UNIVERSITÉ DU QUÉBEC À MONTRÉAL

INTERACTIONS ENTRE LE PEUPLIER FAUX-TREMBLE ET L'ÉPINETTE NOIRE
EN FORÊT BORÉALE DE L'OUEST DU QUÉBEC

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AVANT-PROPOS

Ce mémoire de maîtrise est formé d'un chapitre rédigé en anglais sous forme d'article scientifique. Je suis l'auteur principal de cet article et j'ai réalisé la récolte et la compilation des données, de même que les analyses statistiques et la rédaction de l'article. Alain Leduc et Yves Bergeron ont conçu le projet initial et ont élaboré avec moi le design expérimental alors que Michael J. Papaik a collaboré avec moi aux analyses statistiques. L'unique article de ce mémoire, intitulé «*Tree growth response to trembling aspen proximity in eastern canada black spruce-feathermoss forest*», est en préparation pour soumission à *Ecological Applications*.

TABLE DES MATIÈRES

LISTE DES FIGURES

viii

LISTE DES TABLEAUX

LISTE DES ÉQUATIONS

RÉSUMÉ

En forêt boréale de l'est du Canada, les pessières à mousses sont souvent pourvues de peupliers faux-trembles qui s'y retrouvent parsemés en petits îlots. Ces pessières sont alors aménagées de manière à confirmer leur vocation principale, en tentant de réduire du mieux possible la présence de tremble lors des pratiques d'éclaircies précommerciales. Bien que des études suggèrent qu'à long terme, le peuplier faux-tremble pourrait augmenter le rendement de ces pessières en limitant l'accumulation de matière organique au sol, des inquiétudes persistent quant à son effet compétitif sur la croissance des épinettes à court et moyen termes.

Cette étude cherche donc à quantifier et préciser les interactions compétitives entre le peuplier faux-tremble et l'épinette noire en mesurant leurs effets sur la croissance radiale. Ces interactions sont étudiées à l'échelle de l'arbre, de manière à évaluer plus spécifiquement l'importance de l'espèce, la taille, la distance, la position et l'abondance des voisins sur la croissance. Plus précisément on cherche à déterminer si (1) la croissance radiale d'une épinette noire mature serait meilleure en présence d'un peuplier faux-tremble que d'une épinette noire voisine, (2) la croissance radiale d'un peuplier faux-tremble mature serait meilleure en présence d'un peuplier faux-tremble que d'une épinette noire voisine, (3) la présence de peupliers faux-tremble en pessière dite « pure » ne diminuerait pas le volume total d'épinette noire dans un voisinage et (4) ni la distance, ni la position des voisins n'influenceraient la croissance radiale des arbres matures dans ces forêts.

Une analyse de compétition est effectuée à partir de la croissance radiale de 373 arbres témoins, répartis sur 122 placettes. Le modèle estime la croissance radiale potentielle maximale et distingue les effets de la compétition pour la lumière de ceux découlant de situations de surnombre. Les hypothèses sont représentées sous forme de modèles alternatifs, créés en retirant certains paramètres du modèle complet. La sélection de modèle, qui utilise les techniques de vraisemblance maximale combinées à la théorie de l'information permet de tester plusieurs hypothèses simultanément et de les comparer entre-elles.

Le meilleur modèle pour l'épinette noire inclut un effet d'ombrage spatialement explicite, mais également un effet de densité indépendant des distances. Celui du tremble exclut quant à lui toutes composantes spatiales mis à part le rayon de voisinage. Les résultats montrent qu'une épinette noire est jusqu'à 4 fois moins affectée par le voisinage d'un tremble que celui d'un congénère de même taille. La dominance des trembles sur les épinettes entraîne cependant certains effets négatifs sur la croissance de ces dernières, particulièrement en tremblaie dite pure. Donc la croissance radiale optimale de l'épinette noire est atteinte en milieu mixte, où les proportions de tremble et d'épinette noire sont équivalentes et où la dominance des trembles est réduite.

La croissance des trembles est quant à elle favorisée en tremblaie pure, où les faibles densités lui sont favorables. Les analyses laissent présager la présence d'un certain effet améliorant du tremble sur la croissance des arbres en pessière. En termes de rendement, on observe un effet additif de ces deux essences; c'est-à-dire qu'on peut ajouter jusqu'à 30 % de tremble dans le peuplement sans diminuer le volume total d'épinette noire.

MOTS-CLÉS : Compétition, épinette noire, peuplier faux-tremble, forêt boréale, analyse de voisinage.

INTRODUCTION GÉNÉRALE

En forêt boréale de l'ouest du Québec, les pessières à mousses sont souvent pourvues de peupliers faux-trembles (*Populus tremuloides* (Michx.)) qui s'y retrouvent parsemés en petits îlots. Ces pessières sont alors aménagées de manière à confirmer leur vocation principale, en tentant d'éliminer du mieux possible la présence de tremble. De même, la valeur économique associée au tremble reste inférieure à celles d'autres espèces boréales telles que l'épinette noire (*Picea mariana (Mill) B.S.P.*) (Pearce 1989). Cette situation donne lieu à des pratiques sylvicoles simplifiant les structures et compositions naturelles des peuplements forestiers (McDougall 1988; Nichols et al. 2006; O'Hara et al. 1994), telles que les éclaircies précommerciales qui éliminent une importante proportion de tremble dans les jeunes peuplements résineux. Pourtant, des recherches tendent à démontrer qu'il existerait un gain en productivité associé à l'aménagement mixte de certaines espèces (Kelty 1992; Légaré et al. 2005a; Loreau et al. 2001; Paré and Bergeron 1996) et encouragent, dans certains cas, le maintien d'espèces de début de succession dans l'aménagement (Connell and Slatyer 1977).

L'industrie forestière priorise traditionnellement les peuplements équiennes et monospécifiques pour une question de simplicité opérationnelle (Kelty 2006; MacPherson et al. 2001; Nichols et al. 2006; O'Hara et al. 1994; Rothe and Binkley 2001). Or, les avantages potentiels reliés à la présence de feuillus en forêt résineuse ne manquent pas : amélioration des conditions de sol, abris pour la régénération, réduction des risques d'attaque d'insectes, amélioration de la stabilité au vent (Kelty 1992; Man and Lieffers 1999; Nichols et al. 2006) et amélioration de la productivité et de la rentabilité. Cette simplification de la composition des pessières affecterait également la biodiversité végétale et faunique (Cannell 1999; DeByle 1989a, b; O'Hara et al. 1994). Le maintien de la composante feuillue en forêt boréale rendrait plus complexe la structure du couvert par rapport à une monoculture résineuse et permettrait d'éviter une perte importante de biodiversité, particulièrement pour ce qui est de la faune ailée (Hobson and Bayne 2000).

Rôle du peuplier faux-tremble en pessière

Il est bien connu que la productivité des pessières diminue de façon importante avec le temps (Gower et al. 1996; Ryan et al. 2004). L'une des causes de cette diminution de productivité est l'accumulation de matière organique, qui engendre une hausse de la nappe phréatique, une baisse de la température des sols et une séquestration des nutriments dans l'épaisse couche de matière organique ainsi formée (Dioumaeva et al. 2002; Fenton and Bergeron 2006; Glebov and Korzukhin 1992; Prescott et al. 2000). L'accumulation de matière organique serait plus accentuée dans les régions sensibles à la paludificiation, comme la ceinture d'argile du Québec et de l'Ontario (Fenton et al. 2005; Taylor et al. 1987). Ce phénomène serait d'autant plus important alors que la fréquence des feux diminuerait dans la région depuis la fin du 19e siècle, où le cycle de feu serait passé de 141 à 326 ans depuis 1920 (Bergeron et al. 2001). Les feux ont, en effet, plusieurs rôles écologiques dont celui de diminuer l'épaisseur de la matière organique en surface (Bergeron et al. 1999).

Dans cette région, le peuplier faux-tremble se retrouve naturellement regroupé en îlots tant dans les pessières de première que de deuxième cohorte (Bergeron and Dubuc 1989; Heinselman 1981; Paré and Bergeron 1995). Ce dernier créerait plusieurs effets positifs sur la productivité des pessières. D'abord, le tremble utiliserait des nutriments que les racines d'épinette situées plus en surface ne peuvent atteindre; le tremble agirait ainsi comme une « pompe nutritive » en les rendant ensuite disponibles en surface par la décomposition de sa litière (Jones and DeByle 1985; Stoekeler 1961). De plus la litière de tremble serait plus facilement décomposable compte tenu de la faible teneur en lignine des feuilles (Kelty 2006; Scott and Binkley 1997), de l'humus alcalin qu'elle génère comparativement aux résineux (Cannell 1999; Paré and Bergeron 1996) et de son caractère nuisible à la croissance des mousses et des sphaignes (Van Cleve and Viereck 1981). Plusieurs études suggèrent que la décomposition de la litière des feuillus en général, par leur composition élevée en nutriments, améliorerait la disponibilité des nutriments dans les sols (Hättenschwiler et al. 2005; Hobbie 1992; Kelty 1992; MacPherson et al. 2001; Man and Lieffers 1999; Wardle

2002) et abriterait une pédofaune plus abondante et diversifiée (Blair et al. 1990; Hättenschwiler et al. 2005; Jones and DeByle 1985). Certains mélanges de litière provenant d'espèces différentes pourraient également par l'intermédiaire de cette pédofaune, libérer davantage de nutriments que chacune des litières prises séparément (Blair et al. 1990; Hättenschwiler et al. 2005). Finalement, en laissant passer davantage de lumière au sol, le tremble réchaufferait la température du sol, améliorant ainsi son activité microbienne et la décomposition et permettant le maintien d'une strate herbacée plus diversifiée. Ainsi, la présence de trembles pourrait freiner le processus de paludification des pessières de la ceinture d'argile et, par le fait même, faciliter la croissance des épinettes noires et en améliorer la productivité à long terme (Fenton et al. 2005).

Coexistence et complémentarité en forêt mixte

À court et moyen termes, les effets de la paludification sur la productivité se feraient moins sentir (Simard et al. 2007) et on pourrait croire de même pour les effets positifs du peuplier faux-tremble, mais ce dernier ne nuirait pas pour autant à la croissance de l'épinette noire. Le concept de niche écologique est à la base des hypothèses émises dans notre étude quant à la coexistence du peuplier faux-tremble et de l'épinette noire. La niche écologique représente la position d'une espèce par rapport aux autres au sein d'une même communauté (Whittaker 1975). Cette position dépendrait de la tolérance de l'espèce au milieu physique et de la façon dont elle utilise les composantes de son habitat (Chase and Leibold 2003). Pour qu'il y ait coexistence stable, une certaine compatibilité est nécessaire en ce qui a trait à l'adaptation des espèces à leur environnement (*fitness*) et à leur utilisation des ressources (niche écologique) (Aarssen 1983; Bengtsson et al. 1994; Hutchinson 1957); on parle alors d'habileté d'association écologique (*Ecological combining ability*) (Harper 1977). Les différences de niches (ou FND pour *Fundamental Niche Differentiation* (Whittaker 1975)) augmentent la compétition intraspécifique par rapport à

4

l'interspécifique et permettent ainsi la coexistence (Harper 1977; Jose et al. 2006; Kelty 1992; Vandermeer 1989; Whittaker 1975).

Au-delà de la coexistence, des espèces peuvent être complémentaires et permettre une utilisation plus efficace des ressources du milieu (Loreau et al. 2001). En milieu forestier, la complémentarité prend souvent source dans la stratification au niveau des cimes (Menalled et al. 1998) et des systèmes racinaires entre les espèces coexistantes (Berendse 1979; Jose et al. 2006; Kelty 1992; Larson 1992; Parrish and Bazzaz 1976; Rothe and Binkley 2001). Autant l'épinette noire (tolérante à l'ombre) atteint une hauteur de cime moindre que celle du peuplier (intolérant à l'ombre) autant son système racinaire reste plutôt superficiel comparativement à celui de ce dernier (Gale and Grigal 1987; Perala 1990; Strong and La Roi 1983; Viereck and Johnston 1990). Ces différences s'accentueraient lorsqu'ils se retrouvent en milieu mixte, selon leur plasticité devant la compétition interspécifique (Jose et al. 2006; Rothe and Binkley 2001). Des différences existent également quant à la captation de lumière tant au niveau qualitatif que temporel. L'épinette noire conserve son feuillage toute l'année, lui permettant d'amorcer sa photosynthèse plus tôt que le tremble au printemps (Constabel and Lieffers 1996). De plus, le tremble utilise plus efficacement la lumière directe alors que les espèces de fin de succession, telle que l'épinette, excellent plutôt à capter la lumière diffuse (Kelty 1992; Perala 1990; Viereck and Johnston 1990).

Quoiqu'il en soit, le bilan des interactions positives et négatives entre ces deux espèces dans un contexte de paludification est encore mal connu. Des études se sont déjà penchées sur l'effet de la présence du tremble sur la croissance des épinettes noires (Fenton et al. 2005; Légaré et al. 2005a; Légaré et al. 2005b) et on observe que la présence de tremble pourrait apporter une certaine stabilité aux pessières, qui seraient autrement plus susceptibles à des pertes de productivité. Toutefois, des doutes persistent encore par rapport au bilan net des interactions entre le tremble et l'épinette, à savoir si la présence de tremble nuirait plus qu'elle n'aiderait la cause des épinettes noires.

Analyse de voisinage

L'observation des interactions entre le tremble et l'épinette noire à plus petite échelle permettrait de déterminer plus précisément le rôle de chaque facteur sur la croissance d'un arbre, tout en évaluant le bilan global des interactions. L'analyse de voisinage est l'une de ces approches qui permettent d'analyser les interactions spatialement et à l'échelle où elles se produisent, soit à l'échelle des individus (Canham and Uriarte 2006; Klausmeier and Tilman 2002). Il s'agit une forme relativement récente d'analyse de compétition n'ayant jamais été employée pour étudier spécifiquement la relation épinette noire/tremble. Cette approche, déjà utilisée en agriculture, a ensuite été appliquée aux communautés végétales par plusieurs études avec une efficacité remarquée (Mack and Harper 1977; Pacala and Silander 1985; Silander and Pacala 1985; Waller 1981; Weiner 1982). L'échelle fine alloue une précision supérieure dans la détermination des effets de compétition restés indécelables à l'échelle du peuplement (Puettmann et al. 1992). Étant donné le grand nombre de calculs nécessaires, cette approche était inimaginable avant les récents progrès informatiques. Ces derniers nous permettent maintenant d'utiliser la modélisation couramment et d'obtenir des résultats dans des délais raisonnables (Latimer et al. 2006; Wang et al. 1995). Le recours à la modélisation se substitue donc aux essais sylvicoles, une méthode reconnue, mais qui requiert plusieurs années d'attente (MacPherson et al. 2001).

Certaines études précédentes ont abordé la relation de compétition du tremble avec l'épinette noire (Légaré et al. 2005a; Légaré et al. 2004, 2005b) ou l'épinette blanche (MacPherson et al. 2001; Man and Lieffers 1999; Wang et al. 1995), mais à l'échelle du peuplement, donc avec moins de précision qu'à l'échelle de l'individu. La cartographie des sites est l'une des variables-clés de l'analyse de voisinage puisqu'elle permet de considérer tous les individus dans ses calculs (Canham et al. 2004; Canham et al. 2006; Latimer et al. 2006; Uriarte et al. 2004). D'abord, du fait de leur immobilité, les arbres interagissent principalement avec leurs proches voisins (Harper 1977; Silander and Pacala 1985; Stoll and Weiner 2000) et la compétition demeure un phénomène agissant directement à l'échelle du

voisinage (Bengtsson et al. 1994; Mack and Harper 1977), particulièrement pour ce qui est de la compétition pour la lumière (Stoll and Weiner 2000). De même, l'importance des aspects spatiaux et locaux reliés à la compétition est ignorée par la majorité des analyses de compétition qui utilise de simples indices de compétition, ce qui limite considérablement leur pouvoir (Stoll and Weiner 2000). Aussi, puisque l'influence d'un arbre sur les propriétés du sol se limiterait généralement à la projection de sa cime au sol (Zinke 1962) et que sa litière influencerait les processus nutritionnels des sols forestiers dans un rayon équivalent à la hauteur de l'arbre (Ferrari and Sugita 1996; Staelens et al. 2003), nous avons tout avantage à examiner ces interactions à l'échelle de l'arbre (Rothe and Binkley 2001).

Objectif et hypothèses

L'objectif principal de l'étude est de quantifier et préciser les interactions nettes entre le peuplier faux-tremble et l'épinette noire en mesurant leurs effets sur la croissance radiale des tiges en pessière à mousse de l'ouest du Québec. Bien que l'emphase soit mise sur l'épinette noire, l'espèce commerciale la plus prisée de ces forêts, le peuplier faux-tremble est également considéré vu l'intérêt grandissant qu'on lui accorde. Plus spécifiquement, cette étude cherche à spécifier l'importance de l'espèce, la taille, la distance, la position et l'abondance des voisins sur la croissance du peuplier faux-tremble et de l'épinette noire. Ces précisions permettent de distinguer les effets compétitifs de surabondance (crowding) de ceux liés à l'ombrage. Les effets de surabondance apparaissent lorsque les tiges environnantes sont en densité suffisantes pour causer des réductions de croissance sur un arbre donné (Whittaker 1975).

En tenant compte de tous les facteurs mentionnés ci-haut, les analyses seront en mesure d'évaluer certaines hypothèses en ce qui a trait à la composition forestière et la configuration spatiale des îlots de trembles en pessière. D'abord, le principe de complémentarité et un possible effet améliorant du tremble dans ces forêts de 90 ans nous poussent à croire que (1) la croissance radiale d'une épinette noire mature serait meilleure

en présence d'un peuplier faux-tremble voisin que d'une épinette noire voisine. Toutefois, pour ce qui est du peuplier faux-tremble, le principe de complémentarité agirait à l'opposé de l'effet améliorant du tremble et l'effet détériorant de l'épinette noire sur la qualité des sols. Considérant également le regroupement des trembles en îlots dans ces pessières, nous croyons que (2) la croissance radiale d'un peuplier faux-tremble mature serait meilleure en présence d'un peuplier faux-tremble voisin que d'une épinette noire voisine. En intégrant également les gradients de taille et de densité observées dans des voisinages représentatifs des forêts de cette région, il nous est possible de spéculer que (3) la présence de peupliers faux-tremble en pessière dite « pure » ne diminuerait pas le volume total d'épinette noire dans un voisinage. Finalement, pour des voisinages tirés de peuplements équiens matures et bien établis comme ici, nous estimons que (4) ni la distance, ni la position des voisins n'influenceraient la croissance radiale des arbres matures dans ces forêts.

L'estimation des paramètres impliqués dans ces relations est effectuée selon les méthodes de vraisemblance maximale (*maximum likelihood methods*), jugées mieux adaptées à ce type d'analyse (Canham and Uriarte 2006; Uriarte et al. 2004). Ces méthodes, combinées à la théorie de l'information (*information theory*), permettent de tester plusieurs hypothèses simultanément et de les comparer entre-elles (Hobbs and Hilborn 2006; Johnson and Omland 2004). Les hypothèses y sont représentées sous forme de modèles et leurs structures et paramètres ont été choisis de façon à représenter explicitement des processus écologiques reconnus (Hobbs and Hilborn 2006; Hobbs et al. 2006). Ici, cette étape est intégrée, à l'intérieur d'une application informatique, à un algorithme d'optimisation par approximations successives ou « recuit simulé » (*Simulated annealing*), pouvant effectuer un nombre élevé d'itérations et permettant des estimations de paramètres plus précises (Goffe et al. 1994; Kirkpatrick et al. 1983). Cette forme d'optimisation a été choisie parce qu'elle est mieux adaptée à la sélection de modèle telle qu'utilisée ici.

CHAPITRE I

TREE GROWTH RESPONSE TO TREMBLING ASPEN PROXIMITY IN
EASTERN CANADA BLACK SPRUCE-FEATHERMOSS FOREST

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1.1 RÉSUMÉ

En forêt boréale de l'est du Canada, les pessières à mousses sont souvent pourvues de peupliers faux-trembles qui s'y retrouvent parsemés en petits îlots. Ces pessières sont alors aménagées de manière à confirmer leur vocation principale, en tentant de réduire du mieux possible la présence de tremble lors des pratiques d'éclaircies précommerciales. Bien que des études suggèrent qu'à long terme, le peuplier faux-tremble pourrait augmenter le rendement de ces pessières en limitant l'accumulation de matière organique au sol, des inquiétudes persistent quant à son effet compétitif sur la croissance des épinettes à court et moyen termes. Cette étude cherche donc à quantifier et préciser les interactions compétitives entre le peuplier faux-tremble et l'épinette noire en mesurant leurs effets sur la croissance radiale. Ces interactions sont étudiées à l'échelle de l'arbre, de manière à évaluer plus spécifiquement l'importance de l'espèce, la taille, la distance, la position et l'abondance des voisins sur la croissance. Une analyse de compétition est effectuée à partir de la croissance radiale de 373 arbres témoins, répartis sur 122 placettes. Le modèle estime la croissance radiale potentielle maximale et distingue les effets de la compétition pour la lumière de ceux découlant de situations de surnombre. Le meilleur modèle pour l'épinette noire inclut un effet d'ombrage spatialement explicite, mais également un effet de densité indépendant des distances. Celui du tremble exclut quant à lui toutes composantes spatiales mis à part le rayon de voisinage. Les résultats montrent qu'une épinette noire est jusqu'à 4 fois moins affectée par le voisinage d'un tremble que celui d'un congénère de même taille. La dominance des trembles sur les épinettes entraîne cependant certains effets négatifs sur la croissance de ces dernières, particulièrement en tremblaie dite pure. Donc la croissance radiale optimale de l'épinette noire est atteinte en milieu mixte, où les proportions de tremble et d'épinette noire sont équivalentes et où la dominance des trembles est réduite. La croissance des trembles est quant à elle favorisée en tremblaie pure, où les faibles densités lui sont favorables. Les analyses laissent présager la présence d'un certain effet améliorant du tremble sur la croissance des arbres en pessière. En termes de rendement, on observe un effet additif de ces deux essences; c'est-à-dire qu'on peut ajouter jusqu'à 30 % de tremble dans le peuplement sans diminuer le volume total d'épinette noire.

MOTS-CLÉS : Compétition, épinette noire, peuplier faux-tremble, forêt boréale, analyse de voisinage.

12

1.2 ABSTRACT

In North-Eastern Canada, black spruce-feathermoss forests often include trembling aspens grouped in small patches. These forests are usually managed as to confirm their main vocation by thinning trembling aspen in premature stands. However the presence of trembling aspen in black spruce stands could increase their yield through ecological niche separation (i.e. lower interspecific competition) and by improving soil conditions. The objective of this study is to define and quantify black spruce and trembling aspen competitive interactions and their effect on tree growth in mature stands. Their interactions are evaluated at tree-scale in order to determine the role of species, size, distance, position and neighbour abundance on tree growth. The neighbourhood analysis uses radial growth of 373 target trees located over 122 plots. The model estimates maximum potential growth and distinguishes shading effects from those due to crowding. While the best black spruce model includes spatially explicit shading effects, crowding effects appear independent of neighbour distance. In contrast, the best trembling aspen model excludes all spatial components other than neighbourhood radius. Results reveal that a black spruce tree is four times less affected by aspen neighbours than conspecifics of similar size. However trembling aspen dominance over spruce trees has negative effects on black spruce growth, especially within "pure" trembling aspen stands. Thus, optimal black spruce growth is reached in mixed environments with equivalent aspen and black spruce basal area. Conversely, trembling aspen growth is best in pure trembling aspen environments where low tree abundance suits it best. Analyses also suggest the possibility of a positive effect of trembling aspen on tree growth in black spruce forests. In terms of productivity an additive pattern is observed between these species: including up to 30 % trembling aspen in black spruce stands does not reduce total black spruce volume.

KEY WORDS: Competition, black spruce, trembling aspen, boreal forest, neighbourhood analysis

1.3   INTRODUCTION

Traditional forestry tends to simplify forest composition by favouring regeneration of the most valuable species (Kelty 2006; Nichols et al. 2006; O'Hara et al. 1994). In North-Eastern Canada, black spruce stands often include trembling aspen stems grouped in small patches. Despite the fact that these species naturally coexist in this region (Chen and Popadiouk 2002; Lecomte and Bergeron 2005), These forests are generally managed to favour spruce by removing the aspen component as much as possible in precommercial stands. However aspen could play an important ecological role in these stands and its decline could reduce black spruce yield (Légaré et al. 2004) and long-term forest productivity (Fenton et al. 2005; Légaré et al. 2005b; Simard et al. 2007).

Considering architectural differences between aspen and black spruce in crown height & length and root system depth (Gale and Grigal 1987; Perala 1990; Strong and La Roi 1983; Viereck and Johnston 1990), such variations in species' traits might lead to resource-use complementarity and improved yield compared to monospecific stands (Kelty 1992; Loreau 1998). In the boreal forest, black spruce litter is relatively resistant to decomposition (Prescott et al. 2000) and over the long term, forested peatlands can develop on flat topography (Crawford et al. 2003; Payette and Rochefort 2001), reducing stand productivity (Simard et al. 2007; Van Cleve and Viereck 1981). In such conditions, the presence of trembling aspen could increase soil organic matter (SOM) decomposition and nutrient cycling (Connell and Slatyer 1977; Paré and Bergeron 1996) and reduce or delay deterioration of growth conditions by sphagnum (Payette and Rochefort 2001). It has been suggested that this potential effect of trembling aspen could increase both black spruce and trembling aspen growth.

Both resource-use complementarity and improvement of soil condition could influence black spruce/aspen interactions but previous growth analysis on this subject were blurred by the great variability of abiotic factors and neighbourhood context between sites within

14

mixed stands (Burton 1993; Légaré et al. 2005a; Loreau 1998; Newton and Jolliffe 1998; Rothe and Binkley 2001). Since competition occurs among individual trees, integrating local variables could considerably reduce uncertainty and more accurately illustrate competition dynamics (Grimm and Railsback 2005; Stoll and Weiner 2000). The use of individual-scale analysis has increased considerably with improvements in computing power (Grimm and Railsback 2005). It allows greater precision in measures of local phenomena such as competitive interactions.

The objective of this study is to explore the effects of competitive interactions between black spruce and trembling aspen on tree growth in unmanaged, mature black spruce-feathermoss forests of Western Quebec. In studying mature forests, we are interested in the cumulative interaction effect between these species, not its development over time. This study focuses on black spruce, the most valuable commercial species in this region. However, interest in trembling aspen has risen over recent years and its dynamics were also considered. Analyses explore several hypotheses concerning different characteristics of these stands, i.e. forest composition and spatial heterogeneity issues. Considering complementarity between the two species and a possible improvement effect of trembling aspen in these 90 years-old forests, we speculate that (1) black spruce radial growth improves in the presence of a trembling aspen neighbour compared to a black spruce neighbour. For trembling aspen however, complementarity effects act oppositely to black spruce soil deterioration effect and aspen improvement effect. This situation, coupled with the fact that aspen trees gather in small groups, raises the hypothesis that (2) trembling aspen radial growth improves in the presence of an aspen neighbour relatively to a black spruce neighbour. At stand level, only the consideration of different densities and tree sizes observed in representative neighbourhoods of these forests allows to draw conclusions regarding the yield of the BS/TA mixture. Using this approach, we expect that (3) the presence of trembling aspen in near pure black spruce stands does not reduce total black spruce volume in a neighbourhood. Finally, in a context of even-aged, mature stands as

those sampled here, we anticipate that within neighbourhood limits (4) neither distance between trees and neighbour position influence the radial growth of mature trees.

1.4   METHODOLOGY

1.4.1   Study area

The area is situated in North-Western Quebec, in the North-Eastern Canadian boreal forest. Sites were located between 78°41'W and 79°9'W longitude and 48°57'N and 49°15'N latitude, covering an area of 1160 km². This region lies within western Quebec black spruce-feathermoss forest domain and extends over the clay belt of North-Eastern Ontario and North-Western Quebec. This deposit was created by clay and silt sedimentation in lakes Barlow and Ojibway during the last glaciation (Vincent and Hardy 1977) and is known for its relatively rich but often poorly drained soils. In the absence of disturbance, SOM accumulates with time, creating favourable conditions for sphagnum growth and paludification (Fenton et al. 2005).

The study region has one of the driest climate in the commercial forest of Quebec (Robitaille and Saucier 1998) and is characterized by total annual precipitation of about 857 mm and a mean annual temperature of 0.8 °C based on the meteorological station of La Sarre (Environnement-Canada 1993). Mean stand age in the region, based on time since fire studies, is 139 years and local fire regime was characterized by large wildfires and a fire cycle of 146 years between 1850 and 1920 and by a longer fire cycle since then (326 years) (Bergeron et al. 2001).

16

1.4.2   Sampling design

A total of 122 neighbourhoods were selected and distributed among 49 forest stands. From those, 23 were conifer-dominated stands (more than 75 % of forest cover in coniferous species), 21 were mixed stands (from 25% to 75% of forest cover in coniferous species), and 5 were hardwood-dominated (more than 75 % of forest cover in hardwood species). Hardwood-dominated stands are scarce in this region characterized by black spruce-feathermoss forests, but near-pure trembling aspen patches also occur within mixed stands, where most of the hardwood-dominated neighbourhoods in this study were sampled. Average stand size is 18.3 ha and plots were separated by a minimum of 50 meters (center to center). This distance was sufficient to set plots in separate trembling aspen clusters within the black spruce forest matrix. Mean plot radius was 11 m (area = 427 m²) and plot size decreased with forest density to reduce sampling effort (Table 1.1). Plot radius was set higher than Lorimer's influence radius calculation, which is equal to 3.5 times a target tree crown radius in hardwood forests (Lorimer 1983), in order to test for this value. According to this calculation, mean influence radius would be 10.0 m for trembling aspen and 4.8 m for black spruce. Finally, DBH was measured on all merchantable size stems (9 cm dbh or more), species were identified and coordinates from plot center were taken for all trees within plot radius. Measures of crown geometry were extrapolated from DBH using allometric relationships (Lambert et al. 2005; Poulin and Messier 2006).

Table 1.1 :   Summary statistics of inventory plots

	Min	Mean	Max
Stand size (ha)	2.2	18.3	53.0
No. plots / stand	1	4.9	14
Plot radius and area (m²)	9 (255)	11 (427)	16 (804)
Plot basal area (m²/ha)	30.3	46.2	68.7

Plots contained on average 3 target trees located at a mean distance of 1.4 m from plot center. Targets (n=373) were mostly black spruce (n=239) to focus on the most valuable species, but aspen targets (n=134) were also selected. Attention was given to enlarge target size gradient as much as possible over merchantable size (9 cm). For each target tree, 2 cores were extracted in order to assess current growth. Radial increment was measured for the last 5 years (2001 through 2006). Going back further in time increased the risks of having different neighbourhood configurations than what was actually measured. As sampling was restrained to these mature stands, it overlooks competitive interactions occurring during active self-thinning phase, which essentially occurs at younger development stages; however, the main objective was to assess cumulative effects of trembling aspen and black spruce interactions in unmanaged forests, not necessarily stand development over time.

Soil organic matter (SOM) is both a cause and an effect in terms of productivity (Grigal and Vance 2000; Prescott et al. 2000; Simard et al. 2007; Van Cleve et al. 1983) and in this region, the presence of trembling aspen has often been associated with low SOM depth (Fenton et al. 2005; Légaré et al. 2005b; Paré and Bergeron 1996). Sampled forest patches are located on productive sites of 90-100 years old originating from wildfires (Bergeron et al. 2004), with generally low SOM levels. SOM depth varies from 3 to 12 cm in selected neighbourhoods. To insure uniformity in initial site conditions, other abiotic soil properties were maintained similar between sites: soil type and texture (heavy clay deposit), slope (< 10 %), and drainage (moderately to near imperfectly drained). The fact that pure black spruce plots remain close to mixed-species plots also helped homogenize site condition. Hence, no site quality variables were included in the growth models.

Since the different hypotheses are concerned with merchantable, mature forests, sampling was restricted to specific forest patch characteristics concerning age, composition, origin, and stem abundance. Sampled stands were 90-100 years old and originated from wildfires that occurred around 1910 (Bergeron et al. 2004). Neighbourhood canopy was generally

18

closed (> 60% of closure) and basal area ranged from 30.3 to 68.7 m²/ha (1.1). In terms of species composition, representation of species other than black spruce or trembling aspen was minimized (max. 25 % of total basal area). Moreover, sampling was conducted along a canopy composition gradient from pure black spruce to pure trembling aspen forest patches (0 to 94 % of total plot basal area in trembling aspen). Target trees were distributed throughout various contexts: vertical dominance (suppressed to dominant) and proximity to closest aspen (0.5 m to 9 m). To limit external effects, a 10 m buffer zone of similar forest conditions was respected outside plot limit. Forest patches that had been disturbed locally in the last two or more years were avoided for sampling. This relative uniformity in stand conditions also reduced the risk of influence by site quality differences (Harper 1977; Légaré et al. 2005a; Légaré et al. 2004).

1.4.3   Tree growth and competition models

The simple set of models presented here is derived from previous studies that have shown its efficacy, parsimony and ecological relevance for different forest ecosystems (Canham et al. 2004; Papaik and Canham 2006). This spatially-explicit individual-based model analyzes competition effects of neighbouring trees on trembling aspen and black spruce radial growth. Specifically, the roles of neighbour abundance, species, tree size, distance, and location as well as their interplay are evaluated in terms of overall competitive effects. While a tree-scale approach has never been used in these forests, it should improve the evaluation of the effect of local factors (vertical dominance, tree location and size) on tree growth.

The full model is partitioned in two distinct parts: non-spatial and spatial components (Figure 1.1). The non-spatial component estimates growth for individual trees as a function of maximum potential growth estimation of a free-standing tree (without neighbours). The spatially-explicit component partition competition effects into the shading effect related to sunlight interception by surrounding canopy and the residual effect of crowding from

neighbouring trees. The crowding model reflects both below-ground competition and above-ground inhibition of crown development. Though it addresses specifically tree abundance-related effects, the crowding model may also indirectly include some shading effects, since large and close trees will inevitably cast more shade than small or distant ones. However, the shading model being the only one using specific x,y,z coordinates of tree crowns, shading effects should mostly be dealt through that model. Hypotheses are essentially addressed through specific parameters (which are indicated in figure 1.1), but the whole model's behaviour also provides insights to discuss on the different hypotheses.
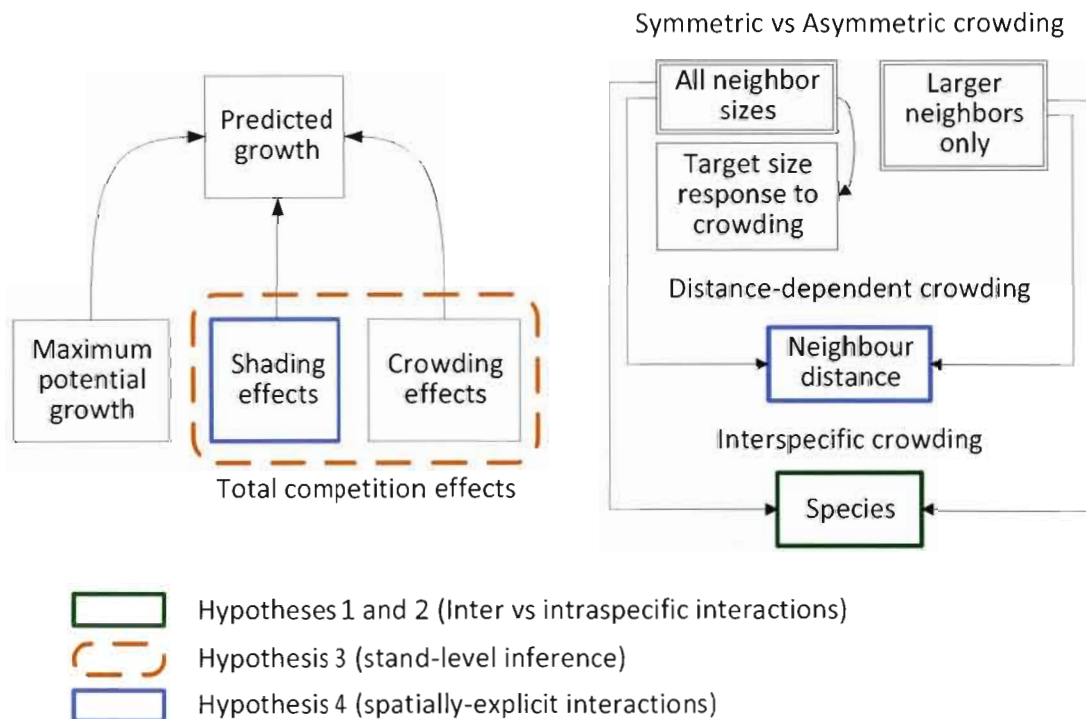
Figure 1.1 : Model structure and hypotheses.

20

The full model is expressed in equation 1-1. Predicted radial growth (RG) and MaxRG (average maximum potential radial growth of target species) are expressed in mm/year whereas other effects are simply expressed as inflation factors varying between 0 and 1. An effect with a value of 1 does not affect growth at all, whereas a value inferior to 1 indicates a decrease in tree growth due to competition.

$$RG(mm/yr) = maxRG(mm/yr) \times \text{shading effect} \times \text{crowding effect}$$

Équation 1.1 :   Full model

1.4.3.1   Potential growth estimation

The average maximum potential radial growth (parameter MaxRG) refers to the growth capacity of a tree as a function of its size and species. It is estimated through a method that extrapolates growth of the best growing trees in a competition-free situation using competitive effects estimation.

1.4.3.2   Spatially-explicit analysis of tree competition

Major determinants of neighbourhood competition are usually neighbour abundance, species, distance, position and size (dbh, height, crown shape) (Larson 1992). Neighbourhood effective radius, the maximum distance at which a neighbour influences growth of a focal tree, is also important in neighbourhood analyses (Burton 1993) and is estimated simultaneously with other parameters. A decay parameter (R) estimates competitive effects decay over that radius. First used by Canham et al. (2004), this method represents an advance over previous neighbourhood studies where effective radius was fixed arbitrarily or decay rate assumed (Burton 1993; Canham and Uriarte 2006; Silander and Pacala 1985; Simard and Sachs 2004).

1.4.3.2.1 Shading effect modeling

As part of hypothesis 4, the shading model integrates over the specific location of neighbours in order to address the spatial dynamics between black spruce and trembling aspen. Shading is distinguished from crowding in the sense that its competition effect is anisotropic around the target tree, conferring all effects to trees located between the target and direct sunlight. Crowding effects are isotropic and remain constant independently of neighbour's angle. The x,y,z tree crown coordinates distinguish the shading model from the crowding model, though both models incorporate common information. The shading model also incorporates size and species of target and neighbour trees through tree crowns representation. Shading effect modeling relies on data sampled in previous studies describing light availability in the canopy (Canham et al. 1999; Canham et al. 2004) and on tree allometry (tree height, crown height and crown width for each species) (Lambert et al. 2005; Poulin and Messier 2006). Aspen and black spruce allometry parameters were previously estimated for the Duparquet area (Poulin and Messier 2006) and from external data (Lambert et al. 2005; Ouellet 1983), respectively.

$$Shading\ effect = exp[-m \cdot \%\ shade]$$

Équation 1.2 :   Shading effect

Where m is a scaling parameter and *% shade* is the proportion of sky area blocked by neighbouring crowns. Shading effect calculated here depends solely on target crown exposition, which is itself determined by neighbouring crowns interference, sun declination at this latitude, amount of growing days and by a cloudiness index. Crown exposition depends on sky area blocked by neighbouring crowns. Sky is represented as an array of 360 cells wide and 90 cells high, each of which is considered either open or blocked to incident light. The simple model represents crowns as two-dimensional opaque panels which avoid the use of expansive and time-consuming GLI (Gap Light Index) data collection which determines species-specific light transmission coefficients (Canham et al. 2004). There is

22

evidence that understory light availability may be better determined by canopy structure and the neighbourhood spatial context than interspecific differences in light transmission through the canopy (Canham et al. 1999). A neighbour crown is considered to be shading a target tree if it is higher than its mid-crown and if it is located between the target and direct sunlight. Vertical dominance is therefore indirectly considered in the shading model.

1.4.3.2.2   Crowding effect modeling

Variables tested within the full crowding model are neighbour species, size, distance and abundance as well as target tree size and species (Equation 1-5). Crowding effect is modulated by a scaling parameter (C) that determines the response of a target tree to the level of neighbourhood competition (Equation 1-4). This index is computed for all trees in a plot, but the optimization algorithm estimates the average distance at which neighbours no longer influence a target tree. This influence radius (R) is not represented in the crowding equation, but it is included in the parameter set for each crowding model run. For i = 1,..., s species and j = 1,..., n neighbors within a radius R, neighborhood crowding index (NCI) on a target tree becomes:

$$Crowding\ effect = exp\left[-C \cdot \left((DBH_t)^\gamma \sum_{i=1}^{s} \sum_{j=1}^{n} \lambda_{ij} \frac{(dbh_{ij})^\alpha}{(dist)^\beta}\right)\right]$$

Équation 1.3 :   Full crowding (NCI) model

The roles of neighbour size and distance are estimated here through their exponent, parameters α and β, which may vary from 0 (no effect) to 4 in order to adjust to field conditions. Parameter α determines how crowding scales to neighbour DBH and β evaluates the decay in the effect of neighbour distance up until neighbourhood radius is reached. As part of hypothesis 4, β addresses the role of neighbour distance in black spruce and trembling aspen interactions. Parameters α, and R are assumed constant for all species of

neighbours to limit total number of parameters. Hypotheses 1 and 2 are addressed through parameter λ, which scales competitive effects depending on neighbour species or functional group. In its complex form, λ is estimated for each neighbour species, but it can also be simplified and estimated for each functional groups or intra/interspecific groups. This parameter is allowed to vary from 0 (no crowding effect generated by a species i) to 1 (maximum crowding effect). Target tree dominance has an important role on tree growth, and although this issue is addressed by the shading model in terms of light availability, there are also advantages to tree dominance in terms of soil resources. Most studies have observed an inversely proportional relationship between target tree size and competitive effects (Canham et al. 2006; Hegyi 1974; Papaik and Canham 2006; Thomas and Weiner 1989). However, as density of black spruce stems can be high, neighbouring aspens may be sensitive to such abundance, regardless of their size advantage. The full model is flexible in this respect and allows both patterns to be tested; by adding an exponent (γ) to the DBH of the target tree, we allow target tree sensitivity to adjust to species and field conditions (Canham et al. 2004; Canham et al. 2006; Papaik and Canham 2006). This parameter ranges from -2 to 2, determining whether bigger trees are more sensitive to crowding ($y > 0$), less sensitive ($y < 0$) or equally sensitive than smaller trees ($y \approx 0$).

Asymmetric competition

As opposed to the full crowding model where competition is symmetric and trees smaller than the target tree may still generate competitive effects, the asymmetric model only considers neighbour trees larger than the target. The magnitude of the effect is not proportional to absolute neighbour size but to the difference in size between the target and its neighbour. This nested submodel also analyzes target tree dominance indirectly through target tree and neighbour size difference. Neighbourhood abundance is thus significantly reduced since many neighbouring trees can be smaller than the target tree. Consequently, parameters C (Equation 1-4) and α adjust to this different context.

$$NCI = \sum_{i=1}^{s} \sum_{j=1}^{n} \lambda_{ij} \frac{\left(dbh_{ij} - dbh_t\right)^{\alpha}}{(dist)^{\beta}}$$

Équation 1.4 :   Asymmetric crowding model

Alternate models were formed by using either eq. 1-4 or 1-6 structures that represent non-nested models (different NCI calculations), by eliminating models or by forming nested models by dropping variables and/or parameters whose presence did not provide any additional information to the model.

1.4.4   Model selection and evaluation

In order to determine the best model, alternate models were compared using model selection procedure as a form of hypothesis testing, based on information theory and the use of the Akaike Information Criterion (AIC). AIC determines the best model based on maximum likelihood and parsimony (Burnham and Anderson 2002; Johnson and Omland 2004). Likelihood methods are a more comprehensive and flexible approach that allows comparison of multiple hypothesis (Burnham and Anderson 2002; Canham and Uriarte 2006). Parameter values were chosen according to their maximum likelihood using simulated annealing, a global optimization algorithm (Goffe et al. 1994). This was done using an application created with Delphi version 6 for Windows (Borland Software 2000).

The fit of alternate models was assessed using two metrics. Bias was measured using the slope of the regression of observed radial growth on predicted radial growth, an unbiased model having a slope of 1. Pseudo R^2 calculated regression between the observed and predicted values as a measure of goodness-of-fit. Alternate models were compared using the corrected Akaike information criterion (AIC_c) for small sample size (Burnham and Anderson 2002). Even if sample size is large enough, it is recommended to use AIC_c systematically (Anderson 2008). The best model and most parsimonious is the one with the

lowest AIC_c score. Strength of evidence for individual parameter estimates is measured with asymptotic two-unit support intervals (Edwards 1992). It is similar to a 95% support limit defined using a likelihood ratio test (Hilborn and Mangel 1997).

To reduce parameter estimate bias, we used multi-model inference (MMI) instead of best model inference (BMI) (Burnham and Anderson 2002). It uses Akaike weights (ω_i), derived from the differences between AIC_c values to evaluate strength of empirical support for the competing models:

$$E(\hat{y}) = \sum_{i=1}^{R} \left(\frac{e^{-0.5 \cdot \Delta_i}}{\sum_{r=1}^{R} e^{-0.5 \cdot \Delta_r}} \right) \cdot E(y_i)$$

Équation 1.5 :   Parameter averaging using Akaike weight

Where Δ_i is ΔAIC_c between the best model and the ith model, R is the number of models used in the analysis, $E(\hat{y})$ is the averaged parameter estimate, and $E(y_i)$ is the best model parameter estimate (Burnham and Anderson 2002). Akaike weight represents the expected probability of model i being selected best with repeated sampling of the same population. MMI is especially recommended when support for the best model (ω_{best}) < 0.9, which means it has less than 90 % chance of actually being the best model and that there is clearly no model superior to others (Burnham and Anderson 2002). When a parameter is absent in some models of a prediction set, they are attributed a neutral value (often 0), which is then included in the averaging computation.

1.4.5   Stand-level considerations

In order to address hypothesis 3 which deals with black spruce yield at stand scale, parameter estimates obtained at tree scale were used to model tree growth along a forest composition gradient. Average tree growth predictions were made using regression models

26

that describe the distribution of average tree size and abundance according to neighbourhood species composition gradient. Based on allometric equations, tree height was estimated from DBH data (Poulin and Messier 2006) and volume of trembling aspen, black spruce and total neighbourhood could also be estimated for different forest composition using Smalian's formula. Since these analyses rely on field measurements, it provides interesting insights into growth dynamics between trembling aspen and black spruce in these stands.

1.5 RESULTS

1.5.1 Range of conditions covered by sample set

The data set covers a variety of neighbourhood contexts in terms of tree abundance, tree size, species composition and spatial configuration that allow estimating growth throughout a wide range of conditions (Table 1.2). An important characteristic of sampled trembling aspen patches is that tree abundance decreases and mean tree size increases for both species as proportion of trembling aspen increases (Figure A.4). This variation makes competitive conditions vary greatly between trembling aspen patches, but the different gradients are covered by the data set (Table 1.2).

Mean radial growth for trembling aspen is 0.79 ± 0.02 mm/year and 0.48 ± 0.01 mm/year for black spruce (with 95 % confidence interval). Trembling aspen trees within the study area experienced a severe forest tent caterpillar outbreak in 2001 (Cooke and Lorenzetti 2006), with a possible aftereffect during the following summer (2002) (F. Lorenzetti, personal communication) (Figure A.6). The bias induced by the outbreak made it difficult to use the last 5 years of growth. Both aspen and black spruce growth were modified since their dynamics are related in these mixed forest patches. As a result, only the last 3 years of growth were used (2003-2005) for modeling.

The entire gradients of vertical dominance and shade conditions were covered within the data set, as calculated by the light model. Mean shade % (with 95 % confidence interval) for trembling aspen ranges from 12.9 ± 6.4 % to 39.4 ± 6.7 % in black spruce and in aspen dominated neighbourhoods, respectively. For black spruce target trees, mean shade % ranges from 37.8 ± 4.4 % to 66.4 ± 4.7 % in black spruce and in aspen dominated neighbourhoods, respectively.

Table 1.2 :   Summary statistics of sampled neighbourhoods

Trembling aspen neighbourhoods

Neighbour species	Neighbour abundance			DBH (cm)			Closest neighbour dist. (m)	
	TA	BS	All	TA	BS	All	TA	BS
Min	1	3	16.0	7.5	7.0	7.0	0.3	0.2
mean	*15.9*	*34.7*	*52.9*	*24.4*	*15.2*	*19.5*	*2.2*	*2.1*
Max	39	130	133.0	54.0	30.6	54	10.0	8.0
Spruce stands*	8.6	77.8	88.1	16.2	13.8	14.1	3.2	1.1
Mixed Stands*	16.7	33.9	53.6	24.1	15.5	18.7	2.1	1.7
Aspen stands*	18.6	10.2	30.7	29.5	15.4	24.1	1.9	3.2
Average	52.9			19.5			2.1	

Black spruce neighbourhoods

Neighbour species	Neighbour abundance			DBH (cm)			Closest neighbour dist. (m)	
	TA	BS	All	TA	BS	All	TA	BS
Min	1.0	1.0	10.0	7.1	6.8	6.8	0.2	0.1
mean	*9.0*	*37.6*	*48.1*	*21.9*	*14.8*	*17.1*	*3.1*	*1.6*
Max	29.0	103.0	106.0	52.0	30.6	30.6	8.5	7.5
Spruce stands*	5.1	52.5	59.4	19.2	14.5	14.9	4.0	1.2
Mixed stands*	12.1	27.0	40.8	23.1	15.2	17.9	2.3	1.7
Aspen stands*	14.4	7.8	23.1	28.9	14.9	23.9	2.1	3.5
Average	48.1			17.1			2.3	

Notes: These numbers were computed for mean neighbourhood radius of 8.7 m for black spruce and 10.6 m for trembling aspen (see table 1.6). TA stands for trembling aspen and BS for black spruce. *For a stand to be classified as pure black spruce, provincial forest regulation (and the present study) allows a presence of trembling aspen < 25 % of total stand basal, between 25 and 75 % of aspen for mixed BS/TA stands, and ≥ 75 % in aspen for trembling aspen stands.

Table 1.3 :   Trembling aspen statistics for asymmetric crowding model

Neighbour species	No. larger neighbors[1]		Extra DBH (cm)[1]	
	TA	BS	TA	BS
Min	0.0	0.0	0.1	0.1
Mean	*9.1*	*3.3*	*6.0*	*2.1*
Max	22.0	50.0	17.4	6.0
Spruce stands[2]	4.7	15.1	4.3	1.8
Mixed stands[2]	8.1	7.9	6.6	2.5
Aspen stands[2]	10.1	1.5	5.8	1.2
Average	12.7		5.2	

Notes: These numbers were computed for mean neighbourhood radius of 10.6 m for trembling aspen (see table 1.6). TA stands for trembling aspen and BS for black spruce neighbours. [1] Number of larger neighbours and extra DBH refer to the asymmetric crowding model which ignores same size and smaller trees to consider only neighbours larger than the target tree (in DBH terms). According to the analyses, this model works only for trembling aspen so these data for black spruce are not presented here. [2] For a stand to be classified as pure black spruce, provincial forest regulation (and the present study) allows a presence of trembling aspen < 25 % of total stand basal, between 25 and 75 % of aspen for mixed BS/TA stands, and ≥ 75 % in aspen for trembling aspen stands.

Soil organic matter (SOM) depth was not intended to form a gradient in this study, but rather a constant, in order to put a focus on the effects of forest composition on tree growth. SOM depth for these productive sites remains relatively low for boreal forest soils (3-12 cm in this sample set). However, despite similar origin and abiotic site conditions, there is still a negative correlation between SOM depth and trembling aspen presence in the canopy for these productive sites (Figure 1.2). This has been observed before in the same area (Fenton et al. 2005; Légaré et al. 2005b).
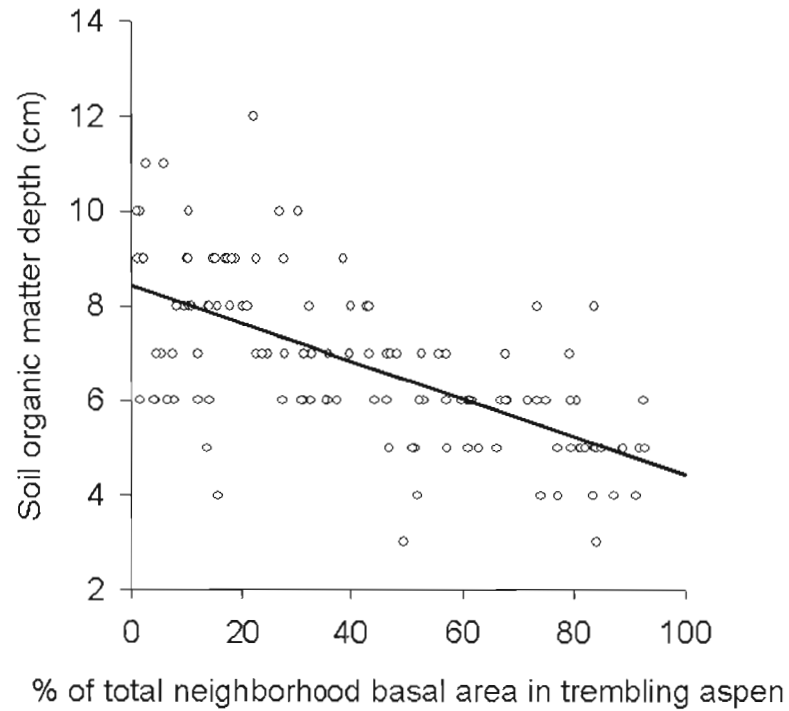
Figure 1.2 :   **Soil organic matter depth distribution along neighbourhood mixture gradient**

<u>Notes</u>: Regression is significant ($P < 0.0001$), equation is $y = 8.44 - 0.04x$, and $R^2 = 0.41$.

1.5.2   Spatial analysis of tree growth

All models give unbiased estimates of growth with a 1:1 relationship of observed over predicted radial growth with intercepts of 0 and best models R^2 were 0.41 for trembling aspen and 0.42 for black spruce (Table 1.4).

Table 1.4 :   Comparison of alternate models using AIC_C

Alternate models		Eq.	Trembling aspen (n=134)				Black spruce (n=239)			
			n/k (k)*	ΔAIC_C	R^2		n/k (k)*	ΔAIC_C	R^2	
Crowding + Shading**			12.2 (11)	16.6	0.39		21.7 (11)	2.5	0.42	✓
Shading only		3	44.7 (4)	73.8	0.04		59.8 (4)	81.3	0.24	
Crowding only**		5	13.4 (10)	14.5	0.39	✓	23.9 (10)	4.7	0.41	
NCI	Asymmetric competition	6	14.9 (9)	2.9	0.42	✓	23.9 (10)	7.1	0.41	
	Target size - independent	7	14.9 (9)	73.9	0.08		23.9 (10)	47.1	0.36	
	Equivalent competitor	8	19.1 (7)	1.2	0.39	✓	26.6 (9)	19.0	0.40	
	Distance - independent	9	**22.3 (6)**	-	**0.41**	✓	**23.9 (10)**	-	**0.42**	✓

Notes: Starting from the full model (Shading + full NCI), submodels are retained for subsequent analyses (marked with a check) if they improve AIC. * n/k stands for the number of data points (n) per parameter (k). A model's reliability improves as this ratio increases. ** Full NCI include species competition index with intra/interspecific groupings. Results in bold represents selected best model.

As explained in the methodology the use of BMI is recommended when support for the best model (ω_{best}) > 0.9. Since neither trembling aspen (ω_{best} = 0.48) nor black spruce (ω_{best} = 0.57) best model has such support, MMI was used to reduce parameter estimate bias (Table 1.5). Nevertheless, MMI parameter values appear consistent with BMI's for both species, increasing our confidence that best models describe accurately the ecological dynamics in these stands.

Table 1.5 : Models included in the prediction set (support based on the relative weight of evidence)

Species	ω_{best}	$\Sigma\omega_i$	N(n)[a]	DBH$_{neighbour}$[b]		Competition model[c]			Shade	Distance	
				Sym.	Asym.	Full	Inter	Equiv		Yes	No
Trembling aspen	0.48	0.99	4 (4)	-	0.99	0.13	0.11	0.76	-	0.52	0.48
Black spruce	0.57	0.90	6 (2)	0.81	0.09	0.17	0.73	-	0.73	0.33	0.57

Notes: ω_{best} represents the support for the best model and $\Sigma\omega_i$ the total support for the whole prediction set (for which $\Sigma\omega_i > 0.9$). [a] N indicates the number of models in the prediction set and n, the number of models for which $\omega > 0.1$. [b] The competition model may consider neighbour DBH (absolute; symmetric competition model) or simply the difference in DBH between the target tree and its neighbours (relative; asymmetric competition model). [c] Competition model stands for the species-specific competition index, whether it considers all species as equivalent competitors (Equiv.), intraspecific and interspecific competition (Inter.) or Trembling aspen, Black spruce and other species separately (Full).

Table 1.6 :   Parameter estimates and support intervals from the AIC$_c$ best model inference (BMI) and multi-model inference (MMI)

Parameters*		Trembling aspen			Black spruce		
		BMI		MMI	BMI		MMI
1	MaxRG	1.21	(1.20, 1.23)	1.25	0.99	(0.98, 1.00)	0.94
2	M		-	-	0.35	(0.34, 0.36)	0.25
3	C	0.21	(0.11, 0.31)	0.25	0.28	(0.18, 0.38)	0.30
4	A	0.42	(0.41, 0.42)	0.33	3.99	(3.95, 4.03)	3.96
5	B		-	0.21		-	0.01
6	γ		-	-	-2.25	(-2.28, -2.23)	-2.22
7	R (m)	8.9	(8.8, 8.9)	10.6	8.7	(8.6, 8.8)	8.7
8	λ_{aspen}		-	0.95	0.19	(0.19, 0.20)	0.21
9	$\lambda_{black\ spruce}$		-	0.86	1.00	(0.99, 1.00)	1.00
10	λ_{others}		-	0.95	0.19	(0.19, 0.20)	0.28

Notes: Support intervals are similar to 95% support limit using a likelihood ratio test and represent the range of parameter values that result in less than a two-unit difference in AIC$_c$ (Edwards 1992). Multi-model inference averages parameter estimates over all prediction set, i.e. 4 different models for trembling aspen and 6 for black spruce (Table 1.5). Some parameters may be absent in the best model but still get MMI estimates since they were present in at least one model in the prediction set. In such cases, it is considered that this parameter has a null value when averaging with other models (Anderson 2008). * See text for details on parameters.

1.5.2.1 Effect of neighbourhood shading and crowding on tree growth

1.5.2.1.1 Shading effects

Shading effect appears only important on black spruce targets, as black spruce best model includes the shading submodel (Table 1.4) and support for shading in the prediction set is important ($\omega_{Shading} = 0.73$) (Table 1.5). Hence, this suggests tree position might bring some information to the model. However, the magnitude of the best model's shading parameter m remains low (0.35) and averaged estimate using MMI even lower (0.25), indicating a limited influence. Furthermore, an analysis made from data with interchanged x,y coordinates on black spruce's best model does not perform much worse than an analysis that uses the right coordinates ($\Delta AIC_c=3.8$, $R^2=0.42$). R^2 and AIC_c score for the black spruce shading only model are the worst of all tested models, meaning it might not provide as much information to the analysis as the crowding model does. This pattern does not occur for trembling aspen targets as all models in the prediction set ignore shading (Table 1.5). The shading model used alone poorly fits the data; moreover, it does not improve the performance of the crowding model (Table 1.4). In fact, crowding only models for both species effectively fit the data (Figure 1.3) and there is overwhelming support for an absence of shading effects on trembling aspen trees ($\omega_{no\ Shading} = 0.99$) and some support on black spruce trees ($\omega_{no\ Shading} = 0.17$).
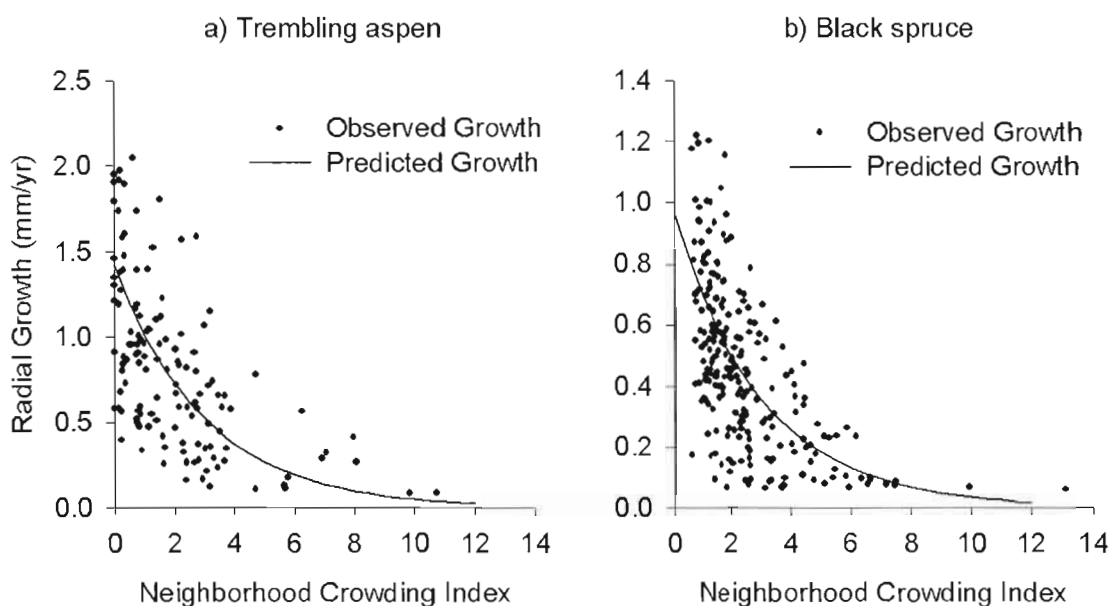
Figure 1.3 : **Distribution of observed growth with neighbourhood competition index (NCI) using a) trembling aspen best model and b) black spruce best crowding only model**

Notes: Predicted over observed regression R^2 are 0.41 and 0.42 for aspen and black spruce maximum likelihood NCI only models, respectively. Included submodels within the NCI model are indicated in Table 1.4.

1.5.2.1.2   Effects of neighbouring tree size and distance

Neighbour size appear not to have much influence for trembling aspen when looking at the high ΔAIC_c and low R^2 values of target size-independent model (Table 1.4). However, when coupled or relativized with target tree size within the best model, neighbour DBH becomes very influent. Similarly, neighbour size importance on black spruce targets declines due to a high α estimate (α_{BMI} = 3.99, α_{MMI} = 3.96) (Table 1.6). Contrasting α values between the two species is due to their different model structure, as trembling aspen model places more importance on fewer larger neighbours (α_{BMI} = 0.42, α_{MMI} = 0.33) (asymmetric competition model) than black spruce model that considers all neighbour trees (competitive response model).

Neither trembling aspen nor black spruce's best model included neighbour distance (Table 1.4). As we stated in hypothesis 4, inter-tree distances should not influence competitive effects within neighbourhood limits and actually, even if there is still good support in the prediction set for distant-dependent NCI models for both trembling aspen (ω_{dist} = 0.52) and black spruce (ω_{dist} = 0.33) (Table 1.5), low β_{MMI} estimates indicate a limited if not absent effect of neighbour distance (β_{TA} = 0.21, β_{BS} = 0.01).

The analysis allows estimating average effective neighbourhood radius, which reaches up to 8.7 m for black spruce and 8.9 m for trembling aspen according to best model inference (Table 1.6). Over that critical distance, neighbours are no longer expected to generate any competition effect on a black spruce tree. However, though MMI and BMI estimates are similar for black spruce, MMI estimate for trembling aspen targets suggests that this influence radius is probably larger than what the best model infers (R_{MMI} = 10.6 m). Influence radius for both species appear larger than previous analyses done in this region

1.5.2.1.3 Relative magnitude of interspecific and intraspecific crowding

According to best model inference, only black spruce distinguishes different neighbouring species; dropping species parameter λ greatly increased black spruce AIC_C (+16.5 units) whereas trembling aspen's was reduced (-1.7 units) (Table 1.4). There is a considerable difference in species-specific competition index between aspen and black spruce neighbours (Table 1.6); effect of conspecifics on black spruce is maximal in the best model ($\lambda_{black\ spruce}$ = 1.00) and more than five times greater than that of heterospecifics' ($\lambda_{aspen/others}$ = 0.19). Averaged parameter estimates using MMI corroborate this pattern and reveal strong evidence in favor of a positive influence of trembling aspen, intraspecific competition being nearly five times stronger than interspecific competition (0.21 for λ_{aspen} > 1.00 for $\lambda_{black\ spruce}$). There is large support that this distinction is made at the intraspecific/interspecific level (ω_{inter} = 0.73), and little evidence (ω_{Full} = 0.17) that black spruce distinguishes competition from conspecifics, trembling aspen and other poorly represented species.

Other species include mainly Jack pine and averaged estimate leans toward jack pine competition effect being slightly stronger than that of aspen ($\lambda_{other\ species}$ = 0.28).

The trembling aspen best model appears indifferent to species and there is strong support for equivalent competitor model with all models in the set ($\omega_{equiv.}$ = 0.76). There is also some evidence that aspen "perceives" different species ($\omega_{species}$ = 0.24). However, when looking at the different competition indices (Table 1.6), black spruce appears scarcely less competitive ($\lambda_{black\ spruce}$ = 0.86) than aspen (λ_{aspen} = 0.95) or other species (λ_{others} = 0.95).

1.5.2.1.4   Competitive response of target trees to crowding

Competitive response to neighbourhood crowding is evaluated through C (Equation 1-4), γ (Equation 1-5) and asymmetric competition model (Equation 1-6). Target tree size inclusion considerably increased model performance for both species (Table 1.4) and was included in all models in the prediction set (Table 1.5). The asymmetric model suits trembling aspen best ($\omega_{asymmetry}$ = 0.99) while the competitive response works better for black spruce ($\omega_{symmetry}$ = 0.81), the main difference between the two structures being that the asymmetric model ignores trees smaller than target. Trembling aspen would then ignore trees in lower levels of the canopy, i.e. mostly black spruce in this case. Actually, for a given DBH, aspen stems are on average 2.8 meters (s.d. ± 0.7 m) taller than black spruce, based on allometric ratios (Lambert et al. 2005; Ouellet 1983; Poulin and Messier 2006). Knowing black spruce may be exceeded in height by lower DBH stems, black spruce best model is indeed sensitive to lower DBH stems, and competitive effects scale up to neighbour basal area (γ_{BMI} = -2.25, γ_{MMI} = -2.22).

1.5.2.2   Hypothetical average neighbourhoods

In the following analyses, hypothetical neighbourhood contexts are generated in order to illustrate the effect of a single parameter or variable (species, abundance, DBH) on tree growth, all other variables being fixed at average neighbourhood conditions. Stem position

and distance does pay any importance in these neighbourhoods, given calibration results discussed earlier. Even if hypothetical neighbourhoods are inferences based on sampled neighbourhoods, they remain artificial contexts; considering interplay between forest variables in mixed environments, an individual effect would be difficult to distinguish within raw neighbourhood data without controlling for other effects. For comparison purposes between species, effects on tree growth are not measured directly in terms of radial growth but in fraction of potential growth (e.g. a fraction of 0.7 meaning growth is at 70 % of maximum potential growth).

Figure 1.4 illustrates the cumulative effect of inter and intraspecific neighbourhood competition on trembling aspen and black spruce potential growth while controlling for the effect of neighbour and target tree size (equally-sized trees; see notes for calculation details). However, the trembling aspen model structure ignores smaller and equally-sized neighbours; controlling for tree size required using only neighbours larger than targets and their mean additional size relatively to targets' (5.2 cm extra on average for aspen targets; Table 1.3). As foreseen in parameter estimates, trembling aspen growth is barely influenced by neighbourhood species composition (Figure 1.4a). Nevertheless, it is markedly affected by larger neighbour abundance; growth at average neighbour abundance is similarly affected as black spruce growth in pure spruce stands. In opposition, influence of neighbourhood species composition alone is important on black spruce growth as it grows better within trembling aspen patches. These trends increase when considering differences in mean tree abundance between stand types (Figure 1.4b).
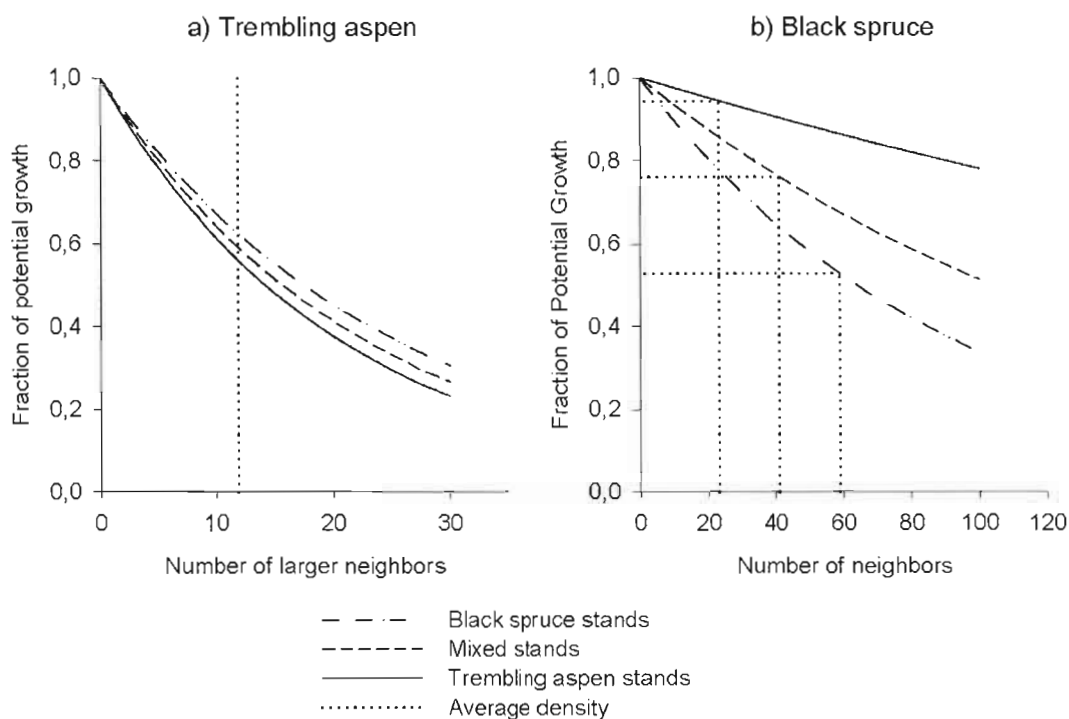
a) Trembling aspen b) Black spruce

Black spruce stands
Mixed stands
Trembling aspen stands
Average density

Figure 1.4 : **Tree species and abundance effect on growth of trembling aspen (a) and black spruce (b) according to averaged parameter estimates (MMI)**

Notes: Fraction of potential growth indicate how much a target trees maximum growth is reduced by competitive effects. Aspen ignores same size and smaller trees; neighbour abundance is measured from trees larger than target (mean of 12.7 larger trees, 5.2 cm larger; Table 1.3). There is little differences in tree abundance between stand types and mean abundance was used for all stand types. Black spruce neighbourhood comprise average-sized trees (17.1 cm) whose mean abundance vary with stand type (black spruce stands: 59.4, mixed stands: 40.8 and trembling aspen stands: 23.1) (Table A.4). Black spruce and trembling aspen stand categories are considered pure and mixed stand has equivalent proportions of both species. Both models used here ignore neighbour location and distance.

One of the main distinctions between trembling aspen and black spruce is their mean size difference (black spruce: 14.4 cm DBH; trembling aspen 23.5 cm DBH) and evaluating overall species effect requires that this size difference be included in the calculation. Figure 1.5 illustrates how species-specific competition strength and size difference combine on an average-sized black spruce target tree. Average-sized black spruce neighbours have a similar

effect as average-sized trembling aspen neighbours but disparity between species increases as neighbours get larger (e.g. 30 cm DBH black spruce neighbour = 0.85 of max. potential growth and 30 cm DBH trembling aspen neighbour = 0.96 of max. potential growth). For both neighbour species, crowding effects due to tree size essentially remain stable until average DBH is reached.
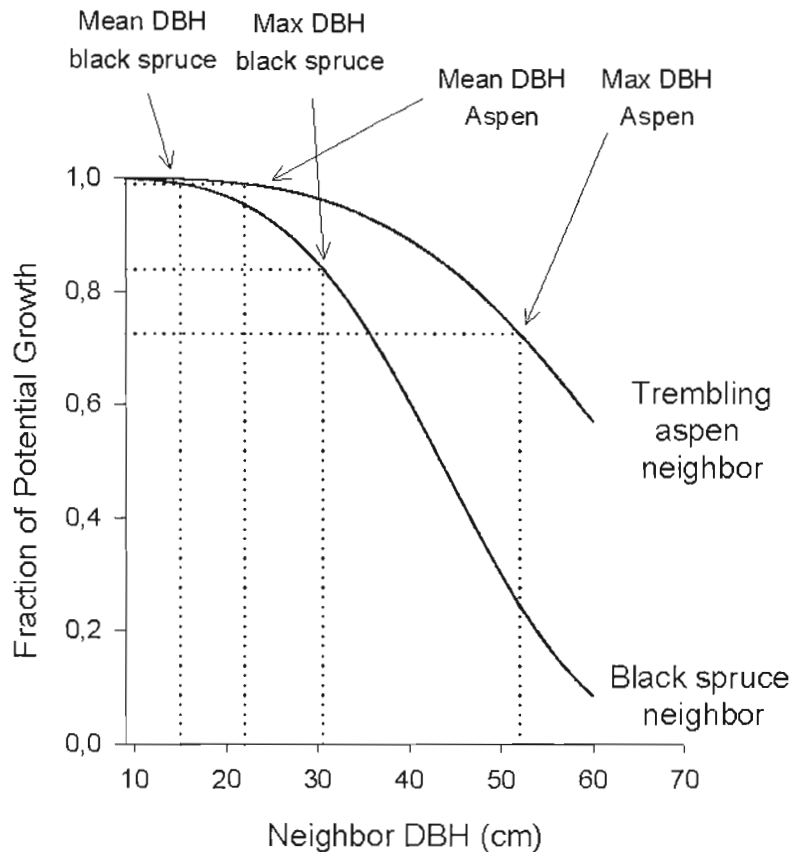
Figure 1.5 :   **Black spruce potential growth variation with neighbour size and species according to averaged parameter estimates (MMI)**

Notes: This figure illustrates the response of an average sized black spruce target (DBH: 14.8 cm) to a black spruce and trembling aspen neighbour tree located anywhere in the neighbourhood of that target. Mean DBH is 21.9 and 14.8 cm, and max DBH is 52.0 and 30.6 cm for aspen and black spruce, respectively (Table 1.2).

1.5.2.3   Stand-level inference

Tree growth relationships with forest composition were assessed using distribution of mean tree size and abundance along the complete forest composition gradient (from pure black spruce to pure trembling aspen neighbourhoods) (Table 1.2, Figure A.4). Despite the fact that average tree abundance and species-related competitive effects decrease in pure aspen forest patches, tree size increases and optimal black spruce radial growth is found at compositions of approximately 60 % trembling aspen (Figure 1.6). A compromise between large neighbours' resource uptake (in hardwood stands) and strong intraspecific competition (in black spruce stands) would then be reached for black spruce in mixedwoods.
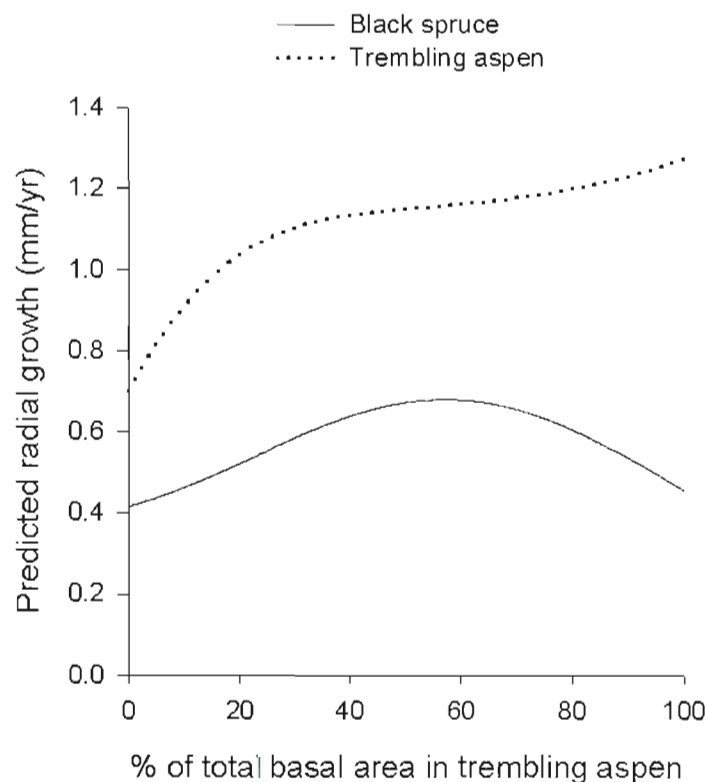
Figure 1.6 :   **Predicted black spruce and trembling aspen radial growth along mixture gradient within an average neighbourhood**

Using observed tree DBH and simulated neighbourhood contexts, the highest total black spruce standing volume is achieved in pure black spruce stands (Figure 1.7). Black spruce volume maintains itself for aspen contents starting from 0 to approximately 25-30 %, with a slight peak in between. Total trembling aspen volume is optimized in pure aspen stands and supports trends observed with growth in mature forests (Fig. 1.6). This supports the additive pattern (Harper 1977) observed by Légaré et al. (2004), where black spruce volume remains stable with an increasing trembling aspen volume in the stand. It also suggests that despite larger black spruce stems found at intermediate aspen proportions, total black spruce volume is reduced due to low tree abundance.

Figure 1.7 : **Total neighbourhood standing volume variation along species mixture gradient**

Notes: Volume measures are based on allometric ratios using observed DBH (see methods section).

1.6   DISCUSSION

1.6.1   Competitive vs. positive effects of trembling aspen presence

Since this analysis does not incorporate soil quality in the model, it is difficult to evaluate precisely the effect of species composition on soil productivity. Nevertheles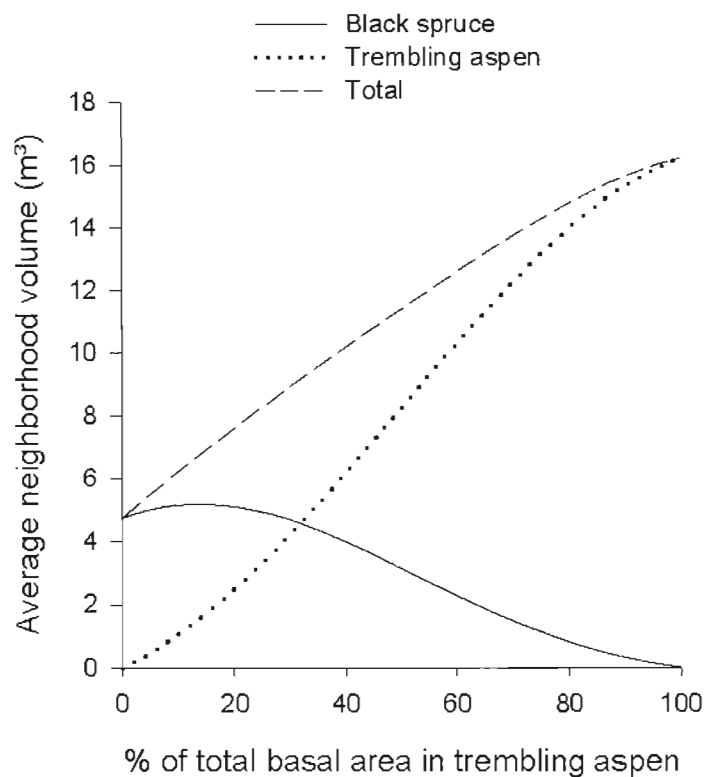s, the negative correlation between SOM depth and aspen content in a stand suggests that trembling aspen accelerates organic matter decomposition. Without this soil factor incorporated in the tree-scale analysis, larger trembling aspen size and growth within pure aspen neighbourhoods is attributed to lower neighbour abundance whereas black spruce improved radial growth appears due to a lower aspen competition index. The fact that trembling aspen best model ignores species difference could mean that, despite niche complementarity with black spruce (as averaged parameters and support for species model tend to show), higher intraspecific competition would be counterbalanced by positive effects of trembling aspen on soil.

The results presented here illustrate that interactions between black spruce and trembling aspen are both competitive and positive at the same time. Still, their competitive interactions are not what we could expect from species that compete for limited resources. Even if it is hard to distinguish niche differentiation effects from trembling aspen positive effects on black spruce growth, the low shading effects of dominant trembling aspen trees measured on sub-canopy black spruce trees argues in favour of niche complementarity with top-canopy trembling aspen. Besides, aspen effect on soil organic matter depth (Figure 1.2) suggests the presence of positive effects on soil decomposition, effects that could easily shift to tree growth improvements (Légaré et al. 2005b). Both phenomenon and the analyses made on black spruce growth in this study supports hypothesis 1 that predicts an improved growth of black spruce in the presence of aspen. Hypothesis 2 was also verified, as trembling aspen growth seems to beneficiate from the presence of conspecifics as well.

Trembling aspen eventually disappears from these stands overtime as forest canopy succession occurs in the absence of major disturbance (Lecomte and Bergeron 2005). Trembling aspen is also more subject to disappear from black spruce stands with time if aspen patch size is relatively small (i.e. less than 200 m diameter) (Laquerre et al. 2010) such as those sampled in this study. Nevertheless, our results from 90 year-old forests suggest that presence of trembling aspen in early succession already favors SOM decomposition. Fenton et al. (2005) have made similar conclusions for older stands as depth generally increases with time since fire. Trembling aspen soil improvement effect might also be more obvious within subsequent cohorts, where SOM accumulation is usually greater (Fenton et al. 2005).

1.6.2 Stand-level considerations

The lower black spruce growth found in trembling aspen stands compared to mixed stands has been previously attributed to higher shading under aspen canopies (Légaré et al. 2004). However, our results indicate that within mature, pure trembling aspen neighbourhoods, shading effects are limited; most black spruce growth reductions would then be due to crowding effects (essentially to large aspen trees increased soil resources uptake). Since tree abundance decreases in trembling aspen stands, magnitude of crowding effects would essentially be related to increased soil resources uptake from large aspen trees found in these stands. Oppositely, trembling aspen growth would be best in pure aspen neighbourhoods where, according to the analysis, their lower tree abundance would be the key factor and not the larger tree size found there. Indeed, black spruce neighbourhoods are where trembling aspen size (and radial growth) is the smallest and consequently, there are far more black spruce stems larger than aspen (15.1 on average) compared to neighbourhoods that contain more trembling aspen (mixed: 7.9, hardwood: 1.5 on average) (Table 1.3).

Patterns observed with radial growth can be evaluated on the long term using DBH as an indicator that resumes overtime growth performances. DBH distribution along neighbourhood coniferous gradient corroborates predicted radial growth for trembling aspen, where maximum DBH is also found in pure aspen stands (Figure A.4). This suggests that trembling aspen growth performance remains optimal when surrounded by conspecifics throughout its whole life cycle, whereas the same is probably not applicable to black spruce. Though there is a slight bell-shaped DBH distribution and lower black spruce DBH in pure spruce stands, there is no clear tendency in cumulative growth over coniferous content in the stand (Figure A.4b). Black spruce growth is maximized in mixed stands at mature stage, but the poor relationship between cumulative growth (DBH) and forest composition indicates that maximum growth at earlier stages may vary. As trembling aspen is mostly sensitive to neighbour abundance, this relationship is clearer than for black spruce whose growth is also influenced by various other variables.

Suppressed trembling aspen trees are rare in these forests since aspen height growth is generally greater than that of black spruce; suppressed aspen stems generally die due to their shading intolerance (Figure A.3a). Black spruce shade increases linearly as target height becomes lower than surrounding crowns (Figure A.3b). Since black spruce vertical dominance in the forest canopy decreases as the proportion of trembling aspen increases, amount of shade on black spruce targets is notably higher in "pure" aspen stands. Even if the light model ignores interspecific light transmission characteristics, Canham et al. (1999) have pointed that spatial configuration, size of canopy trees and the gaps between them are the major drivers of understory light availability. Thus, despite trembling aspen crown's higher light transmission than any shade-tolerant hardwood species (Canham et al. 1999; Messier et al. 1998), black spruce trees are more shaded in pure trembling aspen neighbourhoods due to their position in the canopy.

1.6.3 Spatially-explicit interactions

Spatial components included in the full model are neighbour distance and neighbour crown position. In the model, those two components are associated with distinct competitive effects, i.e. crowding and shading, respectively. Nevertheless, the shading model may address some crowding issues since neighbour distance is indirectly included in tree crown coordinates. The opposite is also true, as the crowding model does integrate some shading aspects, given that vertical dominance is expressed through DBH ratios. However, analyses show that, for these forests, shade is essentially determined by first neighbour's crown size and position and not necessarily by distance of other neighbours. Moreover, results have also indicated that the bulk of crowding effects are dealt with by a tree's competitive status which, in this study, is clearly better explained through the crowding model than the shading model (Table 1.4). Hence, a model structure such as the one used here should distinguish adequately shading from crowding-related competitive effects through the use of their respective spatial attributes.

As trembling aspen is shade-intolerant, most stems are located either above or within the main canopy level (Figure A.3) and in these mature, even-aged stands, aspen is well established and self-thinning is less important than in earlier development stages. Thus, with remaining aspen trees well distributed in space and black spruce crowns below the upper canopy level, trembling aspen may be less affected by light interception from neighbouring crowns. Sampled stands originate from fire and trees of same species have similar sizes, but when focusing on size differences in the crowding model, we captured a great deal of total estimated competitive effects. Measuring canopy openness then added no supplementary information to the model and appeared relatively insignificant compared to competitive status. Therefore, even a more complex light measurement method would probably bring little additional information to the competition model in these stands, as it was observed before (Deutschman et al. 1999). In such a context, distance-independent,

neighbourhood competition models can clearly generate growth predictions as accurate as spatially-explicit models.

Though the best NCI in this case is distance-independent at tree-level, is still needs to use an influence radius at neighbourhood-level since the measured positive effects of trembling aspen are distance-dependent. This is even truer considering the natural heterogeneous distribution of trembling aspen within these black spruce stands, which forces us to incorporate the notion of tree neighbourhood and influence radius. Values obtained here for this influence radius appear higher than studies on the same species (Légaré et al. 2005b) or similar functional groups (Lorimer 1983; Simard and Sachs 2004). This tendency has been noticed with this analysis for other species as well (Canham et al. 2006; Papaik and Canham 2006; Uriarte et al. 2004). This competition radius reflects average neighbourhood context and represents the net effect of all the processes going on between trees. The support in the literature for the ecological relationships used here and the flexibility of this simple estimation method makes it a robust and reliable approach.

1.6.4 Management implications

While total stand black spruce volume is maximized in pure black spruce stands (75-100% black spruce, according to provincial forest regulation), volume per spruce trees is optimized at equal aspen and black spruce proportions. However, profitability is both a question of total stand volume and volume per stem. Indeed, volume per stem reduces production costs and increase product value. Hence, optimal profitability is deeply dependent upon current wood prices and production costs; high wood prices favours higher stand volume whereas high production costs favour higher volume per stem. This optimal proportion may vary with time; a simple profitability analysis performed with local 2008 wood prices and average production costs found maximum profitability to be located at approximately 25 % of total basal area in trembling aspen (data not shown). Cumulative black spruce volume in stand also happens to decrease approximately at that proportion.

Optimal trembling aspen content in black spruce stands also depends on management objectives. Unless economic value of trembling aspen wood increases significantly relative to black spruce's, one might prefer to keep a black spruce vocation in certain stands for economic or operational purposes and maintain trembling aspen proportion low enough to preserve pure coniferous stand designation (i.e. maximum 25% aspen in canopy for Quebec forest regulation. In such cases, our results suggest keeping the maximum aspen proportion allowable (25%) to maintain pure black spruce stands designation in order to maximize profitability, and favour maintenance of biodiversity and other advantages associated with mixed species environments (for trembling aspen in these stands: 25% basal area ≈ 25% canopy area ≈ 18% total stem density). In sample set, mature black spruce neighbourhoods with less than 25 % aspen basal area have 2641 ± 221 stems/ha on average (95% confidence interval), and 410 ± 41 trembling aspen stems per hectare would have to be maintained on the long-term using precommercial and commercial thinning. In practice, this means keeping a ratio comprised between 1 aspen stem for 5 black spruce stems (or other species if applicable) and 1 for 6.

It is also important to keep in mind the risk of encroachment following harvesting in certain stands. For stands with initial trembling aspen content between 5 and 50 %, trembling aspen is expected to gain importance after harvesting (Laquerre et al. 2009). However, in stands prone to paludification, i.e. black spruce stands, Fenton et al. (2005) reported an increase in SOM depth with time, which is most likely to favour black spruce regeneration over trembling aspen. Hence, there appears to be a tradeoff between two long-term management-related risks for these black spruce forests: paludification (associated with low pre-harvest aspen presence) and aspen encroachment (associated with more important pre-harvest aspen presence). Appropriate management decisions will then have to be based on better knowledge of susceptibility to both paludification and encroachment, as these notions need to be clarified from an operational point of vue. Nevertheless, the precautionary principle should be exercised for black spruce stands prone to paludification in order to maintain productivity of these forests. In the light of our results, precautionary

measures should include maintaining 25% of total stand basal area in trembling aspen distributed as evenly as possible.

As traditional forestry shifts to sustainable forest management and managing for complexity becomes an objective in itself, strategic and operational planning should become more complex as well. However, one of this study's main outcomes is the demonstration that this is not always the case. Indeed, results obtained here indicate that black spruce growth is essentially independent of neighbours' position and that mixed species management practices do not necessitate additional efforts in that matter.

Our results support many studies conducted on these species in this region. Associated with the abundant literature describing these stands, the models presented here may be applicable and useful to forest managers. Models remain decision-support tools; simple models may provide as much ecological insight as more complex models but with less time and effort. Without discrediting long term silvicultural experiments, forest management could make greater use of such simple modeling, keeping in mind the uncertainty associated with forecasts and predictions.

CONCLUSION GÉNÉRALE

L'analyse de la compétition à l'échelle de l'arbre démontre qu'en pessière à mousse de l'Ouest du Québec, la croissance de l'épinette noire est effectivement améliorée en présence de peupliers faux-trembles. Une complémentarité semble se manifester entre ces deux espèces en ce qui a trait à la compétition pour les ressources du sol. L'épinette noire croît moins bien en pessière pure puisqu'elle y est affectée par la présence de voisins particulièrement abondants. Bien que l'abondance de voisins soit minimale en tremblaie pure, l'épinette n'y atteint toutefois pas sa croissance optimale, puisque les peupliers faux-trembles qui s'y trouvent dominent largement le couvert et ont des besoins nutritionnels plus importants en raison de leur plus grande taille. Celle-ci croît donc mieux en milieu mixte, où les voisins sont moins abondants qu'en pessière et moins gros qu'en tremblaie. Cette situation ne s'applique toutefois qu'aux forêts matures, puisque la distribution de la croissance cumulative (i.e. diamètre) des épinettes noires en fonction de la composition n'est pas aussi bien définie. Bien qu'on observe un plus faible diamètre d'épinette en pessière pure et une légère augmentation du diamètre moyen en forêt mixte, cette tendance est nettement moins claire. Enfin, si l'on tient compte du volume total d'épinette noire dans un voisinage, il demeure maximal en pessière pure, quoiqu'il se maintienne de 0 à environ 30 % de tremble dans le couvert.

Le portrait est un peu plus complexe pour le peuplier faux-tremble, puisque contrairement à ce que les niches écologiques prévoient, il atteint sa croissance maximale en tremblaie pure. Selon les analyses, il ne serait affecté que par les voisins plus gros que lui, mais étant donné qu'il est lui-même plus petit en pessière, plusieurs épinettes voisines le dépassent en taille. Selon les analyses, la faible abondance de voisins en tremblaie pure expliquerait les meilleures conditions de croissance du tremble dans ce milieu. Ces tendances observées en forêt mature semblent également se vérifier tout au long de la vie de ces peupliers faux-trembles puisque leur diamètre moyen est également maximal en tremblaie pure. Cette situation pourrait également s'expliquer par un effet positif du tremble sur la productivité

des sols (Légaré et al. 2005b). Elle confirme également l'hypothèse 2 quant au fait que le peuplier faux-tremble croît mieux en présence d'autres trembles.

Ainsi l'effet améliorant du peuplier faux-tremble sur les sols sensibles à l'entourbement (Fenton et al. 2005; Légaré et al. 2005b) impliquerait que tant l'épinette que le tremble croissent mieux lorsqu'entourés d'autres trembles. Toutefois, puisque la structure du modèle utilisée n'intègre pas de variable décrivant les conditions du site, il nous est impossible de quantifier avec certitude l'effet améliorant du peuplier faux-tremble.

Contexte spatial

Dans ces forêts équiennes matures, les effets de compétition mesurés dans les voisinages du peuplier faux-tremble et de l'épinette noire s'avèrent être indépendants de la distance des voisins mais également de leur position par rapport au soleil. L'analyse a également permis d'évaluer l'ampleur du rayon de ce voisinage pour le peuplier faux-tremble (10.6 m) et l'épinette noire (8.7 m). À l'intérieur de ce rayon, l'effet compétitif d'un voisin demeurerait inchangé. Cette zone d'influence est estimée à partir de la compétition pour les ressources du sol, ce qui implique qu'elle serait essentiellement déterminée par l'interférence entre les systèmes racinaires de même que par la zone de déposition de la litière des arbres du voisinage. Elle représente également tant les effets négatifs sur la croissance d'un arbre donné que les effets positifs, comme ceux liés à la présence de trembles.

Quant à la faible influence de la position spécifique des voisins sur la croissance de l'épinette noire, elle s'expliquerait avant tout par le fait que dans ces forêts équiennes matures, la lumière ne soit pas un facteur limitant pour la croissance de cette espèce. D'ailleurs, le climat de cette région demeure l'un des plus secs dans le Sud du Québec; sur les sols bien-drainés de cette région (épaisseur de matière organique au sol < 20 cm) le taux de précipitation limite la croissance de l'épinette noire (Drobyshev et al., non-publié). Le peuplier faux-tremble étant quant à lui situé dans l'étage supérieur du couvert forestier

(même en pessière pure), l'ombrage sur cette espèce est pratiquement nul. Ainsi, la structure du couvert forestier et la stabilité du stade de développement de ces forêts expliquerait l'absence d'influence de la position des voisins par rapport aux peupliers faux-tremble.

Quoiqu'il en soit, il est difficile d'éliminer complètement tout effet lié à l'ombrage par les voisins puisqu'aucune mesure directe de lumière n'a été prise. Par contre, les résultats issus de la reconstitution des cimes nous permettent malgré tout d'affirmer que dans ces forêts, l'ombrage a peu d'effet sur la croissance de l'épinette noire et du peuplier faux-tremble également. De même, l'hypothèse 3 statuant qu'un modèle de compétition de voisinage aspatial puisse prédire la croissance aussi efficacement qu'un modèle spatialement-explicite est donc vérifiée.

Répercussions pour l'aménagement forestier

Bien que le volume total d'épinette noire soit maximisé dans les voisinages comprenant de 0 à 30 % de tremble, le volume par tige est quant à lui maximal en forêt mixte, à proportion équivalente de peuplier faux-tremble et d'épinette noire. La rentabilité optimale est grandement influencée par les prix du bois sur les marchés, qui priorisent le volume de bois dans un peuplement (entre 0 et 30 % de tremble), et les coûts de production, qui favorisent de plus grosses tiges (autour de 50 % de tremble). Une analyse faite à partir des prix locaux de bois en vigueur en 2008 et le coût de production moyen a déterminé la rentabilité optimale du mélange tremble-épinette à une proportion d'environ 25 % de peuplier faux-tremble dans le couvert. En termes opérationnels, les peuplements naturels matures échantillonnés correspondants à ces proportions affichent des densités moyennes d'environ 2500 tiges marchandes à l'hectare, donc environ 400 tiges de peuplier faux-tremble à l'hectare (1 tremble par 25 m²). Concrètement, un ratio d'environ 1 tige de tremble pour 5 tiges d'épinette noire devrait être maintenu à long terme au moyen d'éclaircies précommerciales et/ou commerciales. Une telle composante de peuplier faux-tremble

maximise le volume d'épinette noire, tout en conservant la biodiversité et les autres avantages liés à l'environnement forestier mixte.

Bien que les peuplements purs d'épinette noire de la région soient susceptibles de se paludifier en l'absence de tremble, il est également nécessaire de considérer les risques d'enfeuillement suivant les opérations de récolte dans les peuplements plus feuillus. Une composante en tremble avant coupe entre 5 et 50 % du couvert favorise un peuplement de retour plus feuillu après la coupe (Laquerre et al. 2009). Il est nécessaire d'approfondir les connaissances sur les critères de susceptibilité de ces pessières tant à la paludification qu'à l'enfeuillement, de manière à mieux guider leur aménagement. D'ici là, le principe de précaution en vue d'éviter des pertes de productivité par la paludification encourage à maintenir 25 % de tremble dans les peuplements de retour.

Bien que la croissance de l'épinette noire serait indépendante de la configuration spatiale de son voisinage, il faudrait néanmoins s'assurer de répartir les trembles dans le peuplement de retour, de manière à ce que les épinettes ne soient pas à plus de 9 mètres des trembles, soit le voisinage de l'épinette noire. C'est dire qu'une stratégie d'aménagement forestier durable cherchant à maintenir le peuplier faux-tremble dans les pessières ne demanderait pas nécessairement plus d'effort que l'aménagement traditionnel.

Nos résultats corroborent les différentes études faites dans la région sur les interactions entre ces espèces. Considérant les études déjà menées sur cette problématique et cette région, l'utilisation de tels modèles écologiques est dorénavant possible, fiable et avantageuse. Les modèles demeurent toutefois des outils d'aide à la décision et leurs résultats devraient toujours être relativisés par rapport à leur incertitude. Sans discréditer les expérimentations sylvicoles à long terme, l'aménagement forestier gagnerait à utiliser ce type de modélisation écologique relativement simple.

APPENDICE

Model performance and evaluation

Variance in predicted growth increased linearly for both species (Figure A.1). Such heteroscedasticity is common in tree growth studies, as variance due to pests, pathogens, physical damage and suppression and release effects increases with tree growth (Jones and Thomas 2004; Pacala et al. 1994; Papaik and Canham 2006).
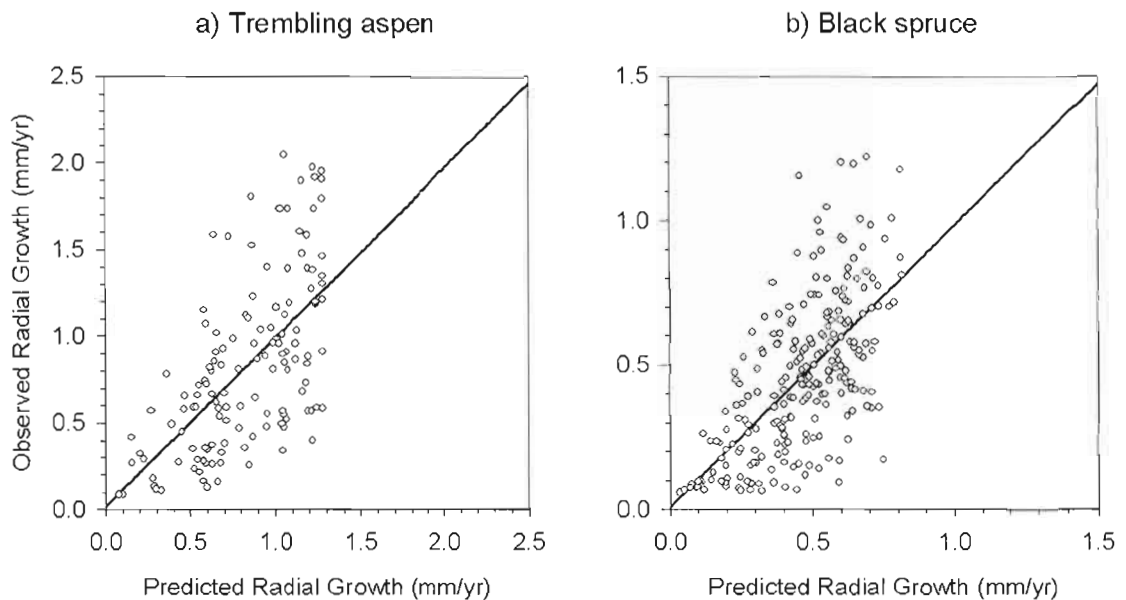

Figure A.1 : Observed/predicted slope for trembling aspen (a) and black spruce (b) selected best models.
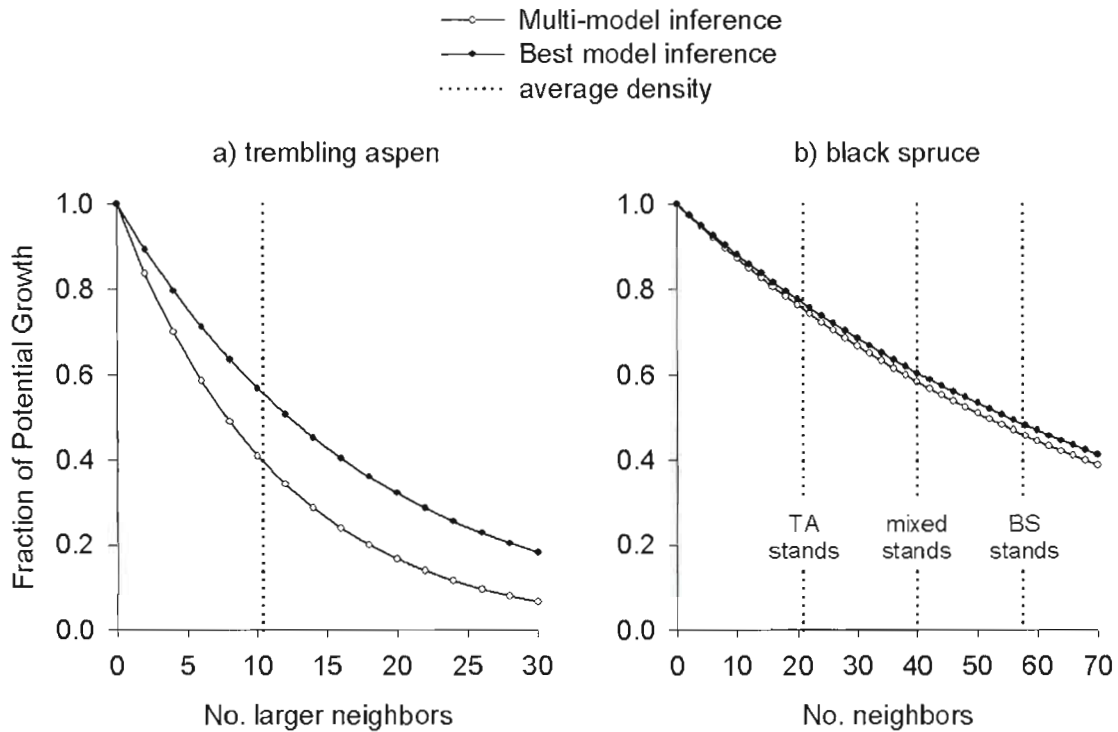
Use of best and multi model inference

Figure A.2 :   Effect of best vs. multi-model inference on neighbour abundance influence

Notes: Analysis based without consideration of neighbour species. For aspen that use asymmetric NCI, neighbours are on average 5.2 cm larger than target tree (Table 1.3).

With multi-model selection methods, the use of best model inference is often biased (Burnham and Anderson 2002, Burnham 2008). The trembling aspen best model results are notably different from multi-model inferences, as seen with neighbour abundance effect on growth (Figure A.2). Aspen's BMI lower performance may be caused by bias due to a smaller sample size compared to black spruce. The better black spruce BMI estimates may also be due to species composition, as sampling effort for this species was concentrated in pure black spruce stands. Lower bias related to the use of BMI has been observed in neighbourhoods where one species is clearly more abundant (Papaik and Canham 2006). In

addition to their smaller sample size, trembling aspen targets are better distributed along coniferous gradient. Nevertheless, inference based on the single best model appears to underestimate the effect of competition for both species at different degrees. Predictions based on model averaging (MMI) may be less accurate but they are expected to be closer to true parameter values of the whole population from which the sample was taken (Papaik and Canham 2006).

Growth and environmental gradients

Figure A.3 illustrates competitive status of both species in the canopy in relation with neighbourhood shade percentage.

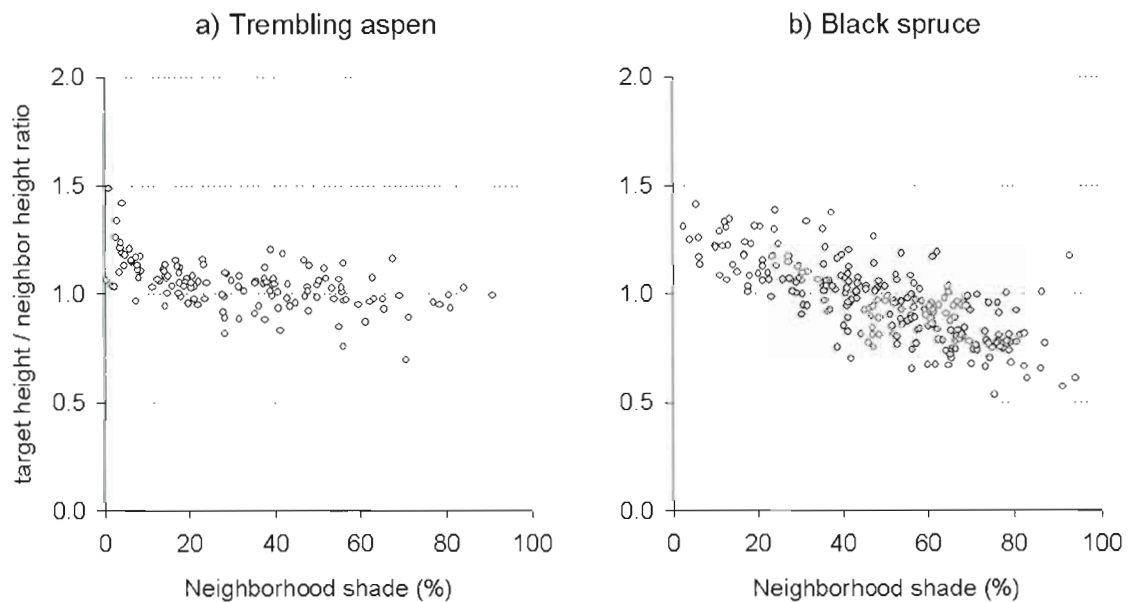**Figure A.3 :**   **Neighbourhood shade percentage as a function of target/neighbour height ratio for trembling aspen (a) and black spruce (b).**

Notes: Tree height was computed using the same allometric equations as described in the shading section.

As discussed before, suppressed live trembling aspen stems are rare in sampled mature stands and neighbourhood shade is not necessarily correlated with this species' competitive status. This may explain why the results indicated a poor correlation of trembling aspen growth performances and neighbourhood shade percentage. Black spruce shading, however, is much more representative of its vertical dominance, as one would expect from a sub-canopy species. This correlation corroborates the support given to shading in black spruce prediction set. This figure also shows that crown reconstitution by the shading model seems to recreate proper shade conditions and that these conditions are widely covered in our data set for black spruce target trees.

Figure A.4 demonstrates how various neighbourhood characteristics (DBH and stem abundance) are distributed along forest composition gradient. These distributions are particularly important for neighbourhood-level inference, which essentially looks at the evolution of black spruce and trembling aspen interactions with forest composition. DBH distribution is also a good indicator of the cumulative effect of black spruce and trembling aspen competition dynamics.
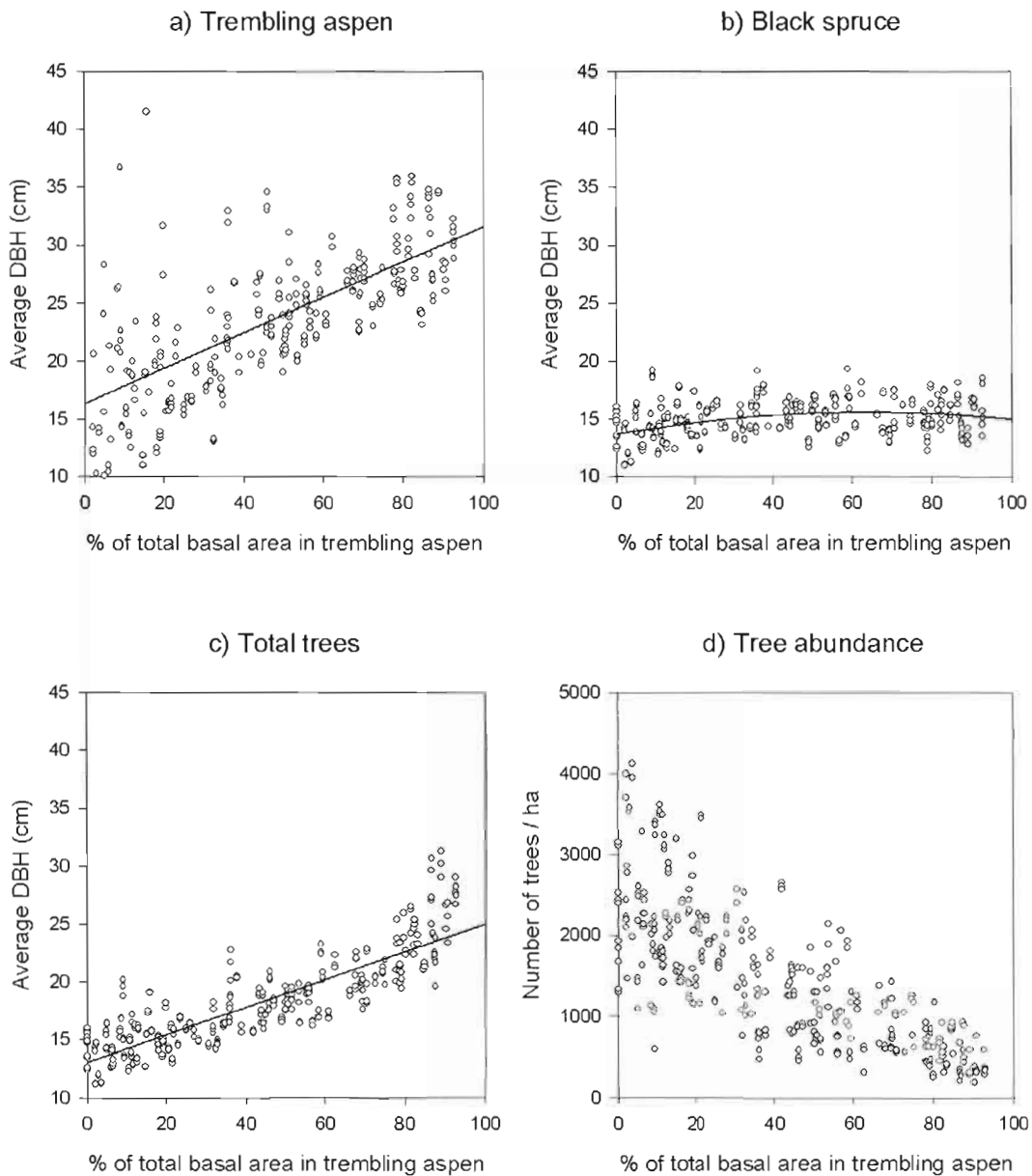
Figure A.4 : Tree size distribution for (a) trembling aspen, (b) black spruce, (c) all trees and (d) tree abundance distribution with trembling aspen percentage.

Notes: All four regressions are significant ($P < 0.0001$). Equations and R^2 for the regressions are   a) $y = 16.35 + 0.15x$, $R^2 = 0.44$;   b) $y = 14.48 + 0.02x - 0.0005(x - 40.98)^2$, $R^2 = 0.13$; c) $y = 13.04 + 0.12x$ $R^2 = 0.74$; and d) $y = 2410.9 - 22.87x$, $R^2 = 0.59$.

Mean radial growth for trembling aspen is 0.79 ± 0.02 mm/year and 0.48 ± 0.01 mm/year for black spruce (with 95 % confidence interval) (Figure A.5). Trembling aspen trees within the study area experienced a severe forest tent caterpillar outbreak in 2001 (Cooke and Lorenzetti 2006), with a possible aftereffect during the following summer (2002) (F. Lorenzetti, personal communication) (Figure A.6). The bias induced by the outbreak made it difficult to use the last 5 years of growth and only the last 3 years of growth were used (2003-2005) for modeling.
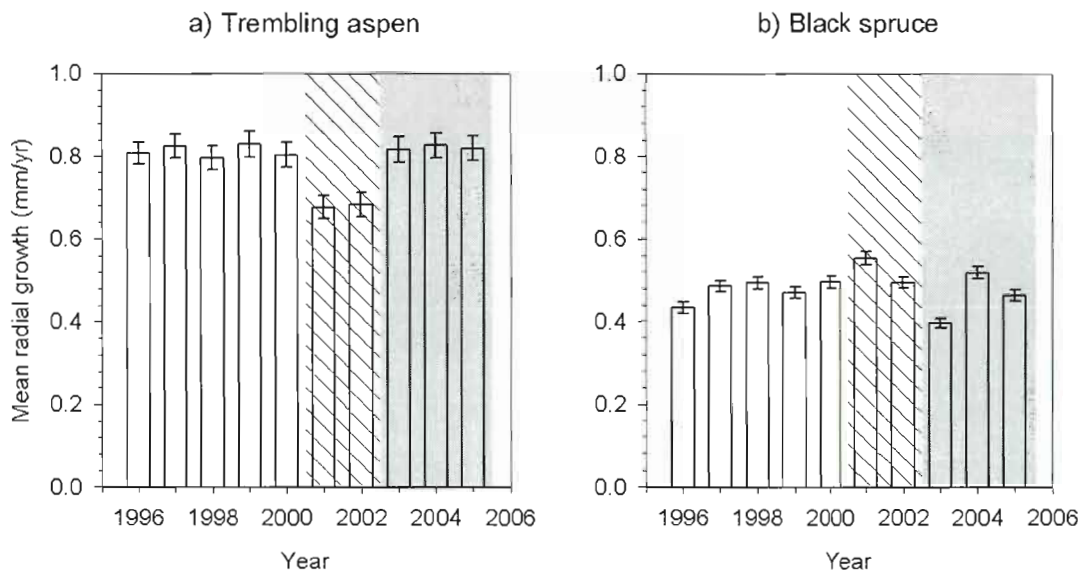
a) Trembling aspen   b) Black spruce

Figure A.5 :   **Mean annual radial growth distribution and standard errors for the 1996-2005 period.**

Notes: Standard error is shown with error bars. Hatched zone represents the period of forest tent caterpillar outbreak (2001) and its aftereffect on trembling aspen and indirectly black spruce growth. These years were excluded from the analysis. The zone in gray illustrates the three selected years where growth was averaged and analyzed (see text for details).

Both aspen and black spruce growth were modified since their dynamics are related in these mixed forest patches as Figure A.6 illustrates. As reported in the discussion, light might not be a limiting factor to growth in these stands and considering the low amount of effective

precipitation in this region (Robitaille and Saucier 1998), Drobyshev et al. (2009, unpublished work) mentioned that for soils with low SOM like in this data set, water might be limiting tree growth. Figure A.6 shows the relation between spruce and aspen growth for the 1996-2006 period and the drought code for the region. Drought code was computed using BioSIM's weather module, a system predicting insect development using daily weather time series (Régnière 1996).
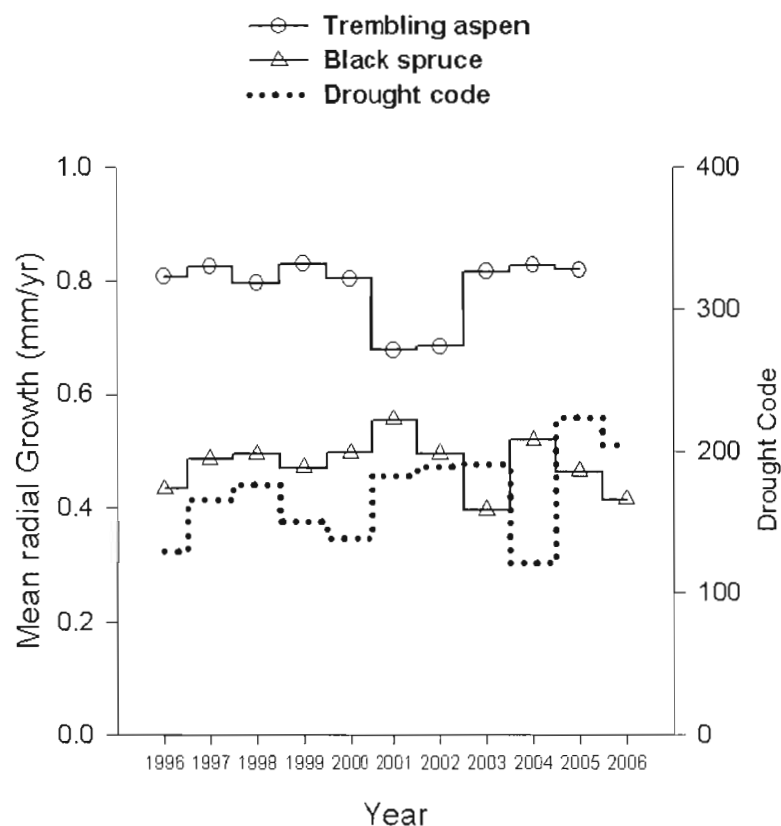

Figure A.6 :   **Mean radial growth evolution for 1996-2006 period in relation with local drought code. Gray zone represents growth years used in study.**

Trembling aspen doesn't appear to be very influenced by climate variations and its growth is relatively constant outside outbreak years. This could be explained by its faster fine root

production vs. black spruce that could improve its water uptake (Finér et al. 1997). Black spruce growth appears much more variable and dependent upon seasonal climate. Whether this is due to drought level, this is not clear from this analysis but an undefined climatic factor is expected to influence importantly black spruce productivity in these forests; its inclusion in the model could improve growth predictions.

Black spruce allometry calculation

Shading effect modeling is based on a simplified light reconstitution model (Canham et al. 1999; Canham et al. 2004) and on tree allometry equations (tree height – Eq. A-1, crown height – Eq. A-2, and crown width – Eq. A-3) (Lambert et al. 2005; Poulin and Messier 2006). Trembling aspen allometry parameters were taken from the forest dynamics model SORTIE-ND (Pacala et al. 1996) calibration report for Duparquet area in North-Western Quebec (Poulin and Messier 2006). Black spruce allometry parameters were estimated using the same calculation but from external data (Lambert et al. 2005; Ouellet 1983).

$$Height = 1.35 + (H_1 - 1.35) \times (1 - e^{-(B \times DBH)})$$

Equation A.1 :   **Tree height (in meters)**

$$Crown\ radius = C_1 \times DBH^A$$

Equation A.2 :   **Tree crown radius (in meters)**

$$Crown\ depth = C_2 \times Height^b$$

Equation A.3 :   **Live crown depth (in meters)**

Where H_1 is the maximum height for a given species, B is the initial slope of the regression between height (m) and DBH (cm), C_1 is the slope of the regression between crown radius (m) and DBH (cm), and C_2 is the fraction of tree height occupied by live crown. The relationships obtained are illustrated in Figure A.7 and parameter estimates reported in Table A.1.

Table A.1 : Parameter estimates for trembling aspen and black spruce allometric equations

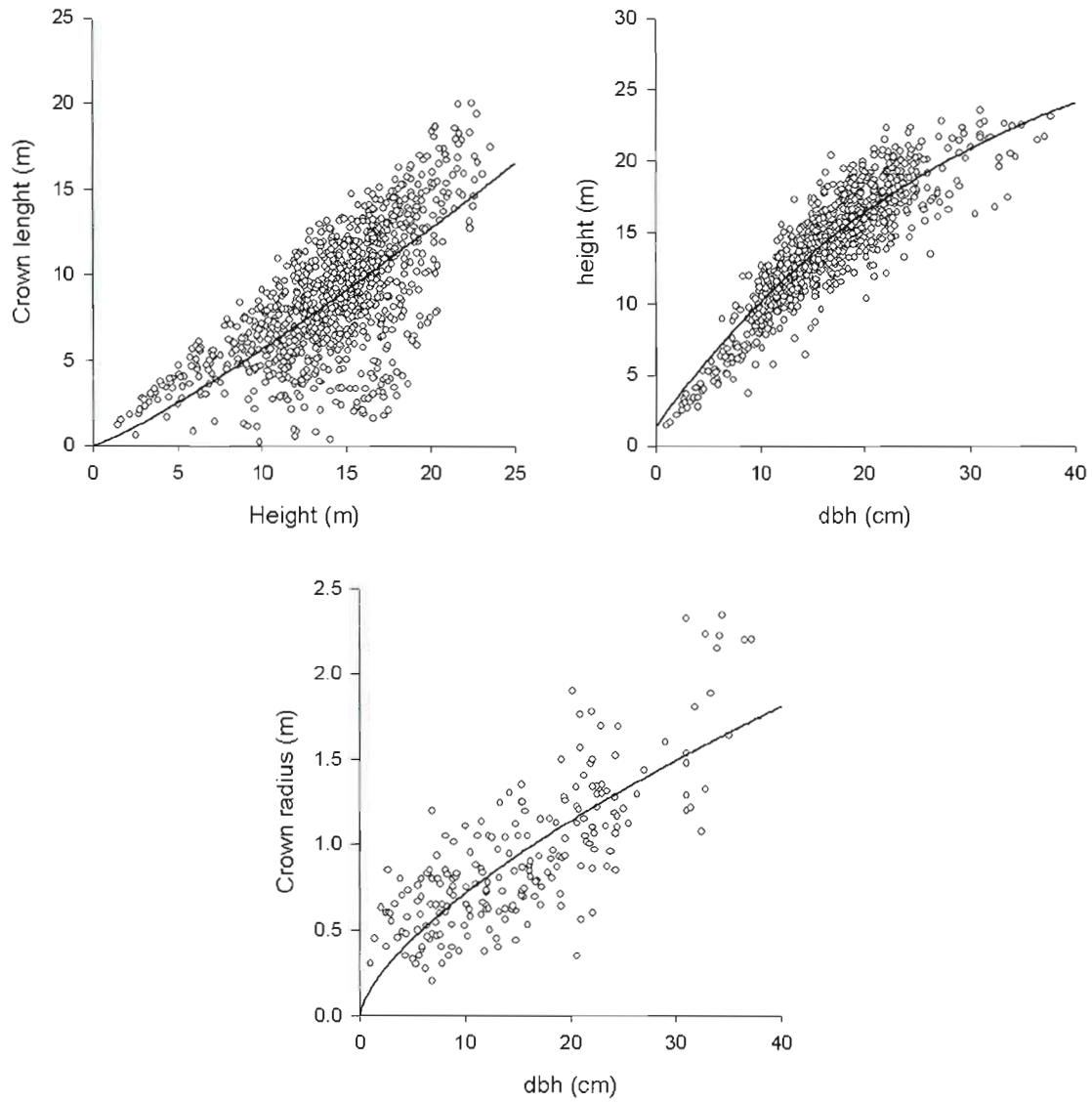| Species	H_1	B	C_1	a	C_2	b
Trembling aspen	26,26	0,067	0,092	0,761	0,262	1,110
Black spruce	32,00	0,034	0,153	0,669	0,384	1,169

Figure A.7 :   Allometry relationships for black spruce height, crown length and crown radius (data from Lambert et al. 2005 and Ouellet 1983).

Target tree size impact on potential growth

Although size effect is usually considered as one of the main growth determinants (Canham et al. 2004; Canham et al. 2006; Papaik and Canham 2006), our data show that it might as well be absent from mature stands. Size effect is relevant in cases where sampled target trees are distributed along a wide size range so that tree size influence on growth is significant. Few large, slow growing trees are found in managed forests and this absence of size effect could be generalized to most commercial species in managed forests. Size range is also reduced considering that small, non-merchantable stems (< 9 cm) were also excluded from sampling. Moreover, as most sampled stands were fully stocked, small trees encountered were mostly suppressed and slow growing. Thus, the relationship between growth and target tree size obtained here is confounded with a "suppression effect" of smaller slow-growing stems found in mature stands (Figure A.8). Results show that analyses of target tree size effect on growth may have been limited by this narrow size and stand age gradient (data not shown). Consequently, potential tree growth was assumed to be independent of target tree size throughout all subsequent analyses.
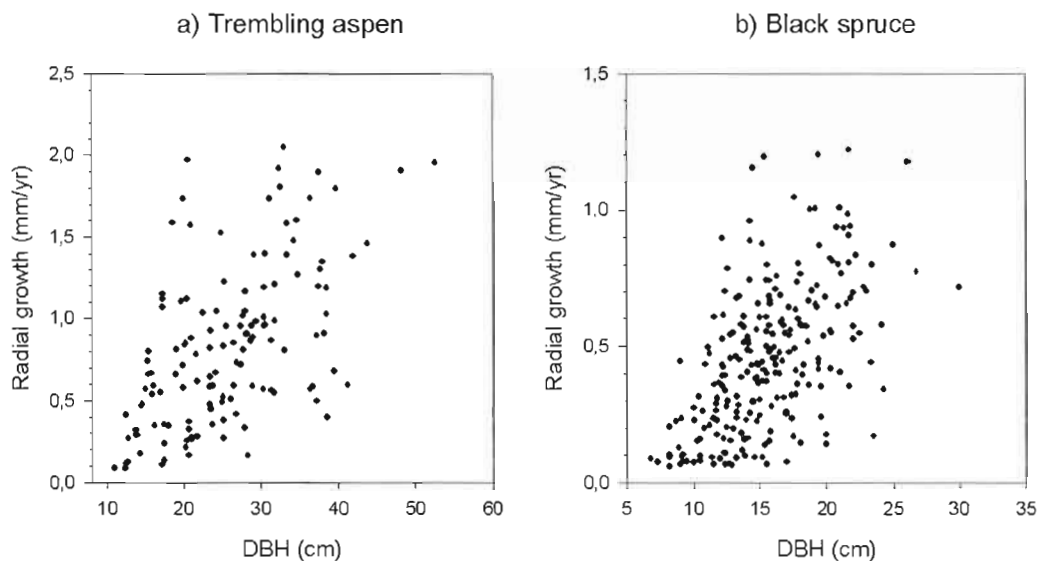

Figure A.8 :   Observed radial growth distribution as a function of target tree DBH.

Considering the absence of size effect in the data set (La Sarre data set), an exploratory analysis using permanent plots data was conducted and reveals that there might be a substantial size effect with a maximum potential growth located within the range of sampled DBH for black spruce (max. radial growth at approx. 15 cm DBH) and trembling aspen (max. radial growth at approx. 28 cm DBH) (Figure A.9 and A.10). There is also support for size effect on aspen trees in a study conducted in Duparquet area, where maximum radial growth was found around 27 cm DBH (Papaik et al. unpublished work). However, size effect analyses in permanent plot data were not conclusive enough to apply their parameter estimates to La Sarre data set analysis. Age and stand structure distribution in La Sarre data set might not be as spread as the model needs to detect a consistent size effect. Nevertheless, the performance of both species' best models remains very good without this effect.
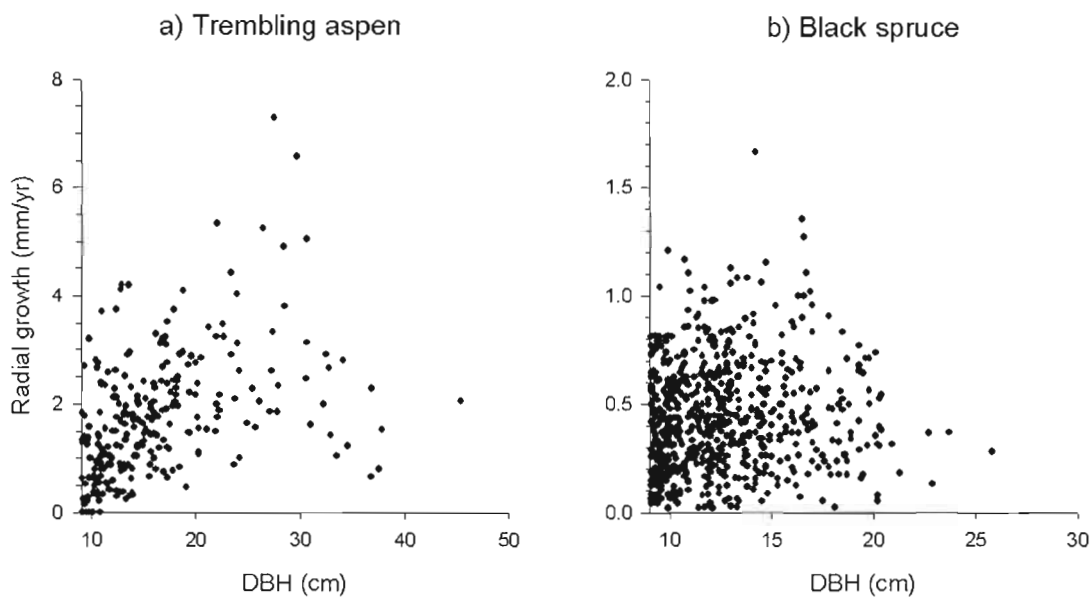
a) Trembling aspen   b) Black spruce

Figure A.9 :   **Radial growth distribution along tree size gradient using permanent plots data**
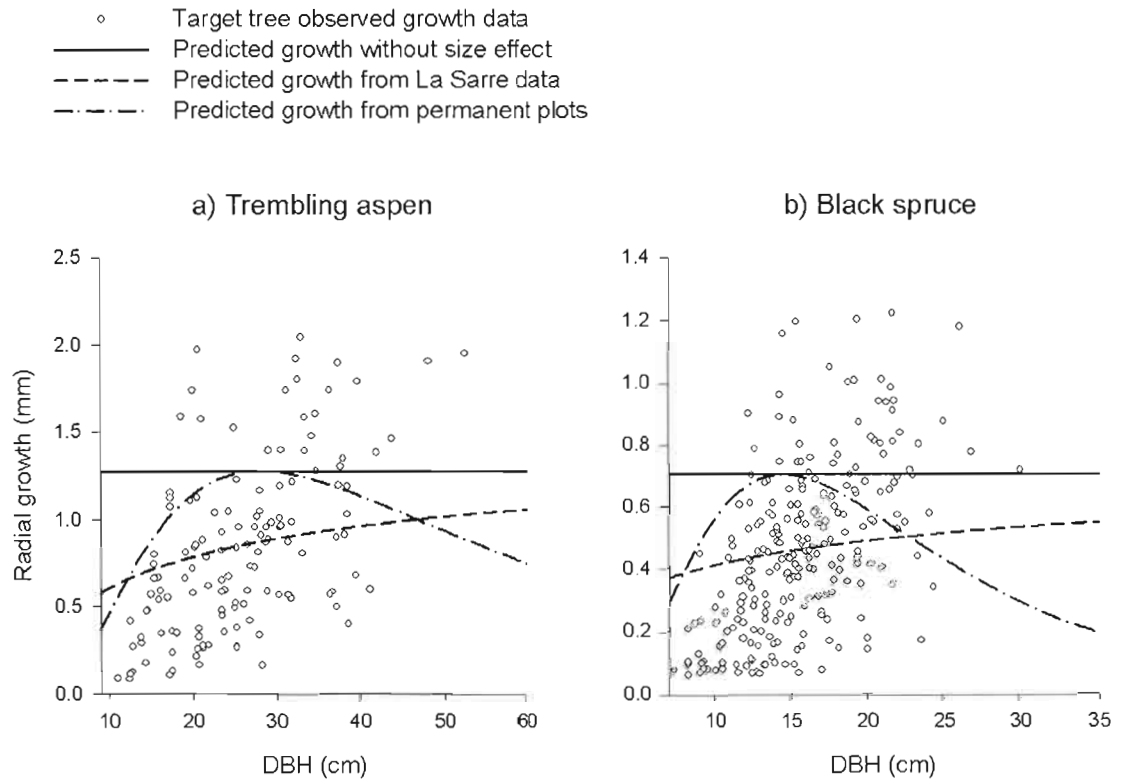
Figure A.10 : Size effect estimation from La Sarre data and permanent plots

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76

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