, stemwood growth was related to an increase in GE. Growth distribution along the stem, driven by cambial activity, was related to the necessity to increase the taper for mechanical stability purposes due to the greater W_F at mid-crown. For black spruce, thinning led to an immediate decrease in SVI due to thinning shock. We noted an increase in SVI and in i_{Vtr} respectively the third and the fourth year after thinning with no changes in GE, W_F , and FD_w . In addition, its SVI was evenly distributed along the stem. For both species, there was no thinning effect on W_{BW} , L_{cr} , and LCR. In conclusion, jack pine was shown to be more responsive than black spruce, which is consistent to their known autecology.

3.3 Introduction

Thinning of forest stands induces a sudden increase in resource availability to residual trees (Aussenac 2000), leading to physiological and morphological modifications such as increases in stemwood growth and changes in crown structure (Weiskittel et al. 2007; Zeide and Gresham 1991). Models based on functional relationships such as the pipe model (Shinozaki et al. 1964) have emerged as suitable methods to analyze tree response to changing resource availability (Perttunen et al. 1996, 1998; Mäkelä 1997). However, these models usually assume that crown shape and stem profiles are independent of the surrounding environment and we lack information on how crown and stem structures react to changes in resource availability.

The ratio of stemwood production per unit of leaf area, known as growth efficiency, has been proposed as a means to assess tree vigour and its response to resource availability (Waring 1983; Stoneman and Whitford 1995). Growth efficiency depends on species, stand structure and previous stand disturbance (Maguire et al. 1998). In addition, growth efficiency depends on crown structure (Smith and Long 1989; Kuuluvainen 1992) or silviculture (Stoneman and Whitford 1995; Maguire et al. 1998). Growth efficiency has been shown to increase when canopy undergoes decreasing competition for light (Waring 1983; Gilmore and Seymour 1996) as is the case following thinning (Brix 1983; Blevins et al. 2005). Thinning generally leads to an increase in live crown ratio (LCR) as a direct consequence of the slowing down of recession of crown base and an increase in crown length and width, resulting in an increase in crown volume (Assmann 1970). Also, thinning generally leads to an increase in crown foliage area (Yu et al. 2003), and in foliage biomass (Blevins et al. 2005). Hence, in seeking to maintain a constant foliage to sapwood ratio, stem basal area usually increases in trees (Assmann 1970). Therefore, it appears to be worthwhile to address changes in crown structure while studying growth efficiency patterns in response to thinning.

When a stand is suddenly opened, stems also respond to increases in wind exposure and adjust their taper by following a constant-stress model of stem growth (Dean and Long 1986). Following thinning of oak stands, a greater annual volume increment was found for the stump

section compared to upper stem sections and DBH was generally found to be more responsive to environmental stimuli than the higher parts of the stem (Duff and Nolan 1953; Fajvan et al. 2008). Heterogeneous patterns of growth distribution along the stem are closely linked to stem mechanical stability and water conductivity (Mokany et al. 2003) as well as crown shape (Muhairwe 1994). This last element is intimately linked to vertical foliage distribution, which is not constant and might cause stem sections to experience different growth rates (Forward and Nolan 1961).

Jack pine (*Pinus banksiana* Lamb.) and black spruce (*Picea mariana* (Mill.) B.S.P.) are two species of great commercial interest in the eastern Canadian boreal forests, and thinning of mature stands would be considered as a means to increase individual stem biomass and diameter growth (Weetman 1971; Barbour et al. 1994). Previous studies have shown that thinning increases radial growth at breast height for jack pine (Barbour et al. 1994) and black spruce (Weetman 1971; Yang and Hazenberg 1992; Thorpe et al. 2007) but information about growth distribution along the stem above and below DBH is lacking. Increase in wood production has been related to foliage efficiency in Douglas-fir (*Pseudotsuga menziesii* (Mirb) Franco) (Brix 1983); yet, direct measurements of jack pine and black spruce needle efficiency two years after thinning have shown no gain in leaf level photosynthetic efficiency (amount of C uptake per unit of leaf area or mass per second) (Goudiaby et al. 2011_a).

The objective of this study was to quantify growth distribution patterns along the stem after thinning in the light demanding jack pine and the shade tolerant black spruce. By relating branch and foliage biomass and density patterns within crown to stem growth, we will show how the proximity to stem of foliage and branches influences stem growth distribution in the context of thinning. Finally, by relating stemwood increment to foliage, known as growth efficiency, we will evaluate changes in tree vigour occurring subsequently to thinning.

3.4 Material and Methods

3.4.1 Study area

The study was conducted in the Abitibi-Témiscamingue region of Northwestern Quebec. The region is part of the Canadian boreal forest (Rowe 1972). The climate is continental with an average daily temperature between 0.8 and 1.2 °C. Annual mean precipitation ranges from 671 to 899 mm with a maximum monthly average of 113 mm falling in July (Environment Canada 2009). The topography is relatively flat and the elevation ranging from 300 to 350 m. Balsam fir (*Abies balsamea* (L.) Mill.), black spruce, white spruce (*Picea glauca* (Moench)), jack pine, and trembling aspen (*Populus tremuloides* Michx.) are the dominant tree species in the region.

3.4.2 Experimental design

Five jack pine and four black spruce stands were selected among stands targeted for operational commercial thinning within the region (Table 3.1). Stands were even-aged and originated from forest fires. Jack pine stands were growing on fluvioglacial surface deposits. Soils consisted of sandy or loamy sands and were well drained with a 10-20 cm organic matter layer of feathermoss origin. Jack pine stands were between 48 and 82-year-old with site index between 16.2 and 17.2 m at 50 years (Table 3.1). The initial stand basal area was between 24.4 and 35.5 m² ha⁻¹ while relative basal area removed varied from 5.6 % to 56.4 % (Table 3.1). Black spruce stands were situated on poorly drained heavy clay deposits covered by a raw humus and litter a 10-20 cm thick layer. Black spruce stands were between 93 and 95-year-old with site index between 15.4 and 17.0 m (Table 3.1). Initial basal area ranged from 34.8 to 41.8 m² ha⁻¹ with a relative basal area removed varying from 19.2 to 68.0 % (Table 3.1). Separate experiments were conducted for jack pine and black spruce. Each experiment was designed as a completely randomized block experiment with three levels of thinning intensity - intensive with a density of 0.4 relatively to initial stand density (Grenier et al. 2001), moderate (relative densities of 0.5), and a control (no-thinning). Thinning from below was applied to 4 ha plots (experimental units) in each block by removing small, poor quality, and low vigour trees (Grenier et al. 2001).

Table 3.1 Natural jack pine and black spruce site characteristics from control stands. In parentheses, we present the range (minimum - maximum) of diameter at breast height over bark, tree height, and live crown ratio of experimental plots close to sample trees

Site names	Location	Density ^a	$G_{1.3}^b$	SI_{50}^c	Stand age ^d	Tree height (H_{tr} , m)	DBH ^e	LCR	Crown width (m)	S-Y_T ^f	S-Y_M ^g
Jack pine											
Castagnier-Nord	N48° 48' W77° 55'	2400	24.4	17.16	48	15.79 (12.25 – 15.98)	15.39 (3.87 – 18.33)	0.37 (0.38 – 0.55)	4.24	Aut-1998	Sum-2004
Clérycy	N48° 18' W78° 39'	2975	29.6	16.94	70	17.40 (10.67 – 20)	17.30 (3.65 – 21.7)	0.37 (0.25 – 0.43)	4.96	Aut-1998	Sum-2004
Dollard	N48° 20' W77° 03'	3300	26.6	16.85	53	16.98 (10.83 – 14.88)	14.86 (5.9 – 16.9)	0.41 (0.29 – 0.44)	5.94	Win-1999	Sum-2004
Duprat-Est	N48° 23' W79° 07'	4125	35.5	16.18	53	15.94 (11.55 – 15.70)	14.41 (5.4 – 16.94)	0.40 (0.23 – 0.46)	4.26	Win-1999	Sum-2004
Figüery	N48° 26' W78° 11'	2400	28.0	16.84	82	19.39 (13.50 – 19.00)	18.91 (4.02 – 22.9)	0.37 (0.22 – 0.49)	5.70	Aut-1998	Sum-2004

Table 3.1 Continued. Natural jack pine and black spruce site characteristics from control stands. In parentheses we present the range (minimum - maximum) of diameter at breast height, tree height, and live crown ratio of experimental plots close to sample trees

Site names	Location	Density ^a	$G_{1.3}^b$	SI_{50}^c	Stand age ^d	Tree height (H_{tr} , m)	DBH ^e	LCR	Crown width (m)	S-Y_T ^f	S-Y_M ^g
Black spruce											
Castagnier-Sud	N48° 45' W77° 50'	1800	35.8	17.02	95	20.11 (14.93 – 19.73)	18.93 (8.80 – 24.62)	0.15 (0.28 – 0.49)	4.82	Win-2001	Aut-2006
Miniac-Sud	N48° 52' W78° 10'	2800	38.9	15.87	93	17.57 (12.38 – 17.75)	16.07 (6.77 – 23.03)	0.34 (0.34 – 0.37)	3.36	Win-2000	Aut-2005
Quévillon	N49° 06' W76° 59'	2150	34.8	16.40	93	18.53 (9.38 – 23.29)	16.15 (4.63 – 22.40)	0.58 (0.42 – 0.44)	5.84	Win-1999	Sum-2005
Vassal	N48° 51' W77° 45'	2450	41.8	15.43	93	19.83 (12.33 – 18.25)	15.42 (7.13 – 22.65)	0.36 (0.38 – 0.55)	4.80	Win-1999	Sum-2005

Note: Number of individuals (n) is 10 for jack pine and 8 for black spruce.

Meaning of superscripts is given below.

^a Number of stems per hectare, in-between trails.

^b Initial stand basal area ($m^2 ha^{-1}$): average of two 10×20 m experimental plots. In each experimental plot, basal area was computed from all individuals.

^c Site Index (tree height (m) at age 50, $N = 6$) for jack pine (Standard Error: SE = 0.409) and black spruce sites (SE = 0.565), calculated after Chapman-Richards model adapted with Pothier and Savard (1998) coefficients.

^d Average age (year) at zero cm tree height obtained from six sample trees per site

^e Average diameter over bark (cm) at breast height (1.3 m)

^f Season-year of thinning (Wint = winter; Aut = autumn; Sum = summer – end for jack pine and beginning for black spruce)

^g Season-year of tree sampling and measurements.

3.4.3 Plot measurements

In each experimental unit, 10×20 m permanent sampling plots were positioned between two consecutive skidding trails at a rate of four plots in moderate and intensive treatments and two plots in the controls. All stems higher than 1.3 m were identified, tagged, and their DBH measured to estimate residual basal area (G_a). Intensity of thinning, expressed as basal area harvested (G_h), was obtained by the difference between initial basal area ($G_{1.3}$) and G_a . In order to estimate $G_{1.3}$, stump height and diameter over bark were measured and incorporated to equation 3.1 to estimate DBH of felled trees. Equation 3.1 was derived from a logarithmic regression between stump height and DBH as provided by Alemdag and Honer (1977):

$$\text{DBH} = D_{sp} (a \ln(H_{sp}) + b) \quad 3.1$$

where DBH is diameter at breast height over bark, D_{sp} the stump diameter over bark, H_{sp} the stump height, and a and b species-specific coefficients provided by the regression analysis. The coefficients a , and b were respectively 0.0819 and 0.5837 for jack pine, and 0.089 and 0.5478 for black spruce.

3.4.4 Sample tree measurements

Six years after thinning, two dominant trees per experimental unit were felled in the vicinity of sampling plots (30 jack pine, 24 black spruce). Total tree height and height to crown base were measured to the nearest cm, and DBH to the nearest mm. The crown base was defined as the lowest whorl having at least one living branch and separated from upper living whorls by one dead whorl at the most (Mäkinen and Isomäki 2004). All living branches were numbered and their position on the main stem recorded, as well as branch length and diameter (2 cm from stem insertion). Tree crown was then divided into upper, mid, and lower sections and four branches per section were randomly sampled along with the upper one tenth section of the crown. Each sample branch or crown top was stored in an individual bag for

foliage and branchwood biomass measurements done in the laboratory. All remaining branches were removed and 1.5 cm thick disks were taken at 0 m, 0.3 m, 0.6 m, 1 m, 1.3 m, 2 m, and at all consecutive one-metre intervals along the stem for stem analyses.

3.4.5 Stem measurements

On each cross-sectional stem disk, annual tree ring width measurements were performed on four paths with WinDendro™ (Regent Instruments Inc., Quebec City, QC, Canada) to the nearest 0.01 mm. The first path was positioned at 22.5° from the longest cross-sectional radius and the three other consecutive paths perpendicularly placed to the precedent one (Zarnovican 1985). Stem analysis data were compiled with the Winstem software (Regent Instruments Inc., Quebec City, QC, Canada), where annual height increment was estimated using the algorithm of Carmean (1972). Values of total annual stemwood volume increment (i_{vr}) were obtained from stem disk measurements and extrapolation between disks performed with WinDendro™ and Winstem™.

3.4.6 Estimation of total tree foliage and branchwood biomass

In the laboratory, sample branch as well as tree top foliage and branchwood biomass were obtained after the samples were dried at 65 °C for 48 hours. Models for individual branch foliage and wood biomass were developed by means of mixed linear models (SAS Institute version 9.1, Cary, NC, 2002) using dry biomass of sampled branches as dependant variables and branch length, diameter, and branch relative depth into crown as predictors. Branch relative depth into crown (H_{br}) was defined as the ratio of distance from stem apex to crown length (Maguire et al. 1998).

Blocks were also included in the models as random factors. Crown sections nested within trees and plots was treated as a repeated factor. All variables were log-transformed and multicollinearity among predictor variables tested prior to analyses by using variance

inflation factor using the REG / VIF procedure. Normality assumption was verified by visual inspection. Variance explained by a given individual predictor variable was assessed according to Singer (1998). Parameters significance was based on Type 1 (sequential order) hypothesis. Thereafter, the retained model was applied to individual branch measured in the field to estimate its biomass. Total tree foliage (W_F) and branchwood (W_{BW}) biomass were obtained for each tree by adding individual branch foliage and branchwood biomass as well as the crown upper section biomass of foliage and branchwood, respectively.

3.4.7 Annual stemwood volume increment

In order to account for differences in tree size and to link stemwood growth and physiology, stemwood increment was expressed in terms of annual specific volume of stemwood increment (SVI, $\text{cm}^3 \text{cm}^{-2} \text{yr}^{-1}$), derived as the ratio of annual volume increment to cambium surface area of each sampled stem section (Duff and Nolan 1957; Shea and Armson 1972; Lussier et al. 1992). By relating annual volume increment to cambium surface, SVI implies a physiological link to new bole growth by indirectly reflecting the ability of a tree to supply photosynthates to the vascular cambium for xylem production (Newton and Jolliffe 1998). A second benefit of using SVI pertains to allowing for a more valid comparison in relative growth for trees of different ages due to the fact that SVI is, comparatively to relative growth rate, less correlated with tree age (Bevilacqua 2002). Finally, SVI is highly variable across a greater range of tree sizes, suggesting it may be easier to identify the influence of natural or anthropogenic disturbances on tree growth (Bevilacqua 2002).

Specific volume increment was computed for individual stem sections from the base to the top of the stem. We assumed that stem sections between two consecutive stem disks were frustums of cones (truncated cones) and the last top section of the stem was a true cone. The cambium surface along each stem section was computed using mensurational formulas of frustums of cone and cone (Weisstein 2010). Annual SVI was then separately estimated for each stem section according to the formula:

$$SVI = \frac{V_n - V_{n-1}}{\frac{1}{2}(S_n + S_{n-1})} \quad 3.2$$

Where, for each stem section, V is the stemwood volume, S the cambium surface, and n the year.

3.4.8 Crown parameters

3.4.8.1 Crown length, live crown ratio, and height of crown base

Live crown ratio was computed for each single tree as the ratio of L_{cr} to total tree height (Holdaway 1986) directly measured on felled trees. Height of crown base was directly measured on felled trees and corresponded to the length of bare stem (H_s).

3.4.8.2 Foliage and branchwood mass density

Crown foliage and branch distribution within crown are known to provide insights into the occupation of space, light interception efficiency, and competitive effects between neighbouring trees (Kuuluvainen 1992). To account for differences in foliage density within the crown, jack pine and black spruce crowns were divided into ten equal sections. Each crown section was considered as a frustum of a cone and the lower base radius was taken as average branch length. The upper base radius was assumed to be the lower radius of the next upper crown section.

Foliage mass density (FD_w) and branchwood mass density (BD_w) for each crown section were then computed according to Weetman and Harland (1964) and Zeide (1998) as the ratio of foliage mass to the fractal volume it occupies:

$$FD_w = \frac{W_f}{F_v} \quad 3.3$$

$$BD_w = \frac{W_{bw}}{F_v} \quad 3.4$$

where F_v is the fractal volume, W_f the foliage mass, and W_{bw} the branchwood mass.

The relationship between the volume of the crown section and the fractal volume occupied by foliage was assumed to be the volume of the crown section multiplied by the percentage of foliated branches occupying the given crown section.

3.4.9 Stem growth efficiency

Known as growth efficiency (GE, $\text{m}^3 \text{m}^{-2} \text{yr}^{-1}$), the ratio of stemwood increment to foliage surface area is frequently used in order to characterize stem response to silvicultural treatments. Estimation of GE for a given year is based on the ratio of annual stemwood volume to foliage surface area increment occurring the corresponding year (Waring et al. 1980; Brix 1983). We used a surrogated of GE in which foliage biomass is used rather than foliage surface area (Vanninen and Mäkelä 2000; Will et al. 2002) and stemwood biomass replaced stemwood volume. The use of foliage biomass in GE computation allowed for the examination of relative partitioning of stem biomass versus foliage biomass (Will et al. 2002) while the use of stemwood biomass avoided confounding productivity with changes in stem specific gravity that might have occurred with tree age or size (Will et al. 2002). Annual stemwood biomass was computed by multiplying annual stemwood volume increment by wood density of jack pine (469 kg m^{-3} , Park et al. 2009) and black spruce (470 kg m^{-3} , M. Ourais, and A. Koubaa, unpublished data). These wood densities were measured on the same trees as our measurements. Since our measurements did not allow for estimations of year-to-year variation of foliage biomass, we computed GE as the ratio of stemwood biomass

increment over the last three years of growth to total tree foliage biomass assuming that year-to-year fluctuation of stemwood growth caused by other factors than thinning would be minimized. Growth efficiency was then computed on a tree basis according as follows:

$$GE = \frac{S_{3y}}{W_F} \quad 3.5$$

where S_{3y} (kg) is the stemwood biomass increment of the last three years, and W_F (kg) represents the total foliage biomass.

3.4.10 Statistical analyses

To test effects of thinning on i_{Vtr} , SVI, W_F , W_{BW} , W_f , W_{bw} , FD_w , BD_w , GE, H_{cr} , L_{cr} , and LCR (dependant variables), a mixed linear regression model, allowing for random and nested effects was implemented using MIXED procedure of the SAS software package (SAS Institute version 9.1, Cary, NC, 2002). This approach was preferred to means comparison and ANOVA because of the within treatment variability in initial stand conditions and basal area removed. In doing so, we would benefit from each observation (tree level) while taking into account the non-independence of nested effects (trees nested within plots, and plots nested within blocks). The effect of thinning was assessed using relative basal area removed [$G_r = \text{basal area removed} / \text{initial basal area} \times 100$] as independent variable. Relative basal area removed was computed at the plot level while all tree response variables were computed at tree level and used as such in the statistical analysis. Prior to analysis, each predictor variable was regressed on all the other predictors using REG procedure in which VIF statement provided factors used to test multicollinearity among predictor variables. The following general model was used for our analyses:

$$Y_{bpti} = \beta_0 + \beta_1 G_{1.3bp} + \beta_2 G_{rbp} + \beta_3 S_{bpti} + \beta_4 G_{rb} S_{bpti} + \mu_b + \varepsilon_{bpti} \quad 3.6$$

where Y_{bpti} is the dependant variable ($b = \text{block}$, $p = \text{plot}$, and $t = \text{tree}$) for the i^{th} stem or crown section. For the independent variables, β_0 represents the intercept, $G_{1,3}$ the effect of basal area before thinning, G_{rb} the effect of relative basal area removed, and S_{bpti} the effect of section (stem or crown). For the coefficients, β_1 is the regression coefficients associated with $G_{1,3bp}$, β_2 the regression coefficient associated with G_{rbp} , β_3 the regression coefficient associated with S_{bpti} , β_4 the regression coefficient associated with $G_{rb}S_{bpti}$, μ_b the random effect associated with block, and ε_{bpti} an error term.

When measurements were repeated over stem or crown sections (i_{vr} , SVI, W_f , W_{bw} , FD_w , and BD_w), repeated factor analyses were conducted using the ordinal number of stem section (for SVI) or ordinal number of crown section (for FD_w , and BD_w). Finally, to account for between-site differences in natural tree growth performance, the average annual SVI computed from the 5-year period preceding thinning was used as covariate when thinning effect was tested on SVI. The SP(POW) covariance structure for unequally spaced data (Littell et al. 2006) was applied for SVI while for other repeated response variables (FD_w , and BD_w), measurements were equally spaced over the stem allowing us to use an autoregressive structure AR(1). Individual analyses for SVI were done for each year following treatment. Parameters were considered significant at $p < 0.05$ based on Type 1 (sequential order) F -test of fixed effects. For illustrative purposes only, thinning classes were assigned as follows: Class 1: $G_r = 0\%$ (control); Class 2: $1\% \leq G_r \leq 31\%$ (mean = 20.65%); Class 3: $32\% \leq G_r \leq 40\%$ (mean = 37.24%); Class 4: $41\% \leq G_r \leq 66\%$ (mean = 47.87%).

3.5 Results

3.5.1 Annual stemwood volume increment

Relative basal area removed had a significant positive effect on annual stemwood volume increment starting 3 years following thinning for jack pine, and 4 years for black spruce (Table 3.2; Fig. 3.1). For both species, initial basal area did not show any significant effect on annual stemwood volume increment. However, 5-year average stemwood volume increment

before thinning had a significant effect on annual stemwood volume increments for all years after thinning.

Table 3.2 Effects of relative basal area removed on total tree annual stemwood volume increment of jack pine and black spruce 1 to 6 years following thinning using basal area before thinning and 5-year average total stemwood volume increment before thinning as covariates

Predictor	1 year	2 years	3 years	4 years	5 years	6 years
Jack pine						
$G_{1,3}$	0.151	0.238	0.838	0.515	0.538	0.998
i_{Vn-sb}	< 0.001	< 0.001	< 0.001	0.001	< 0.001	< 0.001
G_r	0.984	0.070	0.002	< 0.001	0.002	0.002
Model R^2	0.96	0.89	0.81	0.79	0.75	0.73
Black spruce						
$G_{1,3}$	0.254	0.303	0.981	0.026	0.931	0.530
i_{Vn-sb}	< 0.001	< 0.001	0.002	0.001	< 0.001	< 0.001
G_r	0.074	0.162	0.277	0.012	0.043	0.030
Model R^2	0.90	0.85	0.49	0.65	0.63	0.67

Note: G_r : relative basal area removed, $G_{1,3}$: basal area before thinning, i_{Vn-sb} : 5-year average total stemwood volume increment before thinning.

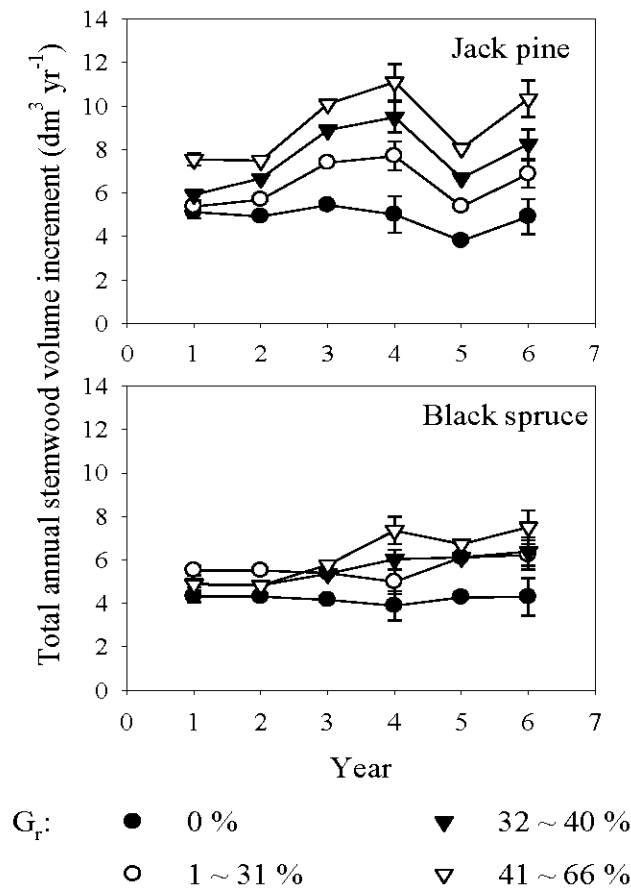


Figure 3.1 Jack pine and black spruce total annual stemwood volume increment 1 to 6 years after thinning modelled through regression analysis. Error bars represent standard errors.

3.5.2 Patterns in specific volume increment along the stem

In jack pine stands, 5-year average SVI before thinning, and height of stem section had highly significant effects on SVI, while initial basal area ($G_{1.3}$) had none (Table 3.3; Fig. 3.2). We noted for G_r , and for the interaction between G_r and height of stem section a significant effect on SVI the second year after thinning and these effects were still significant six years after treatment. In control jack pine stands, average annual SVI between ground level and

8 m remained constant with height and averaged $0.72 \text{ cm}^3 \text{ cm}^{-2} \text{ yr}^{-1}$ the first year following thinning. An increase in SVI with height was observed between 8 and 14 m. This pattern remained constant over the 6-year period. In thinned stands, SVI increased with G_r (Table 3.3). In the second year following treatment, this increase was limited to the base of the tree up to 8 m but with time, the increase in SVI with G_r spread upward (Fig. 3.2). Six years after thinning, differences between control, and thinned stands in patterns of SVI along tree stem were still apparent but limited to 0 up to 10 m height.

Table 3.3 Effects of relative basal area removed and height of stem section on annual specific volume increment for jack pine and black spruce, 1 to 6 years following thinning using basal area before thinning and the average annual specific volume increment of the 5-year period preceding thinning as covariates

Predictor	1 year	2 years	3 years	4 years	5 years	6 years
Jack pine						
SVI_{5b}	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001
$G_{1.3}$	0.188	0.576	0.471	0.114	0.180	0.403
H_{ts}	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001
G_r	0.360	0.022	0.001	< 0.001	0.004	0.017
$G_r \times H_{ts}$	0.883	0.015	0.091	< 0.001	0.009	0.004
Model R^2	0.89	0.86	0.71	0.67	0.65	0.63
Black spruce						
SVI_{5b}	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001
$G_{1.3}$	0.264	0.240	0.763	0.004	0.306	0.089
H_{ts}	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001
G_r	0.075	0.393	0.098	< 0.001	0.002	< 0.001
$G_r \times H_{ts}$	0.003	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001
Model R^2	0.76	0.64	0.53	0.67	0.54	0.68

Note: G_r : relative basal area removed, H_{ts} : height of stem section, SVI: annual specific volume increment, $G_{1.3}$: basal area before thinning, SVI_{5b} : average annual specific volume increment of the 5-year period preceding thinning.

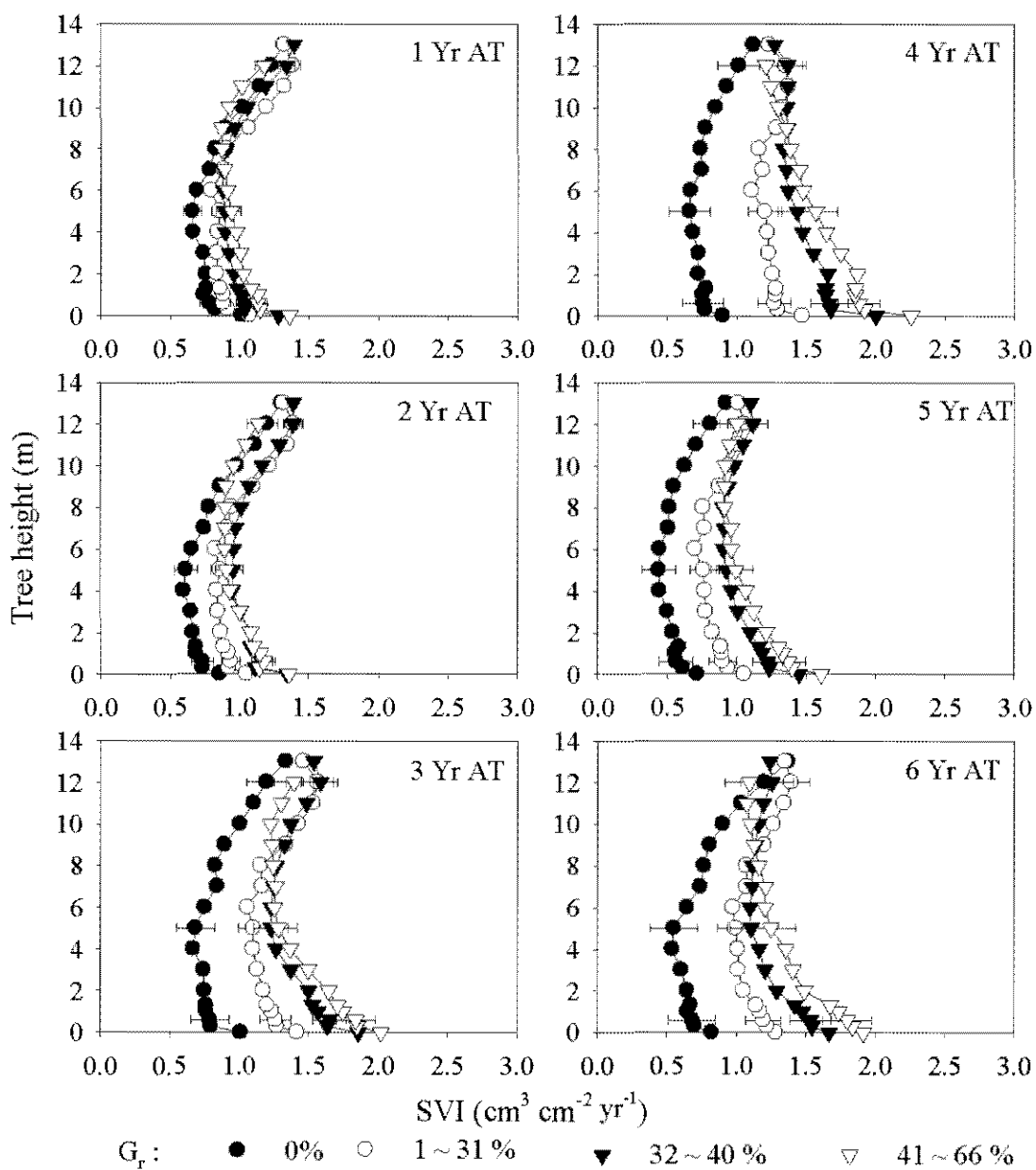


Figure 3.2 Jack pine annual specific volume increment along the bole 1 to 6 years after thinning modelled through regression analysis. Error bars represent standard errors.

In black spruce stands, 5-year average SVI before thinning, and height of stem section had highly significant effects on SVI for all years while $G_{1.3}$ had no significant effect except in year 4 (Table 3.3; Fig. 3.3). During the first three years following thinning, G_r had no significant effect on SVI, whereas its interaction with stem section was significant. In control stands, SVI reached $0.8 \text{ cm}^3 \text{ cm}^{-2}$ at one metre, during these first three years, and remained constant along tree stem. In thinned stands, SVI was 0.60 at 1 m, and remained constant up to 8 m height. Three years after thinning, patterns of SVI with height were similar for all treatments up to 5 m height. From 5 m and higher, SVI increased with G_r . From year 4 to 6, both G_r and the interaction between G_r and tree section were significant. In the fourth and fifth years after thinning, SVI increased with G_r , and the increase was stronger with height for higher G_r .

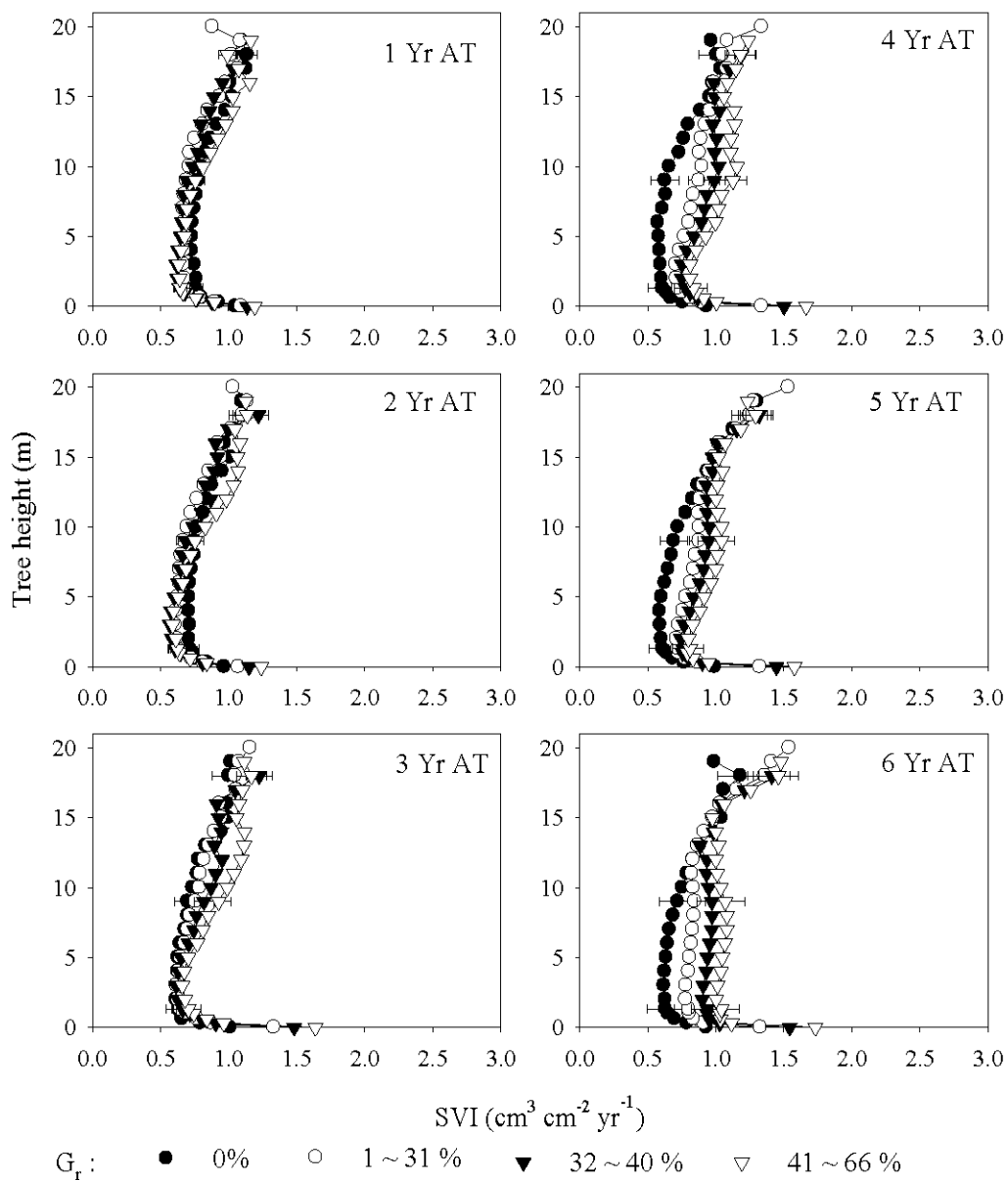


Figure 3.3 Black spruce annual specific volume increment along the bole 1 to 6 years after thinning modelled through regression analysis. Error bars represent standard errors.

3.5.3 Branchwood and foliage biomass prediction models

Foliage and branchwood biomass estimation models were separately conducted for each single site (block) of our experimental design to account for between-site differences. The rationale is that we obtained a marginal significant block effect for foliage ($df = 442$, $F = 2.27$, and $p < 0.06$) and a significant block effect for branchwood biomass ($df = 442$, $F = 7.6$, and $p < 0.001$) for jack pine as well as significant block effect for foliage ($df = 346$, $F = 9.52$, and $p < 0.001$) and branchwood biomass ($df = 346$, $F = 9.48$, and $p < 0.001$) for black spruce.

The models obtained for all separate jack pine sites (Table 3.4) explained at least 67% of foliage biomass and 79% of branchwood biomass and best model predictions reached values as high as 89% and 97% for foliage and branchwood biomass, respectively. For black spruce sites except Castagnier-Sud (Table 3.5), the models obtained for all sites explained at least 52% of foliage biomass and 83% of branchwood biomass and best model predictions reached values as high as 73% and 95%, for foliage and branchwood biomass, respectively. Note that for black spruce, models for Castagnier-Sud site explained 36% of foliage biomass and 41% of branchwood biomass.

3.5.4 Height of crown base, crown length and live crown ratio

In control plots, jack pine live crown length of dominant trees averaged 6.53 m with a LCR of 0.38 while crown length of dominant black spruce trees averaged 6.74 m with a LCR of 0.36. For jack pine and black spruce stems, H_{cr} was respectively located at 10.57 m and 10.71 m from the base of the tree and was not significantly affected by thinning. No significant relationship was found between G_r and LCR of dominant trees for either species. The relationship between G_r and L_{cr} or H_{cr} was not significant either.

Table 3.4 Relationships between foliage and branchwood biomass and branch length, basal diameter, and relative depth into crown for jack pine in different sites. Mixed models linear regression analyses

Effect	Estimate	<i>N</i>	SE	df	<i>t</i>	<i>p</i> > <i>t</i>	<i>R</i> ²	Variance
Castagnier-Nord								
Log-dry-foliage biomass								
Intercept	-10.169	80	1.199	67	8.48	< 0.001	0.67	0.002
Log- <i>L</i> _{br}	1.937		0.166	69.4	11.65	< 0.001		
Log- <i>H</i> _{br}	0.614		0.139	76.3	4.42	< 0.001		
Log-dry-branchwood biomass								
Intercept	-11.456	80	0.964	78	11.89	< 0.001	0.79	0.011
Log- <i>L</i> _{br}	2.286		0.140	78	16.39	< 0.001		
Cléricy								
Log-dry-foliage biomass								
Intercept	-4.770	87	1.237	82.7	3.86	< 0.001	0.89	0.063
Log- <i>D</i> _{br}	-0.350		0.109	79.1	3.20	0.002		
Log- <i>L</i> _{br}	0.574		0.278	82.4	2.07	0.041		
Log- <i>H</i> _{br}	1.683		0.297	82.8	5.66	< 0.001		
Log-dry-branchwood biomass								
Intercept	-1.989	87	0.359	66.9	5.53	< 0.001	0.83	0.010
Log- <i>D</i> _{br}	2.530		0.134	79.5	18.94	< 0.001		
Dollard								
Log-dry-foliage biomass								
Intercept	-1.266	87	0.279	61.7	4.53	< 0.001	0.81	0.010
Log- <i>D</i> _{br}	1.771		0.105	78.6	16.89	< 0.001		
Log- <i>H</i> _{br}	-0.372		0.109	79.8	16.89	< 0.001		
Log-dry-branchwood biomass								
Intercept	-6.379	87	1.153	84	5.53	< 0.001	0.92	0.228*
Log- <i>D</i> _{br}	1.539		0.232	84	6.63	< 0.001		
Log- <i>L</i> _{br}	0.956		0.244	84	3.92	< 0.001		
Duprat-Est								
Log-dry-foliage biomass								
Intercept	-2.318	84	0.355	66.9	6.52	< 0.001	0.81	0.086
Log- <i>D</i> _{br}	2.278		0.130	79.6	17.50	< 0.001		
Log-dry-branchwood biomass								
Intercept	-4.914	84	0.812	80	6.05	< 0.001	0.97	0.067*
Log- <i>D</i> _{br}	1.918		0.194	80	9.90	< 0.001		
Log- <i>L</i> _{br}	0.627		0.186	80	3.37	0.001		
Log- <i>H</i> _{br}	0.227		0.058	80	3.93	< 0.001		

Table 3.4 Continued. Relationships between foliage and branchwood biomass and branch length, basal diameter, and relative depth into crown for jack pine in different sites. Mixed models linear regression analyses

Figury								
Log-dry-foliage biomass								
Intercept	-5.723	92	1.137	88.3	5.04	< 0.001	0.80	0.010
Log- D_{br}	0.903		0.246	88.4	3.67	< 0.001		
Log- L_{br}	1.039		0.249	88.4	4.17	< 0.001		
Log-dry-branchwood biomass								
Intercept	-8.749	92	0.734	87.2	11.92	< 0.001	0.95	0.022
Log- D_{br}	1.132		0.159	86.3	7.14	< 0.001		
Log- L_{br}	1.494		0.160	86.3	9.31	< 0.001		

Note: Formulas are expressed in the form $y = \beta_0 + \beta_1(\text{Log-}D_{br}) + \beta_2(\text{Log-}L_{br}) + \beta_3(\text{Log-}H_{br})$, where y is the natural log-transformed dried foliage or branchwood biomass (g), D_{br} is the branch diameter (mm) at the base, L_{br} is the branch length (mm), and H_{br} represents the branch relative depth into crown. The coefficients β_0 , β_1 , β_2 , and β_3 are respectively the intercept and the estimates of Log- D_{br} , Log- L_{br} , and Log- H_{br} . The variance is for trees nested within plots.

* no random tree effect due to null variance, the variance provided is the one of the residuals
All non-zero parameters were statistically significant at $\alpha = 0.05$.

Table 3.5 Relationships between foliage and branchwood biomass and branch length, basal diameter, and relative depth into crown for black spruce in different sites. Mixed models linear regression analyses

Effect	Estimate	<i>N</i>	SE	df	<i>t</i>	<i>p</i> > <i>t</i>	<i>R</i> ²	Variance
Castagnier-Sud								
Log-dry-foliage biomass								
Intercept	0.188	80	1.086	60.1	0.17	0.863	0.36	0.151
Log- <i>D</i> _{br}	0.897		0.336	76.2	2.67	0.009		
Log- <i>H</i> _{br}	0.115		0.125	57.5	0.92	0.022		
Log-dry-branchwood biomass								
Intercept	0.128	80	0.399	71.9	0.32	0.749	0.41	0.028
Log- <i>D</i> _{br}	1.820		0.155	76.4	11.74	< 0.001		
Log- <i>H</i> _{br}	0.309		0.082	76.9	3.79	< 0.001		
Miniac-Sud								
Log-dry-foliage biomass								
Intercept	-6.195	92	1.806	86	3.43	< 0.001	0.72	0.038
Log- <i>D</i> _{br}	1.784		0.236	87.2	7.55	< 0.001		
Log- <i>L</i> _{br}	0.077		0.292	88	2.64	0.010		
Log- <i>H</i> _{br}	-0.673		0.161	82.8	4.17	< 0.001		
Log-dry-branchwood biomass								
Intercept	-5.940	92	0.767	88.2	7.74	< 0.001	0.83	0.018
Log- <i>D</i> _{br}	1.460		0.208	88.5	7.04	< 0.001		
Log- <i>L</i> _{br}	0.954		0.160	88.8	5.97	< 0.001		
Quévillon								
Log-dry-foliage biomass								
Intercept	-1.206	88	0.393	83.2	3.07	0.003	0.73	0.064
Log- <i>D</i> _{br}	2.080		0.146	82.5	14.29	< 0.001		
Log-dry-branchwood biomass								
Intercept	-4.486	88	0.479	84.3	9.36	< 0.001	0.95	0.034
Log- <i>D</i> _{br}	1.124		0.146	81.4	11.24	< 0.001		
Log- <i>L</i> _{br}	0.716		0.108	81.5	6.65	< 0.001		

Table 3.5 Continued. Relationships between foliage and branchwood biomass and branch length, basal diameter, and relative depth into crown for black spruce in different sites. Mixed models linear regression analyses

Vassal								
Log-dry-foliage biomass								
Intercept	-4.750	93	2.047	88.1	2.32	0.023	0.52	0.065
Log- D_{br}	0.730		0.279	88.4	2.62	0.011		
Log- L_{br}	0.988		0.344	88.3	2.87	0.005		
Log- H_{br}	-0.642		0.192	88.9	3.33	0.001		
Log-dry-branchwood biomass								
Intercept	-4.962	93	0.653	89.8	7.59	< 0.001	0.87	0.016
Log- D_{br}	1.117		0.160	88.7	6.98	< 0.001		
Log- L_{br}	0.959		0.130	89.9	7.38	< 0.001		

Note: Formulas are expressed in the form $y = \beta_0 + \beta_1(\text{Log-}D_{br}) + \beta_2(\text{Log-}L_{br}) + \beta_3(\text{Log-}H_{br})$, where y is the natural log-transformed dried foliage or branchwood biomass (g), D_{br} is the branch diameter (mm) at the base, L_{br} is the branch length (mm), and H_{br} represents the branch relative depth into crown. The coefficients β_0 , β_1 , β_2 , and β_3 are respectively the intercept and the estimates of Log- D_{br} , Log- L_{br} , and Log- H_{br} . The variance is for random trees nested within plots.

* no random tree effect due to null variance, the variance provided is the one of the residuals. All non-zero parameters were statistically significant at $\alpha = 0.05$.

3.5.5 Total tree foliage and branchwood biomass

In jack pine control treatments, total tree foliage and branchwood biomass were 3.89, and 9.80 kg tree⁻¹, respectively. Crown foliage and branchwood biomass were respectively 0.60, and 0.85 kg m⁻¹ of crown length at the crown base, and 0.77 and 1.11 kg m⁻¹ of crown length at the top of the crown. Maximum value of total foliage biomass (1.01 kg m⁻¹ of crown length) was observed at 60% of crown height (14.57 m total tree height from the base and 3.97 m from the crown base). Maximum value of total branchwood biomass was 1.28 kg m⁻¹ of crown length reached at two crown sections 1) 2.64 m height from the crown base and 13.24 m of stem height, and 2) 3.97 m height from the crown base and 14.57 m of stem height. Relative basal area removed and basal area before thinning had no significant effect on jack pine total foliage and branchwood biomass (Table 3.6; Fig. 3.4). In addition, there was no significant effect of relative basal area removed on total tree foliage biomass. However, we noted at mid-crown (3.31 m height from the crown base and 13.91 m of stem height), a significantly greater foliage and branchwood biomass for thinned stands (Fig. 3.4).

For black spruce, total foliage biomass was $5.59 \text{ kg tree}^{-1}$ and branchwood biomass $39.30 \text{ kg tree}^{-1}$ for control treatment. Again for control treatment, total foliage and branchwood biomass were respectively 0.51 and 3.91 kg m^{-1} of crown length at the crown base (0.83 m height from the crown base and 11.63 m of stem height) and 0.56 and 4.27 kg m^{-1} of crown length at the top section of the crown (7.07 m height from the crown base and 17.87 m of stem height). At mid-crown, average foliage and branchwood biomass had maximum values of respectively 0.88 kg m^{-1} and 6.74 kg m^{-1} of crown length (4.15 m height from the crown base and 14.95 m of stem height). However, following thinning treatments, maximum branchwood biomass shifted, relative to control experiment, to the top of the crown (15.21 - 20.70 kg m^{-1} of crown length). It is also at the top of the crown that we noted a greater difference in branchwood biomass between control and thinning treatments. Relative basal area removed and basal area before thinning did not have any significant effect on total foliage and branchwood biomass (Table 3.6; Fig. 3.4). In addition, G_r had no significant effect on foliage or branchwood biomass at any crown section.

Table 3.6 Effects of relative basal area removed, ordinal number from base to top of crown section and their interaction on total tree foliage and branchwood biomass of jack pine and black spruce 6 years following thinning

	Num df	Den df	<i>F</i> value	<i>p</i> > <i>F</i>	Variance
Jack pine					
Total foliage biomass					
<i>G_r</i>	1	226	6.62	0.011	0.01
<i>H_{cr}</i>	8	226	7.13	< 0.001	
<i>G_r × H_{cr}</i>	8	226	1.07	0.383	
Total branchwood biomass					
<i>G_r</i>	1	226	5.38	0.021	0.02
<i>H_{cr}</i>	8	226	3.71	< 0.001	
<i>G_r × H_{cr}</i>	8	226	0.79	0.613	
Black spruce					
Total foliage biomass					
<i>G_r</i>	1	187	1.50	0.222	n.r.
<i>H_{cr}</i>	8	187	5.98	< 0.001	
<i>G_r × H_{cr}</i>	8	187	0.56	0.808	
Total branchwood biomass					
<i>G_r</i>	1	187	2.97	0.087	40.97
<i>H_{cr}</i>	8	187	2.15	0.034	
<i>G_r × H_{cr}</i>	8	187	1.11	0.360	

Note: *G_r*: relative basal area removed, *H_{cr}*: crown section.

Basal area before thinning (*G_{1.3}*) was not significant and was then removed from all the final models as explanatory variable. Variance represents that of the random block effect. n.r.: no random block effect due to null variance.

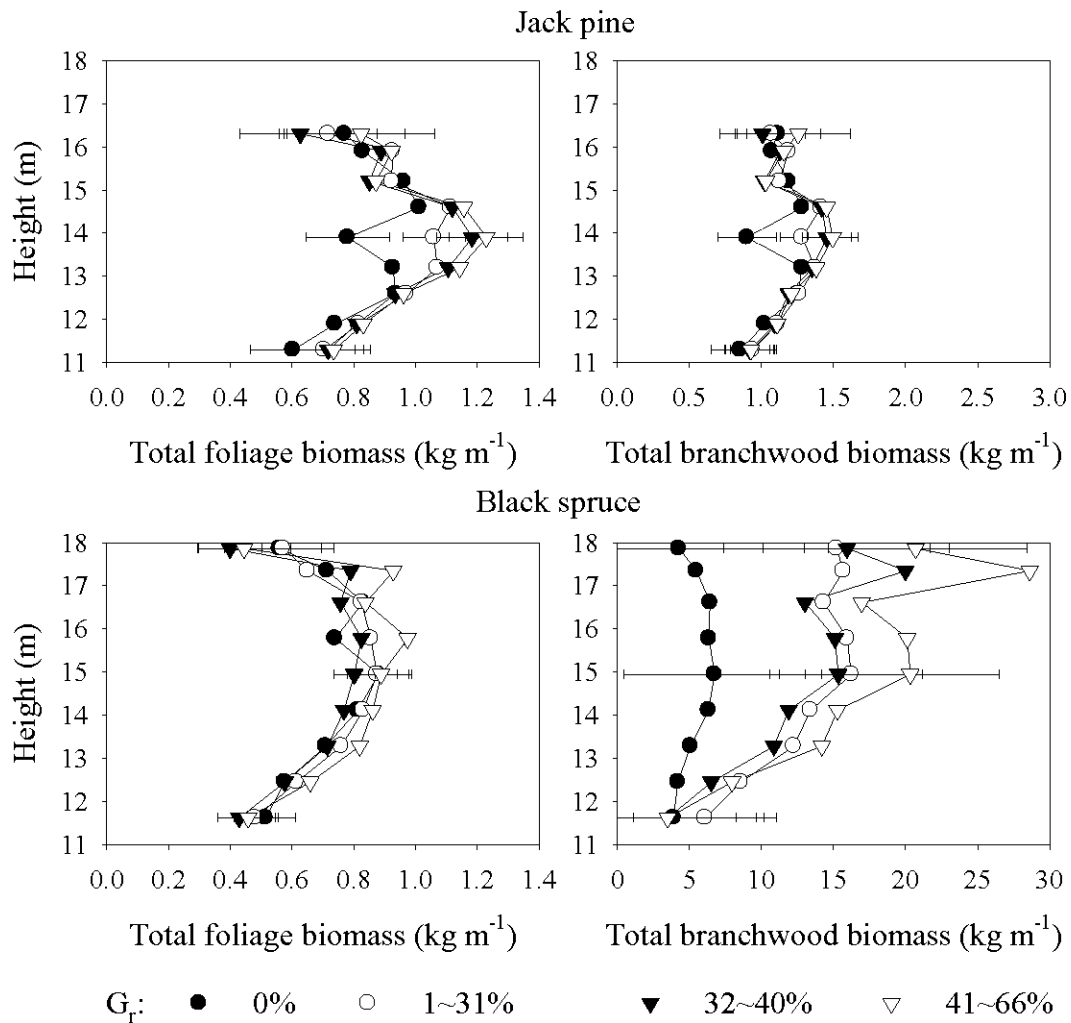


Figure 3.4 Total foliage and branchwood biomass expressed per metre of stem length for jack pine and black spruce, 6 years after thinning modelled through regression analysis. Error bars represent standard errors. Only selected error bars are presented for sake of clarity.

3.5.6 Foliage and branchwood mass density

For jack pine, only crown section had significantly positive effects on FD_w as FD_w increases with G_r and tree section (Table 3.7; Fig. 3.5). No interaction between G_r and tree section was

found and the model explained 68% of FD_w variance. For BD_w the pattern was similar: crown section had a significant effect on BD_w . The interaction between basal area removed and ordinal number of crown section had no effect on BD_w and the model explained 61% of BD_w variance.

For black spruce (Table 3.7; Fig. 3.5), only crown section had a significant effect on FD_w and the model explained 60% of FD_w variance. We noticed an exponential increase in FD_w from the base up to the top of the crown. For BD_w the pattern was similar: crown section had a significant effect on BD_w . The model explained 74% of FD_w variance.

3.5.7 Growth efficiency (GE)

Jack pine displayed a significantly positive relationship between G_r and GE ($R^2 = 0.78$, $df = 21$, $F = 9.2$, $p = 0.006$). For black spruce ($R^2 = 0.86$), there was no significant relationship between G_r and GE (Fig. 3.6).

Table 3.7 Effects of relative basal area removed, ordinal number from base to top of crown section and their interaction on foliage mass and branchwood mass density of jack pine and black spruce 6 years following thinning using block as a random effect

	Num df	Den df	<i>F</i> value	<i>p</i> > <i>F</i>	Variance
Jack pine					
Foliage mass density					
G_r	1	226	3.46	0.064	0.03
H_{cr}	8	226	19.29	< 0.001	
$G_r \times H_{cr}$	8	226	0.97	0.460	
Branchwood mass density					
G_r	1	226	2.56	0.111	0.02
H_{cr}	8	226	15.74	< 0.001	
$G_r \times H_{cr}$	8	226	0.55	0.817	
Black spruce					
Foliage mass density					
G_r	1	187	0.01	0.936	0.05
H_{cr}	8	187	9.54	< 0.001	
$G_r \times H_{cr}$	8	187	0.36	0.941	
Branchwood mass density					
G_r	1	187	0.34	0.562	n.r.
H_{cr}	8	187	3.39	0.001	
$G_r \times H_{cr}$	8	187	0.76	0.637	

Note: G_r : relative basal area removed, H_{cr} : crown section, FD_w : foliage mass density, BD_w : branchwood mass density.

Basal area before thinning ($G_{1.3}$) was not significant and was then removed from all the final models as explanatory variable. The variance represents the one of the random block effect; n.r.: no random block effect due to null variance.

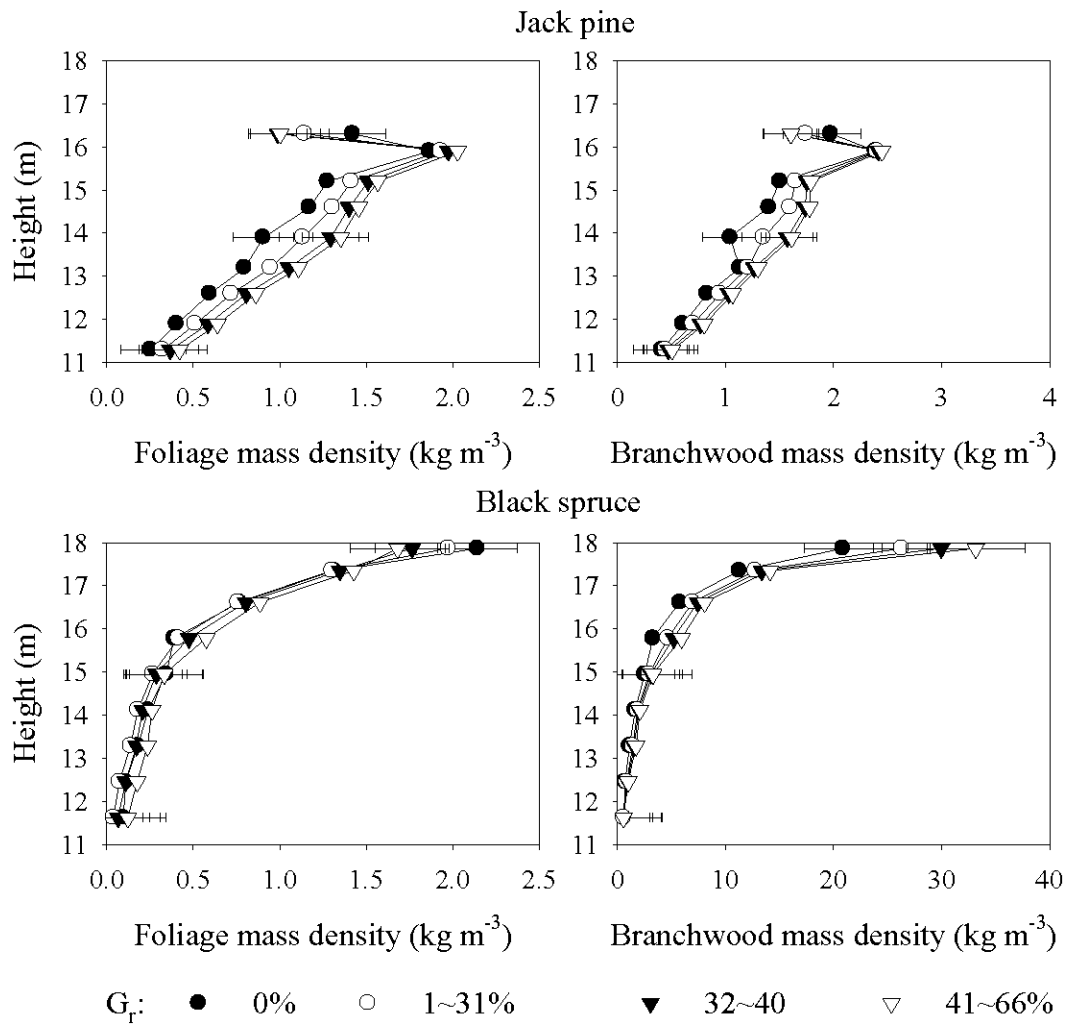


Figure 3.5 Foliage and branchwood mass density expressed per metre of stem length for jack pine and black spruce 6 years after thinning modelled through regression analysis. Error bars represent standard errors. Only selected error bars are presented for the sake of clarity.

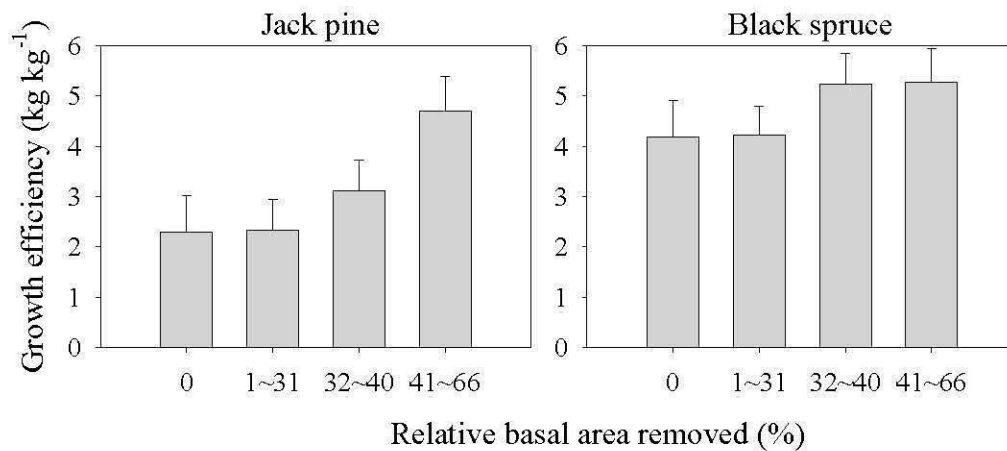


Figure 3.6 Jack pine and black spruce growth efficiency 6 years after thinning obtained from mixed model outcomes. Error bars represent standard errors.

3.6 Discussion

As expected, jack pine reacted earlier and was more responsive to thinning than black spruce for most of the variables measured. Our results are consistent with earlier findings which showed, in response to thinning, a faster and a greater jack pine diameter growth (Barbour et al. 1994) in comparison with black spruce (Weetman 1971). Furthermore, our study provided new evidences on some of the mechanisms responsible for these patterns. For jack pine, enhanced growth in response to thinning mostly occurred at the stem base and the increase in stemwood growth after thinning was associated with increases in foliage biomass at mid-crown and growth efficiency. Black spruce displayed a more uniform growth pattern along its stem while keeping its foliage biomass, foliage density within crown, and growth efficiency unchanged following thinning.

The significant increase in jack pine annual stemwood increment was consistent with the greater GE that has occurred after thinning. Usually, an increase in GE indicates a greater photosynthetic production per unit of foliage area, an increase in the proportion of carbohydrates allocated to stemwood growth or an increased allocation to stem growth for a

given photosynthetic production. Waring et al. (1980) showed that increased GE, go hand in hand with an increase in tree vigour. Although foliage density has been shown to be the most important single factor characterizing GE and growth allocation to stems (Vanninen and Mäkelä 2000), such statement does not agree with what we found for jack pine. For black spruce, stemwood increment following thinning could be related to an increase in tree productivity meaning there was a proportional growth of foliage and stemwood (constant allometry) so that GE remained constant following thinning.

The pattern of growth distribution along the stem displayed by jack pine, in response to thinning, has been previously described for other conifers and was related to a shift of growth downwards on the stem (Karlsson 2000; Peltola et al. 2002; Tasissa and Burkhart 1997). By contrast, black spruce displayed maximal growth at the base of the stem (< 1 m), and a more consistent growth along the rest of the stem, similar to the pattern previously described by Zenner (2008) for *Pinus strobus* L. a moderately shade-tolerant species. According to Assmann (1970), stem growth distribution such as we observed for jack pine pattern is typical of vigorous growth driven by cambial activity, or richer sites while the pattern displayed by black spruce is typical of poor growing conditions. In any case, jack pine always has a more vigorous growth than black spruce when their site conditions are similar.

The consequence of such a stem growth distribution in response to thinning is an increase in jack pine stem taper. This is in accordance with the results of Sharma and Parton (2009), which predicted that density affected jack pine taper more than black spruce taper. According to Muhairwe (1994), the downward shift of growth, is closely related to crown size, which in turn is related to stand density. Hence, it is probable that increase in foliage biomass at mid-crown of jack pine requires more taper in order to maintain its mechanical stem stability. However, black spruce did not change its foliage biomass so that changes in taper would not be necessary to support the crown. Black spruce stem growth distribution was interpreted as an adaptative trait for moderately shade-tolerant species to enhance tree stability, as well (Zenner 2008).

The negative response to thinning of stemwood growth, such as the one initially observed for black spruce, has previously been reported for other conifers and has been referred to as “thinning shock” (Harrington and Reukema 1983). The occurrence, duration, and severity of thinning shock were related to thinning intensity, site quality, and tree species, vigour, and age (Harrington and Reukema 1983). Black spruce “thinning shock” could be related to the upward shift in stemwood growth. Harrington (unpublished data) also found that temporary reduction in growth occurred when allocation of photosynthates is redirected but to sustain increases in crown diameter growth instead. Other behaviours may also be linked to thinning shock. The first hypothesis is a potential shift to greater belowground biomass allocation at the expense of stem growth. The second hypothesis suggests that a “thinning shock” could partly be related to a flux of carbohydrates from residual trees to stumps of thinned trees through root grafts, upsetting the physiological balance of residual trees (Eis 1972). Occurrence of root grafts in black spruce stands have been reported by A. Desrochers (unpublished data) to affect between 37.5 and 81.25% of trees between 40 and 88-year-old and between 8.05 and 14.88 cm in diameter.

The current research has provided interesting insight into how jack pine and black spruce respond to thinning in terms of SVI, GE, total foliage and branchwood biomass and foliage and branchwood mass density. Although response patterns to thinning agree with the general statement that jack pine is more responsive to environmental stimuli than black spruce (Hébert et al. 2006; Goudiaby et al. 2011_a), we may suspect possible effects of a between-species age difference because average jack pine age spanned 48-82 whereas black spruce displayed an average age range of 93-95. However, conflicting evidence was provided on age effect. While Skovsgaard and Vanclay (2008) showed that sensitivity to thinning usually increased with increasing age, Bebbler et al. (2004) did not find any age effect on eastern white pine (*Pinus strobus* L.) subjected to thinning. Moreover, in our experiment, despite the average age differences between jack pine and black spruce, stems remained of comparable ontogenetic maturity as jack pine reaches commercial maturity at more or less 90 years and black spruce at around 110 years.

Our experiments have been restricted to dominant trees and logic suggests that suppressed trees may respond differently, at least in terms of response intensity. The choice of dominant trees is justified by the fact that commercial thinning from below, as it is usually conducted, aims at removing suppressed trees so that only dominant trees remain in thinned plots and the only way to make a comparison with a control is to do it using dominant trees.

3.7 Conclusion

Quantification of functional relationships between aboveground tree compartments has allowed us to contrast mechanisms of jack pine and black spruce stem response to increases in resource availability in the context of commercial thinning. Jack pine displayed higher plasticity and greater stemwood increments than black spruce in response to thinning and could offer jack pine better opportunities when the silvicultural management objective is to increase tree growth. Black spruce had a slower response to thinning but was likely to keep a more consistent taper in contrast to jack pine so that, it would be ideal when the thinning objective is to produce logs with lower taper. However, differences observed between jack pine and black spruce need to be qualified because black spruce stands were growing on poorly drained soil that could have accounted to some extent for observed differences in growth performance in response to thinning. The initial negative response of black spruce to stand opening deserves to be studied more closely in relation to belowground compartments and processes. Since calibration of process-based growth models requires insight into biomass partitioning and crown shape, as well as spatial distribution of photosynthetic elements and branches within the crown, results from this study will provide substantial valuable inputs for model parameterization, at least for the processes in which the aboveground compartments are involved.

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CHAPITRE IV

EFFECTS OF THINNING ON JACK PINE (*PINUS BANKSIANA* LAMB.) AND BLACK SPRUCE (*PICEA MARLANA* (MILL.) B.S.P.) GROWTH – RESULTS OF SIMULATIONS USING CROBAS¹

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¹ Préparé pour soumission à Forest Ecology and Management

4.1 Résumé

Une préoccupation de l'industrie forestière au Québec est de pouvoir ajuster les traitements sylvicoles en fonction d'objectifs de production prédéfinis. Notre objectif était alors de répondre à cette préoccupation en proposant un modèle permettant de simuler des scénarios d'éclaircie et de voir l'effet sur la croissance. Pour cela, nous avons adapté au pin gris et à l'épinette noire, deux espèces d'intérêt commercial, un modèle du nom de CroBas. CroBas est un modèle de croissance d'arbre qui incorpore la relation entre la surface latérale et la biomasse de la cime dans un modèle de bilan de carbone, qui prend en compte le modèle tubulaire, permettant une caractérisation des tiges marchandes. Nous avons développé un module supplémentaire qui traite de l'allocation de carbone dans la tige. Quatre scénarios d'éclaircie, en fonction du pourcentage de surface terrière prélevée (G_r), ont été testés: 1) Classe 1: $G_r = 0\%$ (témoin), 2) Classe 2: $1\% \leq G_r \leq 31\%$ (moyenne = 20,65 %), 3) Classe 3: $32\% \leq G_r \leq 40\%$ (moyenne = 37,24 %), et 4) Classe 4: $41\% \leq G_r \leq 66\%$ (moyenne = 47,87 %). Le modèle a été adapté avec succès aux deux espèces, car la hauteur et le DHP des arbres s'ajustent bien à ceux de leurs homologues provenant des tables de production (Pothier et Savard, 1998) sur une période de simulation de 120 ans. Les accroissements en DHP (i_{DHP}) et en hauteur (i_{Hind}) simulées sont prédits avec plus de 80 % de précision pour un biais de seulement 0,01 à l'exception de celui de i_{DHP} du pin gris qui est de 0,03. Sur une période de simulation de 20 ans, nous avons obtenu à l'échelle de l'arbre du pin gris de la classe 1 à la classe 4 d'éclaircie, des accroissements respectifs en DHP de 17,5 cm, 19,8 cm, 20,4 cm et 21,5 cm, en hauteur de 18,9 m, 19,7 m, 20,0 m et 20,5 m et en volume de tige de 177,8 dm³, 236,9 dm³, 255,1 dm³ et 291,1 dm³. L'épinette noire a eu respectivement de la classe 1 à la classe 4 d'éclaircie, des accroissements respectifs en DHP de 15,0 cm, 16,2 cm, 16,4 cm, et 17,3 cm, en hauteur de 19,7 m, 20,1 m, 20,3 m et 20,6 m et en volume de tige de 130,0 dm³, 154,5 dm³, 181,1 dm³ et 161,3 dm³. À l'échelle du peuplement, les simulations ont montré que l'éclaircie entraîne un accroissement en surface terrière, en volume et en indice de surface foliaire chez le pin gris comme chez l'épinette noire. Indépendamment de l'espèce, l'accroissement en volume du peuplement ne permet jamais d'atteindre les volumes d'avant éclaircie.

4.2 Abstract

One concern of forest industry in Quebec is to be able to efficiently adjust silvicultural treatments for given production objectives. In this study, our objective was to provide a model that simulates thinning scenarios and gives growth outcomes. Hence, we adapted a model named CroBas to jack pine and black spruce, two species of commercial interest. CroBas is a tree growth model that incorporates the relationship between crown surface area and foliage biomass in a carbon balance model, together with the principles of functional balance and pipe-model, which allows for merchantable stem characterization. We added a module that addresses carbon allocation to stem. Four thinning scenarios, based on percent of basal area removed (G_r), are tested: 1) Class 1: $G_r = 0\%$ (control), 2) Class 2: $1\% \leq G_r \leq 31\%$ (mean = 20.65%), 3) Class 3: $32\% \leq G_r \leq 40\%$ (mean = 37.24%), and 4) Class 4: $41\% \leq G_r \leq 66\%$ (mean = 47.87%). Model calibrations were successful for both species and modelled stem height and DBH visually matched with their counterparts derived from Pothier and Savard's (1998) growth and yield tables over a simulation period of 120 years. Simulated DBH (i_{DBH}) and height (i_{Htr}) increments were predicted with efficiencies for both species generally higher than 80% and bias about 0.01 except for jack pine i_{DBH} , which was 0.03. Over a 20-year period simulation, we obtained for jack pine at the tree scale, for class 1 to class 4 of thinning, respective increases in DBH of 17.5 cm, 19.8 cm, 20.4 cm, and 21.5 cm, in height of 18.9 m, 19.7 m, 20.0 m, and 20.5 m, and in stem volume of 177.8 dm³, 236.9 dm³, 255.1 dm³, and 291.1 dm³. Black spruce showed from classes 1 to 4 of thinning, respective increases in DBH of 15.0 cm, 16.2 cm, 16.4 cm, and 17.3 cm, in height of 19.7 m, 20.1 m, 20.3 m, and 20.6 m, and in stem volume of 130.0 dm³, 154.5 dm³, 181.1 dm³, and 161.3 dm³. At the stand scale, simulations showed that thinning led to an increase in basal area, volume, and leaf area index for both jack pine and black spruce. However, irrespective of species, increase in stand volume was not enough to reach the total volumes displayed before thinning application.

4.3 Introduction

A reliable and quantitative prediction of stand response to environmental changes that follow silvicultural treatments is a crucial issue for sustainable forest management (Sheriff, 1996). While commercial thinning is widely conducted in the Canadian eastern boreal forests, response to treatment is rarely addressed beyond rough biomass or volume estimates. Such an approach does not allow decision-makers to adapt silvicultural treatments to given production objectives because it remains difficult to extrapolate results to different ranges of sites or tree conditions than those observed, while ignoring tree morphological attributes and physiological processes. Growth models can overcome these limitations and have received considerable attention (Perttunen et al., 1996, 1998; Mäkelä, 1997; Sievänen et al., 2000). However, modelling requires advanced knowledge of processes that drive tree growth and of functional relationships between tree functional parts (roots, stem, branches and foliage), as well as large amounts of data (Le Roux et al., 2001). In this study, we will use a functional-structural model, which is based on morphological and physiological aspects of tree growth (Perttunen et al., 1996, 1998; Mäkelä, 1997; Sievänen et al., 2000). Functional-structural models have proven to substantially increase our ability to predict tree response to changes in stand conditions beyond those provided by field trials.

CroBas, developed for *Pinus sylvestris* by Mäkelä (1997), is based on the computation of tree growth in units of carbon derived from net assimilation, which depends on tree photosynthesis, respiration and pattern of C allocation within tree functional parts. Interestingly, CroBas addresses tree structure in relation to stocking density, which is relevant to thinning treatments. In Canada, Raulier et al. (2003) and Raulier (2006) have successfully adapted CroBas to balsam fir (*Abies balsamea* (L.) P. Mill.) by incorporating an additional function (Raulier, 2006) aiming at characterizing merchantable stems growth.

The aim of this paper is to parameterize and calibrate CroBas for jack pine and black spruce boreal stands of Northwestern Quebec and to assess its capability to predict tree growth and C allocation in relation with changes in stand density. We also added a module provided by Raulier (2006) to characterize the merchantable portion of the tree stem. We developed an

additional module that addresses carbon allocation to stemwood. Model parameterization was conducted using information gathered during field trials (Goudiaby et al., 2011_a, 2011_b, unpublished information) as well as published information, and parameters estimated by trial and error or based on functional or allometric assumptions.

4.4 Materials and Methods

4.4.1 Study area

All our study sites were located in Abitibi-Témiscamingue, a region of Northwestern Quebec. The region is part of the Canadian Boreal forest (Rowe, 1972). The climate is continental with average daily temperature between 0.8 and 1.2 °C. Annual total average precipitation ranges from 671 to 899 mm with a maximum monthly average of 113 mm falling in July (Environment Canada, 2009). Topography is relatively flat and elevation varies from 300 to 350 m. Stands were all even-aged and originated from forest fire. Jack pine stands were growing on fluvio-glacial surface deposits. Soils were well-drained sands or loamy sands with 10-20 cm organic horizons of feathermoss origin. Black spruce stands were situated on poorly drained heavy clay deposits with 10-20 cm organic horizons.

4.4.2 Experimental design

For all plots, thinnings from below were done on 1 to 4 ha plots (experimental units) by removing trees that were small, of poor quality, and of low vigour. Two to four 200 m² permanent plots were sampled in each experimental unit before and after treatment application for basal area (G_b) estimation.

For gas exchange measurements, two separate experiments were conducted, one for jack pine and another one for black spruce according to a completely randomized block design each. Relative densities of 0.5 (moderate thinning, 50 % of trees removed) and 0.4 (intensive

thinning, 60 % of trees removed) were targeted for black spruce and 0.4 (moderate thinning, 60 % of trees removed) and 0.3 (intensive thinning, 70 % of trees removed) for jack pine using density management diagrams (Grenier et al. 2001). Measurements were conducted for jack pine in the Township of Landrienne (block 1 [48°32'45" N; 77°49'04" W]; block 2 [48°32'21" N; 77°49'21" W]) and for black spruce in the Townships of Bacon (block 1: 49°24'31" N; 78°39'42" W), and Rainboth (block 2: 49°22'16" N; 78°31'37" W).

For tree growth and crown structure, two other experiments were separately conducted for jack pine and black spruce. The experiments were completely randomized block designs with three levels of thinning intensity based on percent of basal area removed (intensive = 60%, moderate = 40%, and a no-thinning control = 0%) replicated within stands (blocks) five times for jack pine and four times for black spruce. Within each block, two to four permanent 200 m² sampling plots were identified. Effects of thinning were studied six years following treatment by harvesting two stems per experiment plot from all the experiment for a total number of 30 stems of jack pine and 24 stems of black spruce.

4.4.3 Needle photosynthesis and respiration measurements

Two years after thinning, gas exchange measurements were carried out on two trees in each experimental plot using a portable gas exchange system Li-6400 (LI-COR Biosciences, Lincoln, Nebraska) for a total number of 12 trees per species. For a complete description of experiments and measurements, see Goudiaby et al. (2011_a).

4.4.4 Biomass and crown measurements

Stands were measured for tree diameter at breast height over bark (DBH) for basal area estimation, and for tree height immediately and five years following thinning in two to four permanent 200 m² sampling plots. Stemwood volume increment was measured one to six years following thinning, and total tree foliage and branchwood weights, as well as crown

length, were assessed six years following thinning in the same large scale experiment. For a complete description of experiments and measurements see Goudiaby et al. (2011_b, submitted). All data of the experiments for a given species were divided into two batches and separately used for parameterization and validation of the model. Stands characteristics are presented in appendix 4.A, and appendix 4.B.

4.5 Model description

CroBas is a structural functional, carbon balance model of tree growth described in detail by Mäkelä (1997). Although a step-by-step parameterization procedure is presented in appendix 4.C, we are providing a brief description of the model below. CroBas is based on carbon balance, and the following three relationships: 1) a constant ratio of foliage weight (biomass) to cross-sectional sapwood area at the base of the crown as implied by the pipe model (Shinozaki et al., 1964), 2) a functional balance, which assumes a constant fine root to foliage weight ratio (Brouwer, 1962), and 3) an allometric relationship between crown surface area and foliage (fractal dimension of the crown) (Zeide and Gresham, 1991).

In CroBas, a tree is considered to be a combination of five functional parts: foliage, branches, stem, transport roots, and fine roots. Foliage is responsible for C uptake by photosynthesis, branches and stem are responsible for the tree structure, transport roots are for anchorage, and fine roots ensure water and nutrients uptake.

Weight of branches, stem, and transport roots were computed based on the pipe model using volume equations (Mäkelä, 1997):

$$W_i = \varphi_i \times \rho_i \times H_i \times A_i, \quad i = b, t \quad 4.1$$

where W is the weight, H the height, A the cross-sectional sapwood area, φ the form factor, and ρ the wood density. The subscript i refers to the functional part involved (f for foliage, b

for branch, s for stem, t for transport roots, and r for fine roots). Foliage weight (W_f) is computed using allometric relationship between crown surface area and foliage area density. Fine root weight (W_r) is determined from W_f using functional balance principle, according to the foliage to fine root ratio (α_r), which is site specific. Note that CroBas simulates site fertility by varying foliage to fine root ratio. Wood density was assumed to be, for a given species, the same for branches, stem, and transport roots.

The second step of the model specification requires computing C balance (Fig. 4.1). To account for shading effect in the stand, CroBas assumes a maximum rate of stand photosynthesis per unit of ground area (P_0), and this maximum is asymptotically approached according to an exponential function as the leaf area index of the stand increases. Therefore, photosynthesis was computed from maximum photosynthesis and leaf area of the stand. Tree respiration is the sum of maintenance and growth respiration. Maintenance respiration for each tree functional part depends on climate and biomass. Growth respiration, as indicated by its name, is proportional to growth. Difference between photosynthesis and respiration at the stand scale is the stand net productivity, which is then converted to tree net productivity.

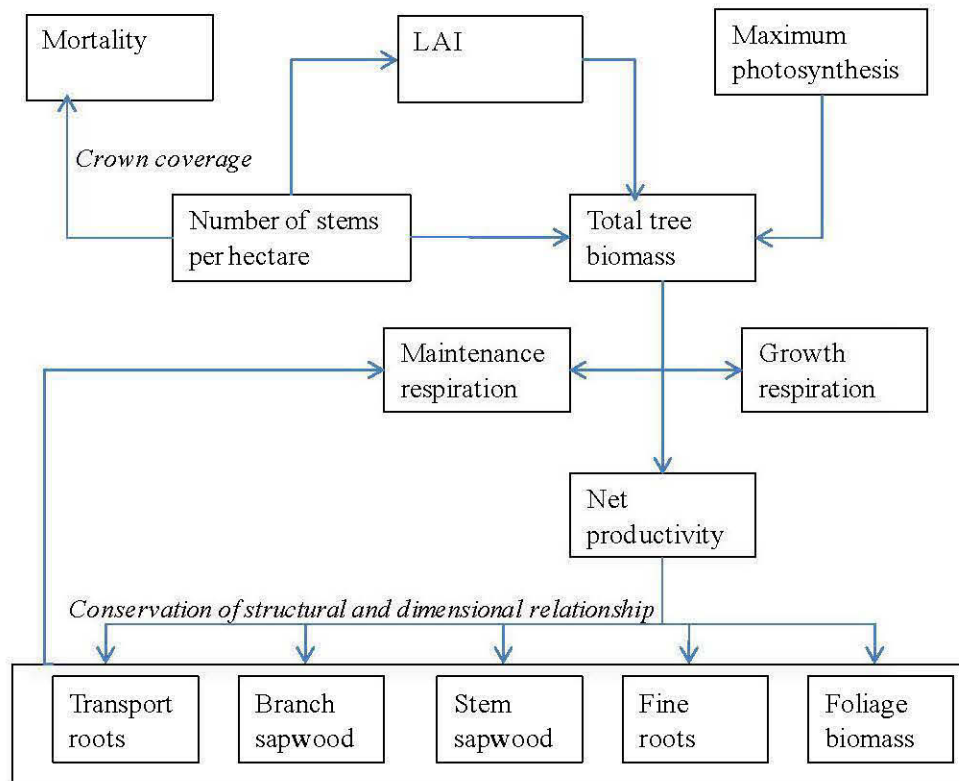


Figure 4.1 Relationship between stand and tree variables at the base of the computation of CroBas carbon balance at tree scale (adapted from Raulier, 2006).

We used a diameter distribution module developed by Raulier (2006) to estimate technical growth (changes in mean diameter and crown length due to thinning) and changes in the merchantable dimension of trees (Appendix 4.C). Carbon allocation to stemwood was expressed as a ratio of carbon (corresponding to stemwood increment) to net carbon uptake at the tree scale (photosynthesis - respiration) within one-year period. Stemwood dry weight was obtained by the product between annual stemwood growth increment and wood density. Stemwood dry weight was then converted into carbon using a conversion factor. Since the model has a yearly time step, all model inputs have been calculated on an annual basis. For initialization, CroBas requires as input parameters: tree height, crown length, number of stems per hectare, and site index.

4.6 Parameterization of the model

Parameterization of the model required 56 parameters for each species. For a given species, 24 parameters were measured in the current experiment or obtained from Goudiaby et al. (unpublished information). The other 22 parameters came from the literature and most of them were adjusted to the site conditions of our experiments. Six parameters were estimated by trial and error and 4 were determined using assumptions based on tree allometry or functions. Although they do not appear in the source code of the model, some parameters were derived from others that have been measured in the field or estimated. All parameters related to increments in DBH, stem height, stem volume, and cross-sectional stem area at breast height used for the validation were measured or came from Goudiaby et al. (unpublished information).

Parameters used for both jack pine and black spruce are provided in the Table 4.1 along with their source. Parameterization used data from control experimental plots that were most likely to represent normal stand conditions. Although comprehensive step-by-step model parameterization is provided in appendix 4.C, we are presenting in the following a brief description of the parameterization. The four following steps were required to parameterize the model: 1) determination of crown foliage weight and leaf area, 2) determination of weight of functional parts of tree, 3) estimation of carbon balance, and 4) merchantable stem characterization.

4.6.1 Crown foliage weight and leaf area

Jack pine and black spruce branch sapwood areas were estimated using Kyker-Snowman and Wilson (1988) allometric equations and values of total branch cross-sectional areas from Goudiaby et al. (unpublished information). Jack pine and black spruce stem sapwood areas were estimated using Bond-Lamberty et al. (2002) allometric equations.

4.6.2 Weight of tree functional parts

We have assumed that all form factors values used for jack pine and black spruce are similar to those defined by Mäkelä (1997). Densities of wood for branches, stem, and transport roots were taken from Park et al. (2009) for jack pine, and from M. Ourais and A. Koubaa (unpublished data) for black spruce. Foliage weight (W_f) for both jack pine and black spruce was taken from Goudiaby et al. (unpublished information). Fine root weight (W_r) was estimated using α_r (Steel et al., 1997) knowing W_f as suggested by functional balance.

4.6.3 Carbon balance

Tree photosynthesis (P) was estimated as in Mäkelä (1997) from maximum rate of canopy photosynthesis (P_0) per unit of ground area and leaf area index (L). Landsberg and Waring (1997) have shown that P_0 depends on quantum efficiency (ε) and yearly photosynthetically active radiation per unit of ground square metre (ϕ_p). Quantum efficiency was set to $0.0018 \text{ kg C MJ}^{-1}$ and to $0.0012 \text{ kg C MJ}^{-1}$ for jack pine and black spruce, respectively (Dang et al., 1998; Goudiaby et al., unpublished information). Yearly photosynthetically active radiation was estimated from yearly global solar radiation using Yin's (1996) model. Fraction of photosynthetically active radiation absorbed by trees was then estimated by multiplying yearly global solar radiation by 0.5 (Jacovides et al., 2003). Specific maintenance respiration rate of foliage, wood and fine roots came from Ryan et al. (1997). Specific senescence rate of foliage was based on maximum needle retention of 3 years for jack pine (personal observation; Sargent, 1897, cited by Schoettle and Fahey, 1994), and 13 years for black spruce (Hom and Oechel, 1983). Specific senescence rate of fine roots was provided by Steele et al. (1997). Specific sapwood area turnover rate per unit of relative pruning was assumed to equal 1 as in Mäkelä (1997). The coefficients β_1 , β_2 , and β_3 used to estimate crown length were determined by trial and error. To estimate carbon allocation to stem, dry weight of stemwood increment was converted to carbon using conversion factor of 0.5 for both jack pine and black spruce. For mortality, data of maximum stand density (N_{\max}), maximum crown coverage (C_{\max}), and ratio of crown radius to crown length (c_b), for both jack pine and black spruce, were taken from Goudiaby et al. (unpublished information).

Table 4.1 List of jack pine and black spruce parameters and their source

Symbol*	Meaning	Jack pine	Black spruce	Unit	Reference
φ_s	Form factor of stemwood in stem below crown	1.0	1.0	-	Theoretical value based on the pipe model assumption
φ_c	Form factor of stemwood in stem within crown	0.75	0.75	-	Based on the conical form
φ'_b	Form factor of stemwood in branches	0.75	0.75	-	Estimate
φ'_t	Form factor of stemwood in transport root	0.46	0.46	-	Nikolova et al. (2009)
c_b	Ratio of crown radius to crown length	0.14	0.20	-	Goudiaby et al. (2011 _b , submitted unpublished information)
c_t	Ratio of transport root length to stem length	1	1	-	Mäkelä (1997)
ρ_s, ρ_b, ρ_t	Density of wood	469	470	kg m ⁻³	Jack pine (Park et al., 2009) Black spruce (Ourais and Koubaa, unpublished data)
α_s	Sapwood area: foliage weight ratio in stem	$2.7 \cdot 10^{-3}$	$1.6 \cdot 10^{-3}$	m ² kg ⁻¹	Goudiaby et al. (unpublished information), stem sapwood area computed after Bond-Lamberty et al. (2002)
α_b	Sapwood area: foliage weight ratio in branches	$3.77 \cdot 10^{-3}$	$3.82 \cdot 10^{-3}$	m ² kg ⁻¹	Goudiaby et al. (unpublished information); branch sapwood area estimated from Kyker-Snowman and Wilson (1988)
α_t	Sapwood area: foliage weight ratio in transport roots	$3.49 \cdot 10^{-3}$	$2.54 \cdot 10^{-3}$	m ² kg ⁻¹	This research, root sapwood area computed after Bond-Lamberty et al. (2002) model
α_f	Fine root: foliage weight ratio	0.15	0.15	-	This research; fine root data from Steel et al. (1997)
β_1	Parameter 1 for crown length estimation	0.4208	0.5656	-	Trial and error
β_2	Parameter 2 for crown height estimation	-0.0503	0.0551	-	Trial and error
β_3	Parameter 3 for crown height estimation	0.1251	0.0862	-	Trial and error
2z	“Fractal dimension” of foliage in crown	2.7	2.4	-	Goudiaby et al. (unpublished information)

Table 4.1 Continued. List of jack pine and black spruce parameters and their source

ξ	“Surface area density” of foliage	0.01	0.02	kg m ^{-2.7} (jack pine) kg m ^{-2.4} (black spruce)	Goudiaby et al. (submitted unpublished information) using Eq. 5c from Mäkelä (1997)
Y	Carbon use efficiency	0.46	0.37	kg C kg ⁻¹ DW	Lavigne and Ryan, 1997
r ₁	Specific maintenance respiration rate of foliage + fine roots	0.18	0.09	kg C kg ⁻¹ DW yr ⁻¹	Ryan et al. (1997)
r ₂	Specific maintenance respiration rate of wood	0.03	0.07	kg C kg ⁻¹ DW yr ⁻¹	Lavigne and Ryan (1997)
s _f	Specific senescence rate of foliage	0.33	0.08	yr ⁻¹	Based on needle lifetime of 3 years for jack pine (personal observation; Sargent, 1897, cited by Schoettle and Fahey, 1994), and 13 years for black spruce (Hom and Oechel, 1983)
s _r	Specific senescence rate of fine roots	1.4	3.3	yr ⁻¹	Steele et al. (1997)
d _{s0} , d _{b0} , d ₀	Specific sapwood area turnover rate per unit relative pruning	1	1	-	Mäkelä (1997)
d _{s1} , d _{b1} , d ₁	Specific sapwood area turnover rate in case of pruning	0.001	0.05	yr ⁻¹	Mäkelä (1997)
ψ_s	Form factor of senescent sapwood in stem below crown	1.0	1.0	-	Theoretical value according to pipe model
ψ_c	Form factor of senescent sapwood in stem inside crown	0.5	0.5	-	Mäkelä (1997)
ψ_b	Form factor of senescent sapwood in branches	0.9	0.9	-	Mäkelä (1997)
ψ_t	Form factor of senescent sapwood in transport roots	0.46	0.46	-	Nikolova et al. (2009)
a _n	Specific leaf area	3.5	4.4	m ² kg ⁻¹	Goudiaby et al., (unpublished information)
P ₀	Maximum rate of canopy photosynthesis per unit area	2.20	1.46	kg C m ⁻² yr ⁻¹	This research, with Goudiaby et al. (unpublished information)

Table 4.1 Continued. List of jack pine and black spruce parameters and their source

a_g	Decrease of photosynthesis per unit crown length	0.11	0.11	m^{-1}	Brooks et al. (1997)
K	Extinction coefficient	0.57	0.52	-	Aubin et al. (2000)
a_q	Parameter related to self-pruning	0.5	0.5	-	Trial and error
ε	Quantum efficiency	0.02	0.03	-	Dang et al. (1998); Goudiaby et al., unpublished
C_{max}	Crown coverage	1.52	1.91	-	Goudiaby et al., unpublished information
f_e	Bark factor	0.225	0.737	-	This paper
$\varphi_{s,tot}$	Parameter for stem volume and basal area \times stem height	0.0578	0.3145	-	This paper
δ	Parameter for quadratic and arithmetic DBH relationship	0.989	0.985	-	This paper
σ_1	Parameter for DBH variance and DBH relationship	0.3827	0.1103	-	This paper
σ_2	Parameter for DBH variance and DBH relationship	0.1661	0.2717	-	This paper
ε_1	Parameter 1 related to quantum efficiency	0.0302	0.0320	-	Trial and error
ε_2	Parameter 2 related to quantum efficiency	0.0023	0.0030	-	Trial and error
ε_3	Parameter 3 related to quantum efficiency	0.0002	0.0005	-	Trial and error

Note: * model parameters have the same symbols as Mäkelä (1997); -: unitless.

4.6.4 Merchantable stems characterization

Merchantable stems characterization (Raulier, 2006) requires data such as quadratic diameter ($\bar{d}_{1.3}$) at breast height, arithmetic diameter ($d_{1.3}$), and amount of parameters (coefficients). All these parameters along with data related to stem mortality, L, and SI came from Goudiaby et al. (unpublished information).

4.7 Calibration of the model

Fine tuning of input parameters was done in order to improve relationships between predicted and observed data using the same observations as those used for parameterization. A visual assessment of the fit between predicted and observed values was conducted and final values given in Table 4.1. For both jack pine and black spruce, foliage weight was increased by increasing fractal dimension (z) or foliage area density (ξ) so that modelled and measured foliage weights coincided. Greater z or ξ increases DBH while, at the same time, decreases stem height and crown length. Lowering z or ξ decreases DBH while, at the same time, increases stem height and crown length. Based on that knowledge, adjustments of z and ξ were always done to obtain acceptable values of foliage weight that allowed for keeping DBH, stem height and crown length in realistic ranges. However, when we increased z and ξ to have foliage weight close to our measured values, stem height and crown length generally decreased below the normal values. This problem was solved by increasing quantum efficiency (ε) and decreasing sapwood area to foliage weight ratio in the stem (α_s). Greater values of quantum efficiency increase DBH as well, so that when varying this parameter we kept a close check on DBH, stem height and crown length to ensure that we remained within normal ranges. When DBH remained high, a slight increase in fine root to foliage weight ratio (α_r) decreased the DBH to fit expected values; this was done in accordance with site quality. Also, there was a negative relationship between sapwood area to foliage weight ratio in stem (α_s) and stem height, and a positive relationship between α_s and DBH. Then, we adjusted α_s when we wanted to simultaneously increase DBH and decrease stem height to normal values, and vice versa.

4.8 Validation of the model

Validation of the model aims at comparing jack pine and black spruce predicted stem height and diameter growth over a period of 120 years with values derived from growth and yield tables (Pothier and Savard, 1998). For either jack pine or black spruce, we used growth and yield tables with SI = 18, for highest merchantable stand density with respective values of

1 191 trees ha⁻¹ and 1 225 trees ha⁻¹ 20-year-old stands. Since the model requires, as input, the total number of stems (merchantable or not), densities were adjusted to 6 000 trees ha⁻¹ for both jack pine and black spruce. Since data related to growth and yield (Pothier and Savard, 1998) were derived from a statistical model, we did not make any formal comparison between simulated and “measured” data but the model comparison was based on a visual assessment of the model by plotting the “measured” and the simulated data in the same graphic to ensure that they have the same range and shape.

Increments in tree height, DBH, cross-sectional stem area at breast height, and tree volume six years following thinning obtained from experimental data were compared with their modelled counterparts. Validation was based on dispersion diagrams of observed versus predicted values. Average model bias (AMB) and model efficiency (EF) were subsequently applied to model outcomes to describe model performance (Pinjuv et al., 2006):

$$AMB = \frac{1}{n} \sum y_i - \hat{y}_i \quad 4.2$$

$$EF = 1 - \frac{\sum (y_i - \hat{y}_i)^2}{\sum (y_i - y_{m_i})^2} \quad 4.3$$

where n is the number of samples, y_i the measured variable, \hat{y}_i the estimated variable and y_{m_i} is the average value of measured variables.

For AMB, a null value indicates no bias in the model whereas EF ranges between 0 (model with poor fit) and 1 (model with excellent fit).

4.9 Model application for commercial thinning over a period of 20 years

Model application to thinning was done through testing thinning scenarios studied by Goudiaby et al. (unpublished information). Four thinning scenarios, based on percent of basal

area removed (G_r), were tested: 1) Class 1: $G_r = 0\%$ (control), 2) Class 2: $1\% \leq G_r \leq 31\%$ (mean = 20.65%), 3) Class 3: $32\% \leq G_r \leq 40\%$ (mean = 37.24%), and 4) Class 4: $41\% \leq G_r \leq 66\%$ (mean = 47.87%). We assessed model goodness of fit by comparing model outcomes of a given thinning scenario with their measured counterparts (Goudiaby et al., unpublished information). Values of the parameters at the beginning (step zero) of the simulation, before any intervention, are given in Table 4.2. Simulations were conducted for 1 to 20 years after thinning.

Table 4.2 Model application for commercial thinning. Values of diameter at 1.3 m, total tree height, crown length and site index used for model initialization i.e. before thinning, and values recomputed by the model immediately after thinning as a function of relative basal area removed

Treatment	G_r	DBH	H_{tr}	H_c	N	SI
Jack pine						
Class 1	0%	16.5	16.5	5.9	3000	16.5
Class 2	$1\% \leq G_r \leq 31\%$ (mean = 20.65%),	18.5	17.0	6.3	1440	16.5
Class 3	$32\% \leq G_r \leq 40\%$ (mean = 37.24%),	19.0	17.2	6.3	1110	16.5
Class 4	$41\% \leq G_r \leq 66\%$ (mean = 47.87%).	19.8	17.3	6.3	630	16.5
Black spruce						
Class 1	0%	13.6	18.0	6.6	3000	16.5
Class 2	$1\% \leq G_r \leq 31\%$ (mean = 20.65%),	15.4	18.5	6.8	1440	16.5
Class 3	$32\% \leq G_r \leq 40\%$ (mean = 37.24%),	15.8	18.6	6.8	110	16.5
Class 4	$41\% \leq G_r \leq 66\%$ (mean = 47.87%).	16.6	18.7	6.9	630	16.5

Note: G_r : basal area removed; H_{tr} : total tree height, H_c : crown length, N: number of stems per hectare, SI: site index.

4.10 Results

4.10.1 Modelled height and DBH compared with volume table outcomes

For both jack pine and black spruce, curves of predicted tree height and diameter at breast height and those provided by growth and yield tables (Pothier and Savard, 1998) displayed a

similar trend (Fig. 4.2). For jack pine, predicted diameters were lower than those from Pothier and Savard's (1998) growth and yield table for ages between 20 and 30 and higher for age above 90 years, whereas black spruce predicted diameters were slightly lower than those of the growth and yield table (Pothier and Savard, 1998) for ages between 20 and 30. For jack pine, the curve of predicted height displayed a trend that matches well with that of Pothier and Savard (1998). For black spruce, predicted height was a little bit higher, between ages 20 and 50, than its counterpart from Pothier and Savard's (1998) growth and yield table.

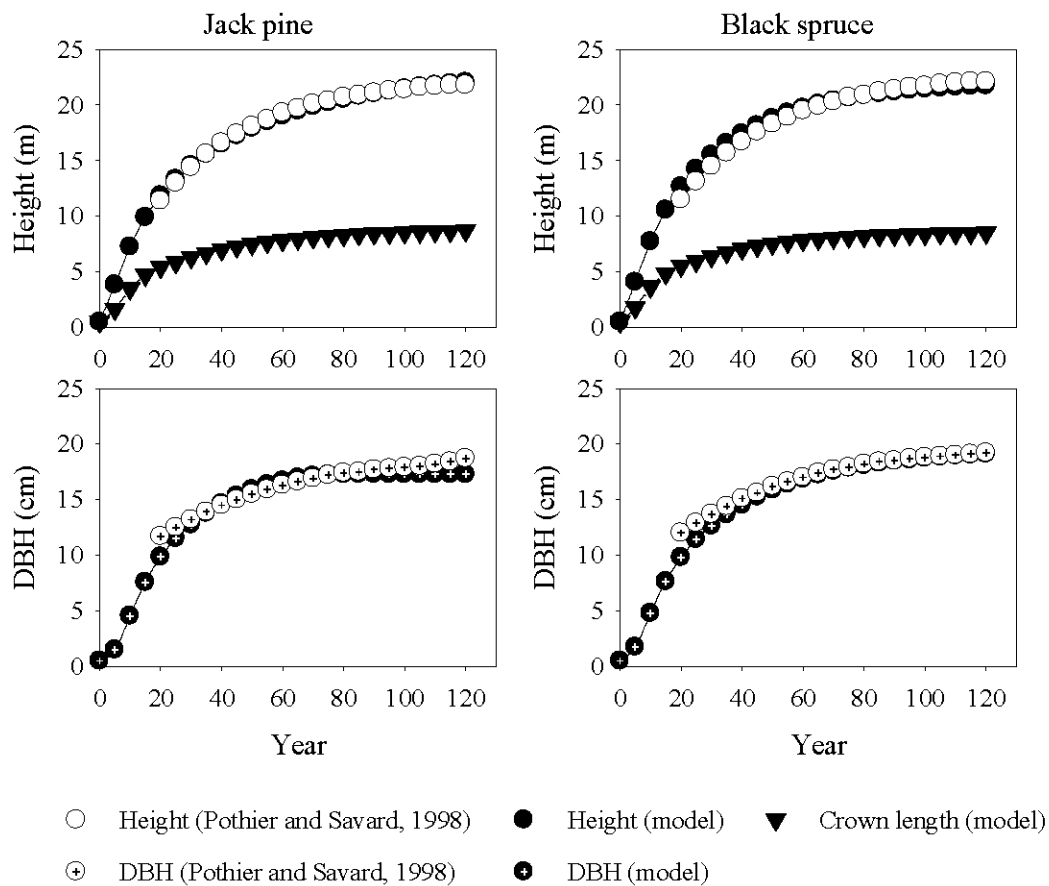


Figure 4.2 Modelled tree height and diameter at breast height for jack pine and black spruce for DBH > 9 cm in relation with their counterparts (except for crown length) derived from growth and yield tables for SI = 18 provided by Pothier and Savard (1998).

Overall tree height and DBH for either jack pine or black spruce displayed asymptotic trends over the 120-year period simulation. Increase tree height over time was very fast at the beginning, as shown by the steep curves, for jack pine (between 0 and 40 years) and for black spruce (between 0 and 50 years) before reaching their slowest growth (not quite a plateau) at age 80 and 50 years for jack pine and black spruce, respectively. Also, tree DBH showed a steep curve at 0-20 year followed by a plateau starting at 60 years for both jack pine and black spruce. For crown length, we had only one experimental value at six years after thinning, and values of jack pine and black spruce provided by the simulation (7.9 m, and 8.4 m, respectively) were within the experimental data range (5.3 m-7.9 m, and 5.4 m-12.0 m for jack pine and black spruce, respectively).

4.10.2 Simulation of the thinning experiments

For both jack pine and black spruce, model outcomes were compared with only one experimental value obtained 6 years after thinning. The simulated diameter, tree height, and volume increments were close to the measured values (Fig. 4.3). For each of these variables, simulations showed, for both jack pine and black spruce, a low bias, a high efficiency, and a high R^2 (Table 4.3).

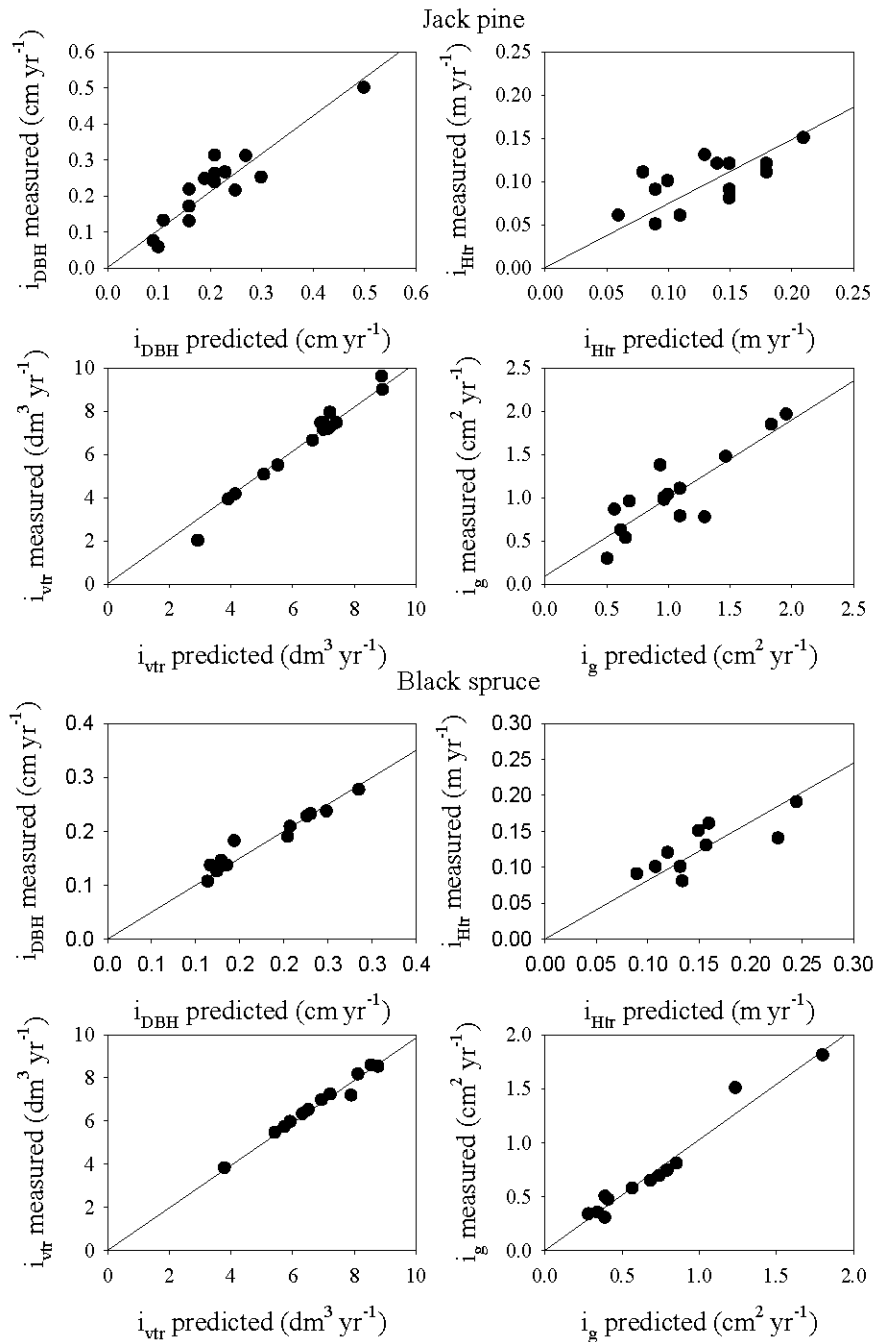


Figure 4.3 Relationship between empirical and modelled variables at the tree scale for increments in diameter at breast height (i_{DBH}), height (i_{Htr}), volume (i_{vtr}), and total cross-sectional stem area at breast height (i_g) for jack pine and black spruce 6 years after thinning.

Table 4.3 Jack pine and black spruce average model bias, model efficiency, and R^2 for annual increments in diameter at breast height, tree height, cross-sectional stem area at breast height, and stem volume

Variables	AMB	EF	R^2
Jack pine			
i_{DBH}	0.03	0.87	0.87
i_{Htr}	0.01	0.89	0.68
i_g	0.02	0.86	0.86
i_{vtr}	0.01	0.85	0.71
Black spruce			
i_{DBH}	0.01	0.82	0.74
i_{Htr}	0.01	0.80	0.70
i_g	0.01	0.81	0.73
i_{vtr}	0.01	0.80	0.72

Note: AMB: average model bias; EF: model efficiency; i_{DBH} : diameter at breast height increment; i_{Htr} : tree height increment; i_g : cross-sectional stem area at breast height, and i_{vtr} : stem volume increment.

At the tree scale and when thinning was simulated, growth due to removing small trees referred to as technical growth occurred and stem height increased by 17.0%, and 17.8%, DBH by 4.9%, and 4.0%, crown length by 6.6%, and 5.4%, and stem volume by 35.4%, and 35.1%, for jack pine and black spruce, respectively (Fig. 4.4; Table 4.2). When thinning scenarios were conducted (class 1 to class 4 scenario) (Fig. 4.4), stem height respectively increased with thinning intensity by 14.4%, 15.7%, 16.4%, and 17.9% after a 20-year period simulation for jack pine, while for black spruce it respectively increased by 9.2%, 8.6%, 9.2%, and 10.1% for a similar period. For DBH, there were for jack pine respective increases of 6.4%, 7.1%, 7.7%, and 8.7%, while for black spruce there were respective increases of 4.1%, 3.8%, 4.8%, and 6.9%. Because stem volume was computed from stem height and DBH, it generally showed the same trend as DBH and height within each species. For both species, thinning increased productivity per tree.

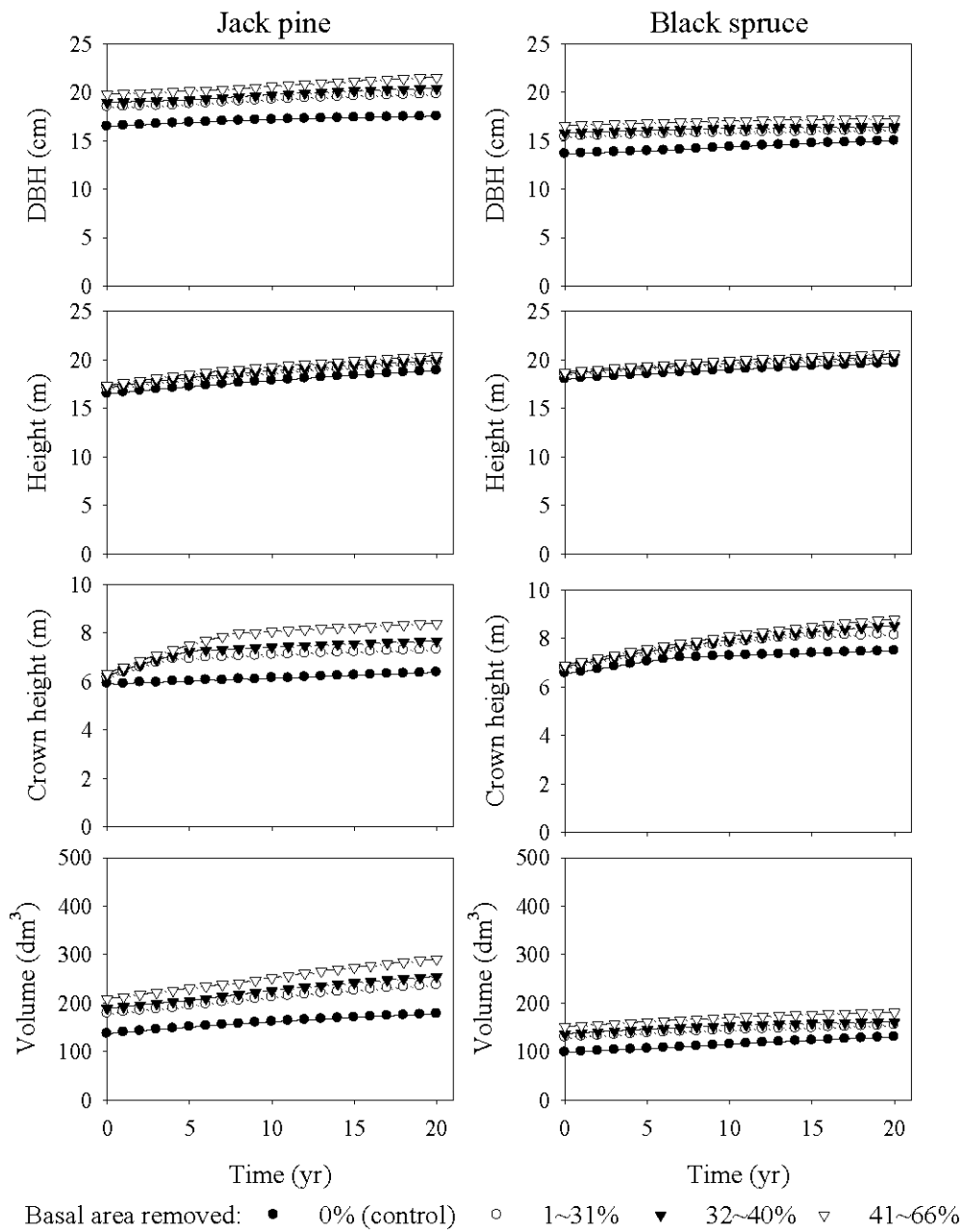


Figure 4.4 Effect of thinning intensity at the tree scale of diameter at breast height (DBH), total height, crown length, and volume for jack pine and black spruce 20 years following thinning.

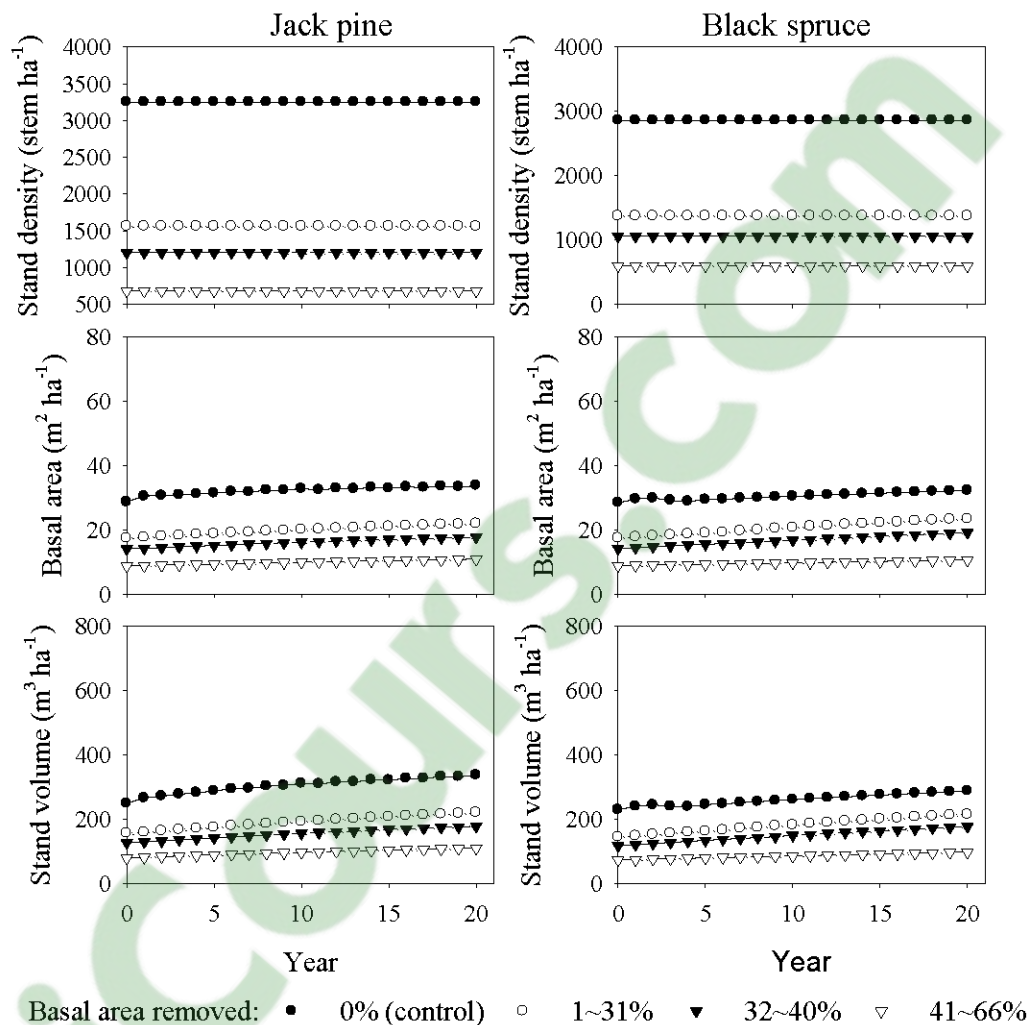


Figure 4.5 Effect of thinning intensity at the stand scale of stem density, volume, and basal area for jack pine and black spruce 20 years following thinning.

At the stand level (Fig. 4.5), the immediate effect of thinning simulation was a general decrease in stand merchantable volume, basal area, and leaf area index. However, when thinning scenarios from class 1 to class 4 were conducted, we noted, 20 years after thinning and relatively to residual basal area, an increase in stand volume respectively of 35%, 37%, 38%, and 38% for jack pine and of 18%, 24%, 25%, and 25% for black spruce. Also, from class 1 to class 4 of thinning, basal area respectively increased by 25%, 31%, 32%, and 32%

for jack pine and by 13%, 20%, 20%, and 20% for black spruce. However, we did not have, for both species, any effect of thinning on stem mortality and total productivity of the stand.

4.10.3 Carbon allocation to stemwood in response to thinning

In the absence of thinning, carbon allocation to stemwood for jack pine and black spruce were 0.37 and 0.25 kg C yr⁻¹ tree⁻¹, respectively (Fig. 4.6). For jack pine, greater thinning intensity led to a concurrent decrease in C allocation to stemwood, reaching 0.27 kg C yr⁻¹ tree⁻¹ for the highest thinning intensity (class 4: 41 < G_r < 66%). For black spruce, thinning did not have any effect on C allocation to stemwood since values displayed for highest thinning intensities (class 3: 32% ≤ G_r ≤ 40%, and class 4: 41 < G_r < 66%), were similar to those of the no-thinning scenario (0.25 kg C yr⁻¹ tree⁻¹). However, we noted a slight decrease (0.24 kg C yr⁻¹ tree⁻¹) for the lowest thinning intensity (class 2: 1% ≤ G_r ≤ 31%).

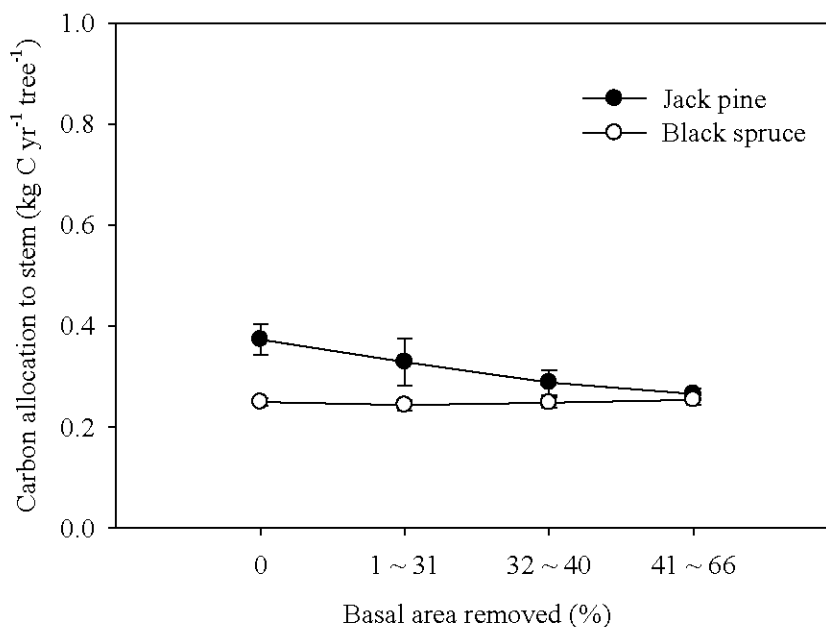


Figure 4.6 Modelled carbon allocation to stem for jack pine and black spruce six years after thinning application.

4.11 Discussion

Adaptations of CroBas model (Mäkelä, 1997) to jack pine and black spruce were successful and simulation outputs seemed realistic. At the tree scale, any intensity of thinning simulation was generally followed, for both jack pine and for black spruce, by an increase in DBH, stem volume and crown length, while tree height seemed to be only very slightly affected. In addition, whatever the thinning intensity, we generally noted an increase in productivity per tree, whereas total productivity of the stand remained unaffected. The fact that jack pine increased its stem growth while decreasing its C allocated to stemwood following thinning is the evidence of total enhanced productivity that offsets the lower priority of C allocated to stem relatively to other tree functional parts. For black spruce, increasing its growth while maintaining its C allocation to stem would likely be suggested by a constant allometry coupled with increase in tree total productivity after thinning. Basically in CroBas, C allocation to stem is driven by crown rise in the sense that self-pruning is stopped or at least slowed by thinning so that crown length increases leading to an increase in stem growth. In a previous paper (Goudiaby et al., 2011_b), the increase in stem volume growth occurring following thinning has been attributed to higher growth efficiency (stemwood growth to foliage weight ratio) and foliage biomass at mid-crown for jack pine, whereas black spruce stemwood growth was hypothesized to be related to an increase in total tree productivity while maintaining a constant allometry. Results provided by the model agree with these findings and/or assumptions. Also, the generally higher DBH, stem volume, and crown length in response to thinning, for jack pine respectively to black spruce, confirms jack pine's higher plasticity in comparison to black spruce.

For either jack pine or black spruce, no thinning effect was noted on total productivity at the stand scale after 20-year simulation. This is due to the fact that we are at northern marginal sites with a late commercial thinning, so that recovery will be more difficult and time consuming than more southern sites location. Such behaviour agrees with what has been reported many times for thinned stands (Pelletier and Pitt, 2008; Mäkinen and Isomäki, 2004). From economic point of view, this is not really a problem since decrease in total stand volume after thinning will be compensated by a higher proportion of valuable sawn timber

owing generally to their significant increase in stem diameter and volume after thinning (Goudiaby et al., unpublished information). In addition, mortality did not generally change much whatever the thinning intensity. In the model, mortality is based on maximum crown coverage and ignores for example senescence and wind-throw, which is likely to occur as thinning intensity increases, and then it is not surprising for stands to not record any mortality when the density is reduced below the maximum stocking. This limitation would to some extent bias merchantable stand volume and basal area estimation mostly for intensive thinning scenario in which wind-throw is likely to occur. In addition, for modelled total stand volume and basal area (merchantable or not), CroBas did not incorporate regeneration. The limitation related to the lack of regeneration would to some extent be buffered by the abnormal lower mortality that is likely to give acceptable ranges at the stand scale for long-term simulations. This is confirmed by the fairly good estimate of stand volume and basal area obtained by Mäkelä (1997) on *Pinus sylvestris* L. and by Raulier (2006) on *Abies balsamea* (L.) Mill.

Jack pine and black spruce calibrations were conducted using data from a network of sites spread all over the Abitibi region of north western Quebec. This region has a variety of site conditions in terms of north-south gradients, and the potential difference in climate conditions, and also in stand age and soil fertility. Although interesting in the perspective of better model inference to a set of different sites, the 20-year simulation conducted would minimize to some extent any effect inherent to these changing parameters.

4.12 Conclusion

The carbon balance model (CroBas) was successfully calibrated for jack pine and black spruce and empirical evidence suggests that the simulation is realistic with low bias and high efficiency. Such a model provides insights into expected tree growth in stands following thinning. Model simulation outcomes confirm the already known better growth potential in response to thinning for jack pine in comparison to black spruce due to their differences in plasticity. Parameters of the model like fine root biomass related to foliage and senescence,

as well as quantum efficiency are sensitive to stand characteristic and fertility. However, in the model, only quantum efficiency was implemented to be a function depending on leaf area and site index. Therefore, our model is to some extent hampered due to the lack of any empirical information mainly about underground functional parts of the trees. Perspectives for model improvement may require addressing more closely this limitation by effective measurements of root dynamics.

Acknowledgements

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Appendix 4.A. Characteristics of jack pine sampling plots used for model parameterization and validation

Site	N_i (tree ha ⁻¹)	N_a (tree ha ⁻¹)	G_i (m ² ha ⁻¹)	G_a (m ² ha ⁻¹)	V_i (m ³ ha ⁻¹)	V_a (m ³ ha ⁻¹)	DBH (cm)	DBH _{dom} (cm)	H _{tr} (m)	H _{dom} (m)	Age	SI ₅₀	L	i_G (m ² ha ⁻¹ yr ⁻¹)	i_{V_a} (m ³ ha ⁻¹ yr ⁻¹)
Castagnier-Nord	2400	2400	31.0	31.0	314.7	314.7	12.2	16.1	13.6	15.8	47	16.8	4.7	0.8	10.4
Castagnier-Nord	2325	1400	34.1	22.2	350.7	332.7	13.3	18.5	n.a.	16.7	48	17.3	4.1	0.7	9.1
Castagnier-Nord	2350	1650	30.0	17.1	285.8	243.9	10.7	19.8	n.a.	16.8	48	17.4	3.6	1.1	11.1
Clérycy	2975	2975	37.6	37.6	386.7	386.7	n.a.	18.9	16.1	17.4	70	15.9	6.5	0.6	6.8
Clérycy	2675	1175	30.9	11.5	288.4	199.0	n.a.	23.0	n.a.	19.5	69	17.9	4.7	1.1	11.8
Clérycy	2475	900	27.5	10.2	360.6	162.7	n.a.	20.4	n.a.	18.2	69	17.0	2.3	0.8	7.2
Dollard	3300	3300	33.8	33.8	278.6	278.6	n.a.	19.0	13.7	17.0	53	17.2	11.1	1.5	21.0
Dollard	3000	1525	27.6	15.0	259.9	228.5	n.a.	n.a.	n.a.	15.7	54	16.0	3.4	0.8	7.9
Dollard	3100	1600	32.6	18.1	283.6	280.3	n.a.	17.8	n.a.	16.9	52	17.3	4.5	0.8	10.1
Duprat-Est	4125	4125	45.3	45.3	372.4	372.4	9.4	16.0	14.0	15.9	53	16.0	7.9	1.2	11.9
Duprat-Est	3850	1525	38.6	18.3	347.8	267.2	9.7	19.5	n.a.	16.3	53	16.3	4.3	1.2	11.4
Duprat-Est	4075	1550	35.0	15.3	308.3	246.0	10.0	18.7	n.a.	16.3	53	16.3	3.7	1.9	18.1
Figury	2400	2400	31.0	31.0	314.7	314.7	n.a.	23.1	17.4	19.4	81	17.1	11.3	1.1	16.2
Figury	3375	1200	34.1	22.2	350.7	332.7	n.a.	21.6	n.a.	18.1	82	15.8	3.8	0.8	9.4
Figury	2550	1125	30.0	17.1	285.8	243.9	n.a.	23.5	n.a.	20.1	81	17.6	4.0	0.9	9.7

Note: L = Leaf area index; n.a. = not available

N_i = Initial stand density (before thinning) (tree ha⁻¹)

N_a = Stand density after thinning (tree ha⁻¹)

G_i = Initial basal area - before thinning (m² ha⁻¹)

G_a = Stand basal area after thinning - Residual (m² ha⁻¹)

V_i = Total stand volume before thinning (dm³ tree⁻¹)

V_a = Total stand volume after thinning (m³ ha⁻¹)

DBH = Diameter at breast height over bark – 1.30 m of stem height (cm)

DBH_{dom} = Dominant diameter at breast height over bark – 1.30 m of stem height (cm)

SI₅₀ = Site index (height (m) at age 50)

i_G = Annual stand basal area increment (m² ha⁻¹)

i_{V_a} = Annual stand volume increment (dm³ ha⁻¹ yr⁻¹).

Appendix 4.B. Characteristics of black spruce sampling plots used for model parameterization and validation

Site	N_i (tree ha ⁻¹)	N_a (tree ha ⁻¹)	G_i (m ² ha ⁻¹)	G_a (m ² ha ⁻¹)	V_i (m ³ ha ⁻¹)	V_a (m ³ ha ⁻¹)	DBH	DBH _{dom}	H _{tr} (m)	H _{dom} (m)	Age	SI ₅₀	L	i_G (m ² ha ⁻¹ yr ⁻¹)	i_{V_a} (m ³ ha ⁻¹ yr ⁻¹)
Castagnier-Sud	1800	1800	45.6	45.6	275.3	275.3	15.1	17.9	16.4	20.1	95	17.1	2.8	0.5	7.4
Castagnier-Sud	2750	1300	50.0	24.8	362.2	194.7	16.5	18.5	24.0	19.2	94	16.4	2.0	0.6	6.1
Castagnier-Sud	2200	775	38.5	13.9	379.4	298.0	15.5	20.4	17.6	20.5	95	17.5	1.6	0.6	6.9
Miniac-Sud	2800	2800	49.6	49.6	395.2	395.2	12.3	13.3	15.5	17.6	90	15.1	4.6	0.8	4.9
Miniac-Sud	3125	1325	50.5	25.3	384.4	210.8	12.7	17.9	22.6	18.3	94	15.6	4.3	0.6	7.9
Miniac-Sud	2350	1075	50.3	23.9	355.8	279.4	15.4	17.0	24.5	19.9	93	16.9	2.7	0.5	7.2
Quévillon	2150	2150	44.3	44.3	288.6	288.6	13.8	14.7	16.0	18.5	93	16.0	6.7	1.1	16.0
Quévillon	2375	1300	43.5	24.2	321.6	185.6	14.7	16.9	15.6	20.2	94	17.1	2.7	0.5	6.8
Quévillon	2425	725	39.4	13.1	344.2	270.3	14.4	16.8	16.4	18.7	91	16.1	2.8	0.4	5.3
Vassal	2450	2450	53.2	53.2	322.3	322.3	n.a.	18.4	n.a.	19.8	94	16.9	6.6	0.9	11.0
Vassal	3425	1425	43.8	19.8	316.8	150.2	n.a.	13.7	n.a.	16.8	91	14.6	3.7	0.7	9.8
Vassal	3650	1025	44.9	20.9	421.2	330.8	n.a.	14.2	n.a.	17.2	93	14.8	2.4	0.7	6.8

Note: L = Leaf area index; n.a. = not available

N_a = Stand density after thinning (tree ha⁻¹)

N_i = Initial stand density (before thinning) (tree ha⁻¹)

G_i = Initial basal area - before thinning (m² ha⁻¹)

G_a = Stand basal area after thinning - Residual (m² ha⁻¹)

V_i = Total stand volume before thinning (dm³ tree⁻¹)

V_a = Total stand volume after thinning (m³ ha⁻¹)

DBH = Diameter at breast height over bark – 1.30 m of stem height (cm)

DBH_{dom} = Dominant diameter at breast height over bark – 1.30 m of stem height (cm)

SI₅₀ = Site index (height (m) at age 50)

i_G = Annual stand basal area increment (m² ha⁻¹)

i_{V_a} = Annual stand volume increment (dm³ ha⁻¹ yr⁻¹).

Appendix 4.C Detailed description and parameterization of the CroBas model

Model description

CroBas is a structural-functional model for a homogeneous forest stand. It is based on allometric relationships between different parts of the tree, which define rules to allocate carbon to different functional parts of the tree. The most important relationships are the pipe model, the relationship between crown width and length, the functional balance between roots and foliage, as well as a constant density of foliage within the crown. These relationships are shown in figure 4.C.1.

Growth of the model is driven by the net carbon uptake and its dynamic allocation to different functional parts of the tree. The model has a yearly time step. Unless otherwise stated, model equations follow Mäkelä (1997).

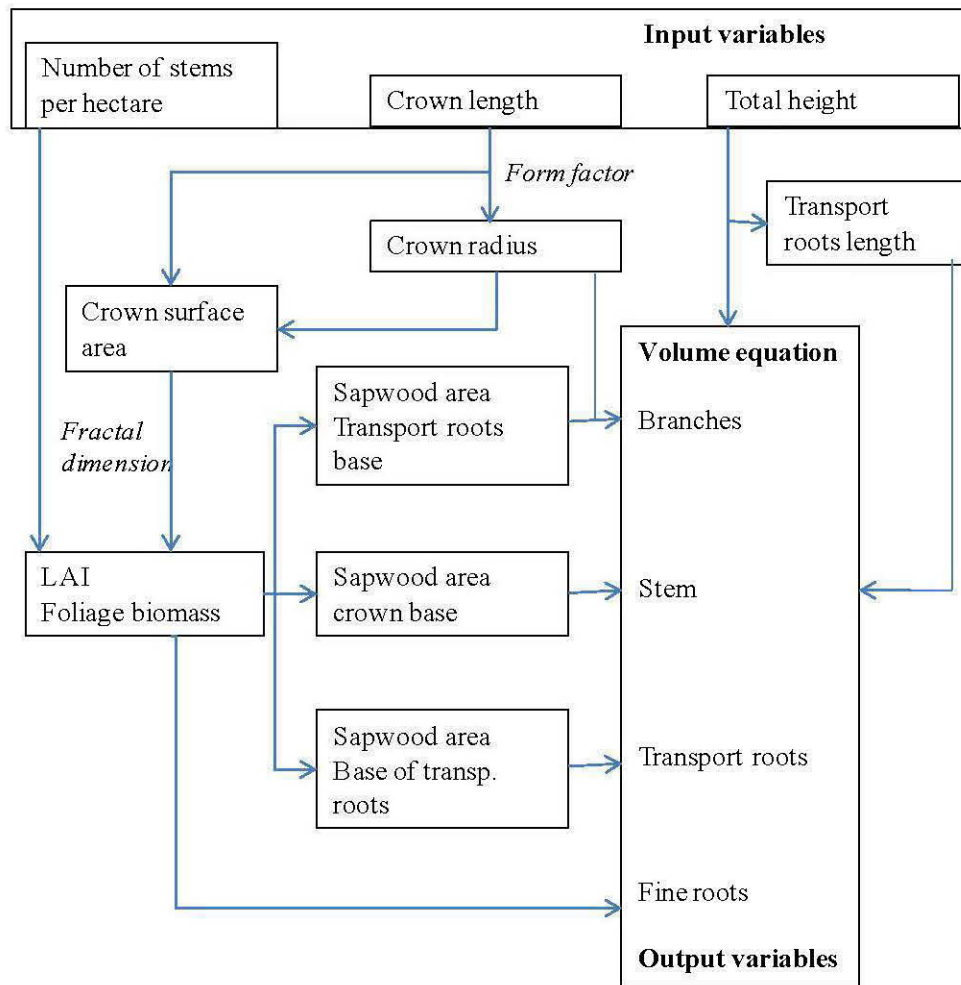


Fig 4.C.1. CroBas structural and dimensional relationships (adapted from Raulier, 2006).

1 Allometric relationship of the crown

1.1 Foliage weight

Foliage weight (W_f) was assumed to be an allometric function of lateral crown surface area (A_c), using fractal dimension (z : an allometric exponent between crown length and foliage weight), and leaf area density of foliage (ξ):

$$W_f = \xi A_c^z \quad 4.C.1$$

In addition, crown radius (H_b) was assumed to be proportional to crown length (H_c):

$$H_b = c_b H_c \quad 4.C.2$$

where c_b is the ratio of crown radius to crown length.

Using Eq. (4.C.1), and Eq. (4.C.2), we derived Eq. (4.C.3):

$$W_f = \xi H_c^{2z} \quad 4.C.3$$

1.2 Weight of fine roots

Based on functional balance, fine roots (diameter < 0.2 cm) weight (W_r) was related to foliage weight by the following equation:

$$W_r = \alpha_r W_f \quad 4.C.4$$

where α_r is the fine root to foliage weight ratio, which is specific to growth conditions of the site.

1.3 Weight of woody parts of trees

Because they have evident geometric dimensions, the weights (W) of branches, stem, and transport roots were computed using height (H) and cross-sectional sapwood area (A):

$$W_i = \varphi_i \rho_i H_i A_i, \quad i=b, t \quad 4.C.5$$

where the subscript i identifies the functional part involved (f for foliage, b for branch, s for stem, and t for transport roots), φ is the form factor of the related functional part, and ρ refers to wood density. We presents in the following the computation procedure of the other variables of Eq. (4.C.5), i.e. H_i , and A_i .

Cross-sectional sapwood area (A_i) determination was based on pipe model, which suggests that there is a constant ratio (α) between sapwood area at a given height and the foliage mass above this height. This ratio exists in branches, in stem, and in transport roots as it is stated by Eq. (4.C.6):

$$A_i = \alpha_i W_f, \quad i = s, b, t \quad 4.C.6$$

where α_i is the ratio of branches, stems, or transport roots to foliage weight.

Due to differences in taper between bare stem (H_s), and stem within crown (H_c), height (H_t) was represented by H_s+H_c . Then, transport root length (H_t) was assumed to be proportional to stem length (H_s+H_c):

$$H_t = c_t(H_s+H_c) \quad 4.C.7$$

where c_t is the ratio of transport root length to stem length.

Using Eq. 4.C.6 and Eq. 4.C.7, weights of transport roots (W_t), stemwood (W_s), and branchwood (W_b) were derived as follows:

$$W_t = \varphi_t \rho_t \alpha_t c_t (H_s + H_c) W_f \quad 4.C.8$$

$$W_s = \rho_s \alpha_s c_s (\varphi_s H_s + \varphi_c H_c) W_f \quad 4.C.9$$

$$W_b = \varphi_b \rho_b \alpha_b c_b H_c W_f \quad 4.C.10$$

2 Carbon balance

At the tree scale, difference between C uptake by photosynthesis (P) and release by respiration (R) divided by carbon use efficiency (Y), provides an estimate of tree net productivity. At the scale of tree functional part, difference between gross growth (G_i) and senescence (S_i) gives an approximation of net growth weight (W_i) of the functional part involved.

2.1 Estimation of photosynthetic production of the stand and trees

To account for interaction between trees within stand and mutual shading effect, photosynthesis of a tree (P) was estimated from maximum rate of canopy photosynthesis (P_0) per unit of ground area and leaf area index (L):

$$P = P_0 \frac{1}{N} (1 - e^{-kL}) \quad 4.C.11$$

where k is the average extinction coefficient, N the stand density, and L the leaf area index computed as the product between specific leaf area (a_n), N , and W_f .

Finally, according to Landsberg and Waring (1997), P_0 can be obtained as follows:

$$P_0 = \varepsilon \phi_p \quad 4.C.12$$

where ε is the quantum efficiency (kg C MJ^{-1} photon absorbed), and ϕ_p the yearly photosynthetically active radiation per unit of square metre ($\text{MJ m}^{-2} \text{yr}^{-1}$).

2.2 Senescence of functional parts and stem mortality

Senescence rates of all the functional parts have to be provided in the model for carbon balance computation. Stand density has to be provided as well since it affects carbon balance due to density effect on tree productivity.

Mortality in CroBas is driven by crown coverage (C), assuming that maximum crown coverage (C_{\max}) coincides with maximum stand density (N_{\max}). We computed C from



Eq. (4.C.13) as the product between crown projection surface area and stand density, which was derived in a second equation that accounted for relationship between crown radius (H_b) and length (H_c) according to crown radius to crown length ratio (c_b). Stand density (N) is not constant over time, but can't exceed a maximum value (N_{max}) corresponding to maximum crown coverage. When tree crowns are getting larger, C concurrently increases but, when C is about to exceed C_{max} , tree mortality is initiated ($N - N_{max}$) so that C_{max} is not exceeded.

$$C = N\pi H_b^2 = N\pi c_b^2 H_c^2 \quad 4.C.13$$

3. Merchantable stems characterization

We focused on merchantable stem diameter (≥ 9 cm). We used Raulier (2006) approach to determine diameter and stem volume, as well as merchantable stem characterization. Tree volume was after derived by applying volume equations.

3.1 Stem diameter distribution

Diameter distribution of even-aged stands approximates a normal distribution curve (Assmann, 1970) and can be characterized by average stand diameter and a standard deviation. Normal distribution principle was used to determine stem diameter ≥ 9 cm. Quadratic diameter ($\bar{d}_{1.3}$) gave a best estimate and was higher than stand average diameter ($d_{1.3}$). It was computed as follows by Raulier (2006):

$$\bar{d}_{1.3} = \delta \times d_{1.3} \quad 4.C.14$$

where δ is a parameter to estimate.

The following equation was used to estimate the variance ($\sigma_{d_{1.3}}^2$):

$$\sigma_{d_{1.3}}^2 = \sigma_1 \times \exp(\sigma_2 \times d_{1.3}) \quad 4.C.15$$

where σ_1 and σ_2 are parameters to estimate.

Average diameter of merchantable stems (> 9 cm) was after estimated as follows:

$$d_{1.3}^{9+} = d_{1.3} + i\sigma_{d_{1.3}} \quad 4.C.16$$

where $d_{1.3}^{9+}$ is the average diameter at breast height for stems ≥ 9 cm, and i is the difference between average diameter for stems ≥ 9 cm and total average stem diameter of the stand.

Number of stems ≥ 9 cm was obtained by the product between total number of stems and the value of the normal distribution function. Volume of stems with DBH ≥ 9 cm was computed by volume equations calibrated from our experimental data, using stem diameter and height.

3.2 Comparison between predicted and measured diameter growth

Empirical increase in stand basal area was computed by multiplying the average tree basal area increment by total number of merchantable stems of the experimental plot divided by the bark factor.

Adjustment between empirical and modelled basal area increment for the overall experimental plots was improved by varying quantum efficiency, computed as follows:

$$\varepsilon = \varepsilon_1 + \varepsilon_2 \times L + \varepsilon_3 \times L \times SI \quad 4.C.17$$

where L is the leaf area index of the stand, SI the site index and ε_1 , ε_2 , and ε_3 parameters to estimate. Values of ε_1 , ε_2 , and ε_3 were obtained by trials and errors allowing a value of quantum efficiency that make the simulated and measured basal area increments to be consistent.

3.3 Technical growth

After thinning, average stem diameter of the stand increases and is referred to as “technical growth” due to the immediate effect of removing stems with lower DBH. Therefore, average stem diameter of the stand has to be computed before any simulation. The computation was based on the same procedure used to determine merchantable stem diameter (Raulier, 2006). Average stem height after thinning was computed using average stem diameter after thinning. Crown length was determined using average stem diameter and height after thinning, and SI.

4 Model parameterization

4.1 Allometric relationship of the tree

4.1.1 Foliage weight

4.1.1.1 “Fractal dimension” of foliage in crown

Foliage weight and the fractal volume it occupies obtained from empirical values, were used to compute fractal dimension. Tree crown was divided into ten sections representing each 10% of the whole crown. For each crown section, foliage weight was estimated by a model

incorporating branch length, its basal diameter and its relative depth into crown (Goudiaby et al., 2011_b, submitted). Fractal dimension (z) was then computed according to Zeide (1998) from the slope of the regression of the logarithm of foliage mass on the logarithm of volume occupied by foliage. This regression is linear if the crown is a fractal and follows the formula (slope = $D/3$) from which the fractal dimension was derived.

4.1.1.2 “Surface area density” of foliage

Surface area densities were calculated using Eq. (4.C.3) with inputs from Goudiaby et al. (2011_b, submitted).

Fine root weight is a function of DBH and was estimated using Rencz and Auclair (1980) allometric equation for black spruce and that of Steel et al. (1997) for jack pine. No adjustment to site conditions was made for lack of data. Fine root to foliage weight ratios were then computed using measured foliage weights of Goudiaby et al. (2011_b, submitted).

4.1.1.3 Specific leaf area

Jack pine and black spruce specific leaf areas were measured on needle randomly sampled from mature stands in the course of photosynthesis measurements. Needles were scanned and their surface areas measured using Winseedle 5.0 software (Regent Instruments Inc., Québec City, QC, Canada) and weighted (Sartorius, BP 210) to the nearest 0.1 mg after drying in a ventilated oven at 65°C for 48 h. Specific leaf area was determined from the ratio of projected needle surface area to needle dry mass (Goudiaby et al., 2011_b, submitted).

4.1.2 Weight of fine roots

Only fine root to foliage weight ratio (α_r) is required to compute fine root weight (W_r) from foliage weight (W_f). Hence, W_r was computed using data from Goudiaby et al. (2011_b, submitted), whereas fine root weight came from Steel et al. (1997). The ratio was after computed and, for either jack pine or black spruce, α_r had a value of 0.15.

4.1.3 Weight of woody parts of trees

4.1.3.1 Form factors of sapwood

Weight of branches, stems and transport roots were computed using volume equations where the inputs were length of the functional part, its cross-sectional sapwood area, and a form factor. We used values provided by Mäkelä (1997) for form factors of sapwood in stem below crown, in stem within crown, in branches, and in transport roots. The form factor of sapwood in transport roots was based on the assumption that there is “no heartwood in transport roots” Mäkelä (1997). However, Nikolova et al. (2009) reported for spruce a sapwood to heartwood ratio of 54%. We used this ratio to correct form factor of sapwood in transport roots.

4.1.3.2 Density of wood

Wood density was measured from trees used for stem analyses. Jack pine wood density averaged 469 kg m^{-3} (Park et al., 2009) and black spruce density averaged 470 kg m^{-3} (M. Ourais and A. Koubaa, unpublished data). Branches, stem and transport roots were assumed to have a similar wood density.

4.1.3.3 Sapwood area: foliage weight ratios

Jack pine and black spruce branch sapwood areas were estimated using Kyker-Snowman and Wilson (1988) allometric equations and values of total branch cross-sectional area from Goudiaby et al. (2011_b, submitted). Jack pine and black spruce stem sapwood areas were estimated using Bond-Lamberty et al. (2002) allometric equations in which sapwood area was estimated as a function of diameter at breast height. Consistent with the pipe model, the cross-sectional sapwood area at stem base was assumed to approximate the cross-sectional sapwood area of transport roots. Sapwood areas at the base of jack pine and black spruce stems were estimated using Bond-Lamberty et al. (2002) allometric equations. Thereafter, sapwood area to foliage weight ratios in branches (α_b), stem (α_s) and transport roots (α_r) were computed according to Eq. (4.C.6).

5 Carbon balance

5.1 Photosynthesis and respiration

Quantum efficiency was set to 0.02 mol CO₂ mol⁻¹ photon absorbed for jack pine and to 0.03 mol CO₂ mol⁻¹ photon absorbed for black spruce (Dang et al., 1998; Goudiaby et al., 2011_a, submitted) and converted for jack pine and black spruce to 0.0018 kg C MJ⁻¹ and 0.0012 kg C MJ⁻¹, respectively.

Yearly photosynthetically active radiation was estimated from yearly global solar radiation. Average daily global solar radiation was computed on a monthly basis from temperature (°C) and precipitation (mm) normals (Environment Canada, 2009) and atmospheric topsolar radiation (MJ m⁻² d⁻¹) for the study sites using Yin's (1996) model. Daily global solar radiation was then integrated over the growing season [days with average daily temperature $\geq 5^\circ\text{C}$ (Environment Canada, 2009)] to obtain the annual estimate. Fraction of photosynthetically active radiation absorbed by trees was then estimated by multiplying

yearly global solar radiation by 0.5 (Jacovides et al., 2003). Yearly maximum rate of canopy photosynthesis was estimated with Eq. (4.C.12).

5.2 Decrease of photosynthesis per unit crown length

Brooks et al. (1997) performed photosynthesis measurements at different heights of jack pine and black spruce trees located at the northern and southern limits of the boreal forest in central Canada. We used these values and the height where the measurements were performed to compute rate of decrease of photosynthesis per unit crown length.

5.3 Light extinction coefficient

For jack pine, a light extinction coefficient of 0.57 was obtained from Aubin et al. (2000). For black spruce, we used the extinction coefficient of 0.52 provided by Pierce and Running (1988) for conifers.

5.4 Carbon use efficiency

Carbon use efficiency was set to $0.46 \text{ kg C kg}^{-1} \text{ DW}$ for jack pine and to $0.37 \text{ kg C kg}^{-1} \text{ DW}$ for black spruce according to Lavigne and Ryan (1997).

5.5 Specific maintenance respiration rate of foliage, wood and fine roots

Estimates of maintenance respiration rate of foliage, wood and fine roots were provided by Ryan et al. (1997) for jack pine and black spruce stands from northern and southern locations of the boreal forest. Also, foliage of jack pine and black spruce temperature response

coefficients (Q_{10}) were set to 2.0 and 2.1, respectively (Ryan et al., 1997). For wood and root respirations of both species, Q_{10} had respective values of 1.6 and 1.9 (Ryan et al., 1997). Respiration rates were adjusted to our sites based on the 1994 mean temperature of the growing season (Environment Canada, 2009).

6 Senescence and mortality

6.1 Specific senescence rate of foliage

Maximum needle retention was set to 3 years for jack pine (personal observations) and to 13 years for black spruce (personal observations; Fraser and McGuire, 1969). Specific senescence rate of foliage (yearly basis) was computed from these values.

6.1 Specific senescence rate of fine roots

Senescence rates of fine roots were set to 1.4 yr^{-1} for jack pine and to 3.3 yr^{-1} for black spruce according to results obtained by Steele et al. (1997) in Saskatchewan, Canada, near the southern limit of the boreal forest.

6.3 Specific sapwood area turnover rate in case of no pruning

Specific sapwood area turnover rate in case of no pruning was computed from our data using the formula from Lo et al. (2001).

$$\text{heartwood area} / (\text{heartwood area} + \text{sapwood area})$$

4.C.18

6.4 Form factors of senescent sapwood

Based on the pipe model theory, a form factor of senescent sapwood in stem below crown of 1.0) and 0.0; in transport roots (assumption of no heartwood) were suggested by Mäkelä (1997). Again, Nikolova et al. (2009) reported a sapwood to heartwood ratio of 54% for spruce. We used this ratio to correct form factors of senescent sapwood in transport roots to 0.46 for both jack pine and black spruce. Form factors of senescent sapwood in stem within crown and in branches were estimated by trial and error.

6.5 Degree of control by crown coverage of self-pruning

Degree of control by crown coverage of self-pruning was obtained by trial and error and was set to 1 for both species.

6.6 Parameter related to self-pruning

Parameter related to self-pruning was obtained by trial and error and was set to 0.6 (unitless) for both jack pine and black spruce.

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CONCLUSION GÉNÉRALE

En raison de la difficulté d'approvisionnement en bois de qualité de l'industrie forestière que traverse le Québec, due à une baisse généralisée du diamètre moyen marchand récolté des espèces d'intérêt commercial, il est préconisé d'avoir recours à des interventions sylvicoles comme les éclaircies commerciales (Coulombe *et al.*, 2004). À la suite de l'éclaircie, la disponibilité des ressources hydrominérales et lumineuses augmente en raison de la redistribution d'une même quantité de ressources entre un nombre plus restreint d'individus résiduels, favorisant pour ces derniers une meilleure croissance. Même si cette réponse positive est illustrée par plusieurs études, certains mécanismes notamment physiologiques et d'allocation de C, restent à confirmer. L'objectif général de la thèse était alors de préciser les mécanismes qui sous-tendent la réponse des arbres à l'augmentation des ressources après éclaircie.

Le choix des espèces d'étude a porté sur le pin gris et sur l'épinette noire, du fait qu'en forêt boréale du l'est du Canada, ce sont les deux espèces d'intérêt commercial les plus importantes. Notre hypothèse générale d'étude était que le pin gris, du fait qu'il est une espèce à croissance rapide et intolérante à l'ombre (Sims *et al.*, 1990), devrait répondre rapidement et intensément à l'augmentation des ressources alors que l'épinette noire, modérément tolérante à l'ombre (Sims *et al.*, 1990) et plus conservatrice devrait être plus mitigée dans ses réponses. Dans son ensemble, la thèse a été organisée autour de quatre chapitres dont le premier a été axé sur une revue de littérature qui a recadré les enjeux historiques de la sylviculture en réponse aux besoins récurrents qu'a connus l'humanité pour ce qui est de l'approvisionnement en bois. Les aspects sylvicoles reliés principalement à l'éclaircie commerciale ont été mis en exergue. Les autres chapitres de la thèse se sont intéressés à des réponses physiologiques (chapitre II), d'accroissement en volume de bois, de modifications de structure de cime et de l'efficacité de croissance (chapitre III) et d'allocation de C au niveau de la tige (chapitre IV). Les échelles temporelles d'étude allaient de la

seconde au jour (chapitre II) et à l'année (chapitre III et IV). Les échelles spatiales allaient de l'aiguille (chapitre II), à l'arbre (chapitre III et IV) et au peuplement (chapitre IV). Nous allons dresser les conclusions qui émanent de ces différentes échelles ainsi que leurs imbrications, ce qui va nous permettre de fournir des recommandations ciblées destinées à ajuster les interventions sylvicoles telles que pratiquées par l'industrie forestière du Québec.

Échelle d'étude spatiale de l'aiguille et temporelle de la seconde et du jour

La réponse à l'éclaircie sur une échelle d'étude spatiale de l'aiguille et temporelle de la seconde et du jour a été abordée dans le second chapitre de la thèse qui a traité des réponses de photosynthèse et de respiration. L'originalité de l'étude a reposé sur les mesures de photosynthèse et de respiration *in situ* sur des individus adultes dans un contexte d'éclaircie commerciale. L'hypothèse spécifique était que l'éclaircie commerciale entraînerait une augmentation de la disponibilité des ressources hydrominérales et lumineuses conduisant à une augmentation de la photosynthèse aussi bien chez le pin gris que chez l'épinette noire, avec toutefois une réponse plus faible chez cette dernière.

Les résultats ont montré que l'éclaircie n'a pas eu d'effet significatif sur les réserves en eau utiles du sol et sur les températures de l'air et du sol aussi bien dans les sites de pin gris que dans ceux d'épinette noire. À l'échelle des aiguilles, l'éclaircie n'a généralement pas affecté la concentration en N et la surface foliaire spécifique. À l'échelle des aiguilles et de la seconde, aucun effet de l'éclaircie n'a été noté sur : le taux de photosynthèse nette à lumière saturante (A_{max}), l'efficacité photosynthétique (α), la photosynthèse au point de compensation (LCP) et la respiration diurne (R_d) chez le pin gris comme chez l'épinette noire. À l'échelle de la journée, il a été noté une augmentation significative de la disponibilité de la lumière dans l'environnement immédiat des aiguilles de pin gris et d'épinette noire mesurées. À cette échelle journalière, la seule réponse significative a été notée chez le pin gris, où une relation positive a été trouvée entre l'éclaircie et le patron de photosynthèse (par unité de surface ou de masse) chez les aiguilles âgées d'un an alors que l'épinette noire n'a pas réagi. La réponse positive à l'échelle journalière observée chez le pin gris a été liée à

l'augmentation de la disponibilité de la lumière et à l'élongation de la durée d'irradiation journalière des aiguilles. Cette étude physiologique revêt un double avantage dont le premier repose sur le fait que nos expérimentations ont porté sur des mesures effectives d'échanges gazeux appliqués à des peuplements adultes malgré la difficulté d'ordre logistique d'atteindre la cime des arbres. Le deuxième avantage est celui d'avoir pu s'assurer d'une meilleure inférence de nos résultats par le fait d'avoir mené nos mesures dans des dispositifs expérimentaux avec des traitements répétés appliqués à des parcelles expérimentales délocalisées spatialement, ce qui n'est pas courant pour des études typiquement écophysiological.

Échelles d'étude spatiale de l'individu et temporelle annuelle

Les échelles d'étude spatiale de l'individu et temporelle annuelle ont été abordées dans les troisième et quatrième chapitres. L'originalité de l'étude a été d'une part la description fine et détaillée de l'accroissement en volume spécifique de bois le long de la tige de même que les changements de structure de la cime et de l'efficacité de croissance (chapitre III) et d'autre part le calibrage d'un modèle processuel de bilan de C (CroBas), lequel a précisé les réponses à l'éclaircie concernant l'allocation de C au niveau de la tige (chapitre IV).

À l'échelle de l'individu, la réponse à l'éclaircie s'est traduite, respectivement chez le pin gris et chez l'épinette noire, par une augmentation de l'accroissement en volume spécifique de bois respectivement à 2 et 3 ans après éclaircie. Toutefois, l'accroissement total en volume de la tige a été noté respectivement à 3 et 4 ans après éclaircie. La différence fondamentale notée entre les deux espèces a été la réponse à l'éclaircie plus rapide chez le pin gris comparativement à la réponse chez l'épinette noire. Chez le pin gris l'accroissement en volume de la tige a été lié expérimentalement à une efficacité de croissance plus importante (chapitre III) alors que celle de l'épinette noire a été liée à une augmentation de la productivité sans modification de l'allométrie de l'arbre (chapitre III). Une autre différence fondamentale entre le pin gris et l'épinette noire a porté sur la distribution de la croissance le long de la tige en réponse à l'éclaircie. C'est ainsi que le pin gris privilégie une réponse en

bas de la tige se propageant en hauteur par la suite alors que l'épinette noire présente une réponse uniforme le long de la tige. De telles caractéristiques indiquent qu'en réponse à l'éclaircie, le pin gris a tendance à augmenter le défilement de sa tige ce qui n'est pas le cas pour l'épinette noire. L'accentuation du défilement à la suite de l'éclaircie constitue pour le pin gris une réaction normale assurant une meilleure stabilité mécanique en raison d'une biomasse foliaire plus importante à mi-hauteur de cime consécutivement à l'éclaircie. Un autre fait marquant a été la réponse négative ou choc d'éclaircie survenue les deux premières années après éclaircie chez l'épinette noire. Le mécanisme à la base du choc d'éclaircie n'a pas été expérimentalement démontré, mais deux hypothèses ont été avancées : 1) un changement dans l'allocation de C entre les compartiments de l'arbre, ou 2) un transfert d'hydrates de carbone des individus résiduels vers les souches via les contacts qu'ils entretiennent au niveau de leurs racines.

Échelle d'étude temporelle annuelle et spatiale du peuplement

L'échelle d'étude spatiale du peuplement associée à une échelle d'étude temporelle annuelle a entièrement été abordée dans le quatrième chapitre à travers des résultats issus de données de simulation du modèle CroBas appliqué au pin gris et à l'épinette noire. Notre hypothèse spécifique était que l'éclaircie n'entraînerait pas, chez le pin gris comme chez l'épinette noire, un accroissement en volume annuel à l'échelle du peuplement à un taux tel que cela lui permettrait de compenser les volumes prélevés. L'originalité de l'approche utilisée a reposé sur le fait d'avoir offert la possibilité de simuler des intensités d'éclaircie et d'en prédire la réponse relative à la croissance en volume de bois et à l'allocation de C au niveau de la tige.

Les résultats de simulation ont montré à la suite de l'éclaircie qu'il y avait généralement chez le pin gris et chez l'épinette noire, une hausse de l'indice de surface foliaire, de la surface terrière et du volume total du peuplement. La hausse s'est maintenue jusqu'à l'horizon 20-ans correspondant au délai de simulation maximum sur lequel a été testé l'effet de l'éclaircie. Pour les deux espèces, l'éclaircie ne permettait pas de revenir à des surfaces terrières et volumes de peuplements d'avant éclaircie. En d'autres termes, il n'existe pas à l'échelle du

peuplement un effet compensatoire relatif à la quantité de matière ligneuse prélevée. En effet, bien qu'un accroissement ait été noté chez les deux espèces, les volumes totaux des peuplements n'atteignaient généralement jamais ceux prélevés lors de l'éclaircie.

Évidemment, la possibilité de simuler des scénarios d'éclaircie, bien qu'intéressante, présente des limites inhérentes à l'adaptation du modèle dont un certain nombre de paramètres entrant dans le modèle a été estimé. C'est le cas par exemple du rapport de la biomasse des racines fines sur celle du feuillage, lequel est spécifique au site, et qui pourrait remettre en cause, dans une certaine mesure, l'application du modèle à des peuplements situés sur des sites différents.

Le pin gris et l'épinette noire, deux espèces aux réponses à l'éclaircie contrastées

Les résultats obtenus ont confirmé la plus forte plasticité du pin gris comparativement à l'épinette noire et ce, aussi bien au niveau de la réponse physiologique que celle liée à l'accroissement en volume de la tige et en biomasse du feuillage et en efficacité de croissance. De telles réponses sont ainsi conformes à ce qui est connu de l'autoécologie des deux espèces et cette dichotomie est illustrée à toutes les échelles spatio-temporelles étudiées. Le pin gris est une espèce de début de succession qui répond rapidement et plus intensément à l'augmentation des ressources à la suite de l'ouverture du peuplement. L'épinette noire quant à elle s'est montrée non seulement plus conservatrice, mais répondait à l'ouverture du couvert plus tardivement et plus faiblement.

Recommandations et perspectives

Des recommandations ciblées passent nécessairement par la compréhension du but initialement poursuivi quand un aménagiste forestier ou un sylviculteur décide de faire une éclaircie commerciale. De prime abord, une éclaircie commerciale est motivée par des raisons purement économiques, celle de pouvoir rentabiliser financièrement une première éclaircie en

récoltant des tiges de diamètre marchand et celle de pouvoir récolter, consécutivement lors d'une deuxième éclaircie, des tiges dont la croissance accrue permettrait d'augmenter potentiellement ses gains à un taux auquel on n'aurait pas pu prétendre si une première éclaircie n'avait pas initialement été menée. Une mise à contribution des connaissances acquises lors de cette étude et qui font état des différences notées entre le pin gris et l'épinette noire permet de formuler un certain nombre de recommandations.

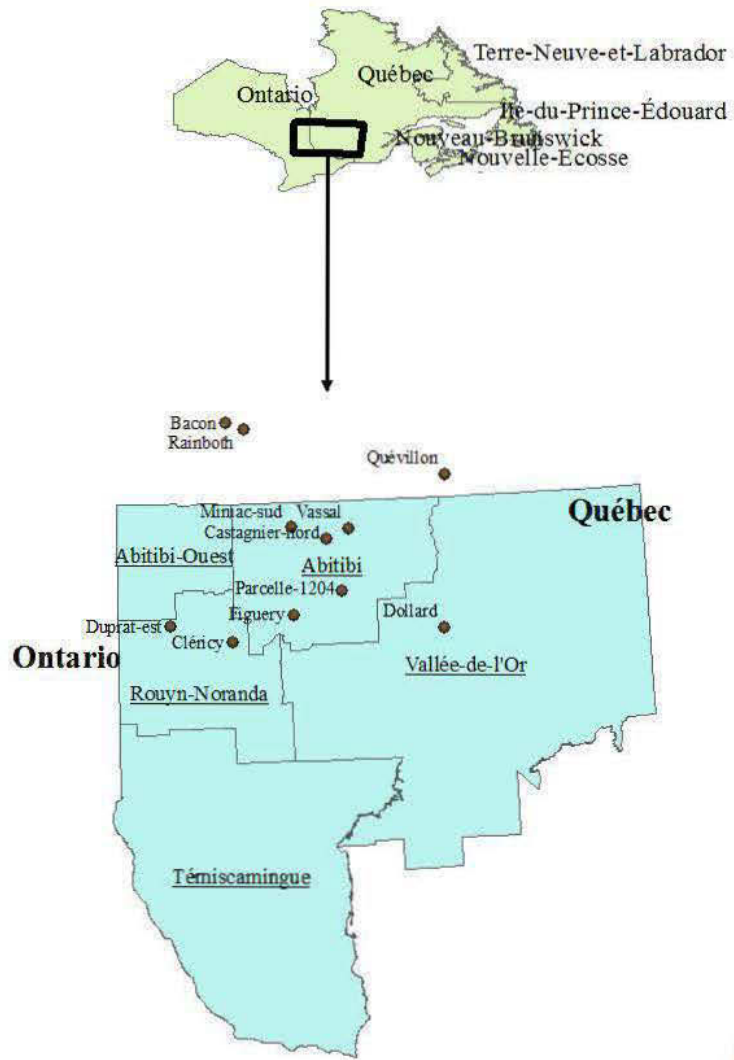
Tout d'abord, les mesures écophysiologicalues que nous avons menées (chapitre II) ont montré que l'augmentation de la lumière après l'éclaircie est avantageuse pour le pin gris qui augmente sa photosynthèse à l'échelle journalière sur les aiguilles de l'année alors que l'épinette noire n'a pas réagi. Ceci devrait avoir des implications pour les sylviculteurs dans leur façon de conduire une éclaircie commerciale. L'éclaircie qui a tendance à libérer les cimes des arbres pour une meilleure interception de la lumière pourrait être privilégiée chez le pin gris. Par contre, l'épinette noire qui a montré moins de réactions au niveau des compartiments aériens nous fait penser que sa réponse à l'éclaircie serait plutôt liée aux ressources du sol. Nous recommandons donc pour l'épinette noire de privilégier une éclaircie qui favoriserait une plus grande distance entre les arbres au sol.

Par ailleurs, à la lumière des résultats obtenus dans le chapitre III, on a obtenu un meilleur potentiel de réponse à l'éclaircie chez le pin gris comparativement à l'épinette noire. De plus, la distribution de croissance reste uniforme tout au long de la tige chez l'épinette noire alors qu'elle se fait de préférence vers le bas chez le pin gris même si elle se propage vers les parties supérieures avec le temps (tendance à l'accentuation du défilement de la tige). Ainsi comme recommandation, le pin gris pourrait être privilégié dans une optique de production accrue pour l'industrie des pâtes à papier dont le défilement n'est pas un critère de qualité. Toutefois, l'un des critères de qualité de l'industrie du sciage est le faible défilement des tiges de sorte que si l'on veut des tiges plus droites, l'éclaircie appliquée à l'épinette noire pourrait être plus intéressante.

Enfin, nos peuplements ont été éclaircis tardivement par rapport à la période propice pour une première éclaircie commerciale et des simulations de 20 ans (chapitre IV) sont justifiées, d'autant plus qu'il est recommandé d'avoir recours à une deuxième éclaircie au moins 15 ans après qu'une première a été effectuée (MRNFP, 2003). Ainsi, il est probable que des peuplements plus jeunes réagissent différemment, par exemple en intensité de réponse, de ce qui a été reporté dans la présente étude. Des éclaircies de peuplements plus jeunes seraient nécessaires afin d'en mesurer l'amplitude de réponse et de les intégrer dans le modèle pour prendre en compte la dimension âge des individus. La fiabilité des simulations s'en trouverait alors maximisée et les biais de prédiction à long terme minimisés.

APPENDICE A

CARTE DE LOCALISATION DE L'ENSEMBLE DES SITES D'ÉTUDE (BLOCS) DE
PIN GRIS (*PINUS BANKSIANA* LAMB.) ET D'ÉPINETTE NOIRE
(*PICEA MARIANA* (MILL.) B.S.P.) DANS LESQUELS ONT ÉTÉ MENÉES LES
MESURES DE PHOTOSYNTHÈSE ET LES ÉTUDES D'ARBRE

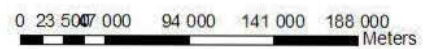


Légende:

En gras: Provinces

En souligné: Municipalités régionales de comté

● Sites d'étude



APPENDICE B

CARACTÉRISTIQUES GLOBALES DES SITES D'ÉTUDE (BLOCS) DE PIN GRIS
(*PINUS BANKSIANA* LAMB.) ET LEURS LOCALISATIONS GÉOGRAPHIQUES

Site	Éclaircie	Longitude (dd mm ss.s)	Latitude (dd mm ss.s)	Dépôt	Élévation (m)	ACAC	AEA	M (an ⁻¹)	N _h (ind ha ⁻¹)	G _h (m ² ha ⁻¹)	V _h (m ³ ha ⁻¹)
Castagnier-Nord	Témoin	N48 48 35.6	W77 54 59.5	4gs	353	1999	2004	0,000	0	0,0	0,0
Castagnier-Nord	Modérée	N48 48 47.4	W77 55 10.2	4gs	352	1999	2004	0,006	925	5,2	199,6
Castagnier-Nord	Forte	N48 48 38.3	W77 55 03.8	4gs	344	1999	2004	0,002	700	4,4	149,1
Cléricy	Témoin	N48 18 12.2	W78 39 10.5	4gs	344	1999	2004	0,012	0	0,0	0,0
Cléricy	Modérée	N48 18 24.1	W78 39 03.8	4gs	358	1999	2004	0,008	1500	13,0	502,4
Cléricy	Forte	N48 18 18.1	W78 39 10.0	4gs	299	1999	2004	0,008	1575	11,8	379,3
Dollard	Témoin	N48 20 36.7	W77 03 30.0	4gs	366	1999	2004	0,002	0	0,0	0,0
Dollard	Modérée	N48 20 19.2	W77 03 34.6	4gs	358	1999	2004	0,002	1475	6,0	231,1
Dollard	Forte	N48 20 33.7	W77 03 30.0	4gs	363	1999	2004	0,000	1500	6,6	289,8
Duprat-Est	Témoin	N48 23 58.6	W79 07 07.2	1a	345	1999	2004	0,001	0	0,0	0,0
Duprat-Est	Modérée	N48 23 42.0	W79 07 16.9	1a	349	1999	2004	0,008	2325	10,8	473,8
Duprat-Est	Forte	N48 23 50.0	W79 07 09.9	1a	352	1999	2004	0,002	2525	11,8	504,5
Figuery	Témoin	N48 26 00.7	W78 11 26.6	1a	368	1999	2004	0,004	0	0,0	0,0
Figuery	Modérée	N48 25 53.6	W78 11 26.9	1a	345	1999	2004	0,015	2175	12,0	580,1
Figuery	Forte	N48 26 06.0	W78 11 28.8	1a	453	1999	2004	0,022	1425	12,7	534,9

Note : pour des raisons d'uniformisation, nous avons maintenu les mêmes abréviations que celles utilisées dans les chapitres II, III et IV.

ACAC : année de croissance après coupe

AEA : année étude d'arbre

dd mm ss.s : degré minute seconde

M : mortalité totale relative (calculée sur une période de 5 ans)

N_h : densité d'individus prélevés lors de l'éclaircie

G_h : surface terrière prélevée lors de l'éclaircie

V_h : volume prélevé lors de l'éclaircie

Le type de dépôts s'inspire de la classification des types écologiques de Blouin et Berger (2002)

4gs : dépôts glaciolacustres de texture grossière

1a : dépôts de till.

APPENDICE C

CARACTÉRISTIQUES GLOBALES DES SITES D'ÉTUDE (BLOCS) D'ÉPINETTE
NOIRE (*PICEA MARLANA* (MILL.) B.S.P.) ET LEURS LOCALISATIONS
GÉOGRAPHIQUES

Site	Éclaircie	Longitude (dd mm ss.s)	Latitude (dd mm ss.s)	Dépôt	Élévation (m)	ACAC	AEA	M (an ⁻¹)	N _h (ind ha ⁻¹)	G _h (m ² ha ⁻¹)	V _h (m ³ ha ⁻¹)
Castagnier-Sud	Témoin	N48 45 16.9	W77 50 48.6	4ga	324	2001	2006	0,00	0	0,0	0,0
Castagnier-Sud	Modérée	N48 45 29.4	W77 50 44.6	4ga	333	2001	2006	0,00	1450	13,7	419,0
Castagnier-Sud	Forte	N48 45 21.5	W77 50 44.9	4ga	307	2001	2006	0,01	1425	15,9	524,8
Miniac-Sud	Témoin	N48 52 49.1	W78 11 02.6	4ga	324	2000	2005	0,00	0	0,0	0,0
Miniac-Sud	Modérée	N48 52 35.3	W78 10 57.4	4ga	303	2000	2005	0,00	1800	15,7	465,2
Miniac-Sud	Forte	N48 52 39.4	W78 10 56.5	4ga	316	2000	2005	0,00	1275	15,8	335,7
Quévillon	Témoin	N49 06 41.0	W76 59 48.5	4ga	282	1999	2004	0,02	0	0,0	0,0
Quévillon	Modérée	N49 06 49.6	W76 59 52.6	4ga	292	1999	2004	0,01	1075	10,8	263,9
Quévillon	Forte	N49 06 36.6	W76 59 47.1	4ga	288	1999	2004	0,02	1700	19,8	395,1
Vassal	Témoin	N48 51 24.8	W77 45 11.9	4ga	312	1999	2004	0,00	0	0,0	0,0
Vassal	Modérée	N48 51 26.4	W77 45 25.7	4ga	309	1999	2004	0,01	2000	18,2	323,9
Vassal	Forte	N48 51 27.2	W77 45 13.2	4ga	322	1999	2004	0,01	2625	18,3	532,0

Note : pour des raisons d'uniformisation, nous avons maintenu les mêmes abréviations que celles utilisées dans les chapitres II, III et IV.

ACAC : année de croissance après coupe

AEA : année étude d'arbre

dd mm ss.s : degré minute seconde

M : mortalité totale relative (calculée sur une période de 5 ans)

N_h : densité d'individus prélevés lors de l'éclaircie

G_h : surface terrière prélevée lors de l'éclaircie

V_h : volume prélevé lors de l'éclaircie

Le type de dépôts s'inspire de la classification des types écologiques de Blouin et Berger (2002)

4ga : dépôts glaciolacustres de texture fine (argile).

APPENDICE D

CARACTÉRISTIQUES DENDROMÉTRIQUES DES INDIVIDUS DE PIN GRIS
(*PINUS BANKSIANA* LAMB.) ÉTUDIÉS

Site	Éclaircie	Age	DHP (cm)	H _{tr} (m)	H _c (m)	H _a (m)	W _f (kg ind ⁻¹)	W _{BW} (kg ind ⁻¹)	V _{tr} (dm ³ ind ⁻¹)
Castagnier-Nord	Témoin	47	16,1	15,8	5,9	123,3	3,2	4,1	141,5
Castagnier-Nord	Modérée	48	18,5	16,7	6,8	150,4	5,6	7,0	209,5
Castagnier-Nord	Forte	48	19,1	16,8	7,3	129,1	5,0	6,3	211,2
Clérycy	Témoin	70	18,6	17,4	6,4	104,9	3,8	6,1	206,5
Clérycy	Modérée	69	23,0	19,5	8,2	155,2	7,6	9,8	331,1
Clérycy	Forte	69	20,4	18,2	7,2	123,4	6,0	7,7	251,0
Dollard	Témoin	53	19,0	17,0	6,9	160,0	5,7	7,3	209,8
Dollard	Modérée	54	17,1	15,7	6,3	145,4	4,2	5,2	163,8
Dollard	Forte	52	17,6	16,9	7,9	155,1	6,3	7,9	196,2
Duprat-Est	Témoin	53	160,0	15,9	6,2	91,1	3,2	4,0	139,2
Duprat-Est	Modérée	53	19,5	16,3	6,8	109,6	5,2	6,7	205,5
Duprat-Est	Forte	53	18,1	16,3	6,8	100,6	5,4	6,5	199,0
Figury	Témoin	81	23,1	19,4	7,1	152,9	7,9	10,7	372,2
Figury	Modérée	82	21,6	18,1	6,5	130,4	6,1	9,3	265,9
Figury	Forte	81	23,5	20,1	6,9	159,4	8,0	11,4	376,5

Note : pour des raisons d'uniformisation, nous avons maintenu les mêmes abréviations que celles utilisées dans les chapitres II, III et IV.

DBH : diamètre à hauteur de poitrine (1,3 m)

H_{tr} : hauteur totale de l'arbre

H_c : longueur de la cime de l'arbre

H_a : rayon de la cime de l'arbre

W_f : biomasse foliaire totale de l'arbre

W_{BW} : biomasse totale des branches de l'arbre

V_{tr} : volume total de l'arbre.

APPENDICE E

CARACTÉRISTIQUES DENDROMÉTRIQUES DES INDIVIDUS D'ÉPINETTE NOIRE
(*PICEA MARIANA* (MILL.) B.S.P.) ÉTUDIÉS

Site	Éclaircie	Age	DHP (cm)	H _{tr} (m)	H _c (m)	H _a (m)	W _f (kg ind ⁻¹)	W _{BW} (kg ind ⁻¹)	V _{tr} (dm ³ ind ⁻¹)
Castagnier-Sud	Témoin	95	17,9	20,1	9,3	1,6	3,4	46,7	276,7
Castagnier-Sud	Modérée	94	18,5	19,2	3,1	1,8	3,3	31,4	290,3
Castagnier-Sud	Forte	95	20,4	20,5	5,2	2,4	4,6	69,3	367,4
Miniac-Sud	Témoin	90	13,3	17,6	5,9	1,2	3,8	23,3	137,2
Miniac-Sud	Modérée	94	17,9	18,3	7,1	1,3	6,9	25,6	262,5
Miniac-Sud	Forte	93	17,0	19,9	8,0	1,5	5,4	27,0	263,0
Quévillon	Témoin	93	14,7	18,5	10,8	2,0	6,7	20,7	179,7
Quévillon	Modérée	94	16,9	20,2	7,8	1,1	4,8	20,5	253,0
Quévillon	Forte	91	16,8	18,7	9,4	1,7	8,3	35,0	234,1
Vassal	Témoin	94	18,4	19,8	7,2	1,5	5,9	66,5	305,4
Vassal	Modérée	91	13,7	16,8	6,4	1,4	5,5	25,1	154,2
Vassal	Forte	93	14,2	17,2	7,1	1,4	5,2	19,6	194,6

Note : pour des raisons d'uniformisation, nous avons maintenu les mêmes abréviations que celles utilisées dans les chapitres II, III et IV.

DBH : diamètre à hauteur de poitrine (1,3 m)

H_{tr} : hauteur totale de l'arbre

H_c : longueur de la cime de l'arbre

H_a : rayon de la cime de l'arbre

W_f : biomasse foliaire totale de l'arbre

W_{BW} : biomasse totale des branches de l'arbre

V_{tr} : volume total de l'arbre.

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