UNIVERSITÉ DU QUÉBEC EN ABITIBI-TÉMISCAMINGUE

INTERACTIONS ENTRE LES ESSENCES FORESTIÈRES DE LA FORÊT BORÉALE DE L'EST DU CANADA, ET CONSÉQUENCES POUR LA SÉQUESTRATION DU CARBONE DANS LA COMPOSANTE AÉRIENNE DES PEUPLEMENTS MIXTES

THÈSE
PRÉSENTÉE COMME EXIGENCE PARTIELLE
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RÉSUMÉ

Bien qu'il soit reconnu que la forêt boréale canadienne contribue de façon non négligeable au stockage du carbone, le fonctionnement des peuplements mixtes demeure mal compris. Ces derniers sont pourtant fréquents dans les forêts naturelles et il existe plusieurs hypothèses qui y prévoient un accroissement du stockage de carbone par rapport aux peuplements monospécifiques : en plus de possibles phénomènes de facilitation, le recoupement des niches écologiques peut se révéler moindre entre individus d'espèces différentes, induisant ainsi une baisse de la compétition et une utilisation plus vaste des ressources du milieu, et donc une augmentation de la productivité. La végétation du sous-bois n'est pas en reste, pouvant être largement affectée – positivement ou non – par la diversité de microhabitats créée par une canopée mixte. Les résultats expérimentaux sur ces sujets sont toutefois peu nombreux et contradictoires, et aucune étude ne semble s'être intéressée spécifiquement au rôle des peuplements mixtes dans le stockage du carbone. C'est pourquoi cette thèse vise à déterminer l'effet du mélange des essences sur la productivité aérienne, mais n'est qu'une partie d'un projet plus vaste qui englobe des études concernant la productivité racinaire et la respiration hétérotrophe du sol, l'objectif ultime étant de modéliser le bilan des flux d'entrée et de sortie du carbone en fonction de la composition spécifique des peuplements forestiers étudiés.

Des peuplements purs et mixtes d'environ 90 ans, issus de feu et peu perturbés, ont été sélectionnés dans deux zones géographiques distinctes : sur la ceinture d'argile abitibienne, au nord-ouest du Québec, et sur des tills au nord-ouest de l'Ontario. Les mélanges étudiés au Québec réunissaient le peuplier faux-tremble et l'épinette noire, et ceux en Ontario comportaient du tremble, de l'épinette noire et du pin gris.

La mesure des stocks de carbone dans les tiges vivantes à 90 ans ont révélé des relations plutôt neutres entre les espèces à l'échelle de la tige individuelle. À l'échelle du peuplement, les stocks de carbone dans les peuplements mixtes ne sont généralement pas différents de ce qui peut être prédit à partir des peuplements purs associés, et les quelques différences observées peuvent être expliquée par l'effet de la densité. Les analyses dendrochronologiques ont toutefois révélé que les relations entre les espèces ne sont pas neutres mais que les effets positifs et négatifs évoluent et s'annulent au fil du temps. La végétation de sous-bois quant à elle n'est guère favorisée par les canopées mixtes. Les plantes vasculaires bénéficient des surplus de ressources apportés par le tremble, mais leur productivité chute drastiquement dès lors que la proportion de conifère augmente. Inversement, les bryophytes qui envahissent les sous-bois des pessières ne tolèrent pas que la proportion de tremble dans la canopée augmente un tant soit peu. Ainsi, la biomasse et la croissance du sous-bois des peuplements mixtes est inférieure à celle de chacun des peuplements purs correspondants.

Une fois tout cela mis ensemble, il apparaît que comparé aux arbres, le sous-bois contribue très peu aux stocks de carbone 90 ans après feu. Au niveau des intrants de carbone en revanche, le sous-bois contribue largement plus, particulièrement les bryophytes dans les pessières en Abitibi et les arbustes dans les tremblaies en Ontario. Par conséquent, l'effet négatif des peuplements mixtes sur la productivité du sous-bois fait en sorte que la productivité aérienne dans les mixtes est plus proche de celle du peuplement pur le moins productif que de celle du peuplement pur le plus productif. La quantité de carbone accumulée après 90 ans dans la biomasse aérienne des peuplements mixtes étudiés est, en revanche, plus proche de la moyenne entre celles des peuplements purs associés.

INTRODUCTION GÉNÉRALE

Préambule

L'attirance des contraires. Un mystère aussi dense et impénétrable que les sombres et chaotiques forêts qui, au-delà de nos habitations, s'étendent plus loin que notre imagination n'ose le concevoir, vision frappante pour celui qui s'extirpe tout juste d'un Ancien Monde depuis longtemps réduit aux seules dimensions humaines. Cette immensité est le théâtre d'une âpre lutte entre les géants qui la dominent. Une lutte bien réelle, bien que se déroulant à une échelle si éloignée de la nôtre qu'il est facile de l'oublier. Une lutte pour la survie, mais qui n'en est pas pour autant dénuée d'une certaine courtoisie, l'entraide semblant aussi présente que la compétition. Et lorsque se joignent différentes essences, ces multiples et contradictoires interactions s'entremêlent en un écheveau encore plus complexe à déchiffrer. Ainsi, les maîtres des sylves couvrent langoureusement leurs plus modestes congénères d'un ombrage aussi protecteur que répressif, tels des maris attentifs et jaloux. Chacun répand de son être sur le sol, tentant de le modeler à son image, démiurges donnant et reprenant à l'envie la manne primordiale.

Ami lecteur, je t'enjoins à voir par-delà l'analytique froideur des pages qui suivent. Car elles furent enfantées par ma fascination envers l'étrange et féconde danse immobile de ces amants cyclopéens qui, trop souvent, se trouvent séparés par l'action de nos mains insensibles.

0.1. OBJECTIF GÉNÉRAL : LA FORESTERIE COMME OUTIL CONTRE LES CHANGEMENTS CLIMATIQUES

Le danger d'un changement climatique global dû à l'émission anthropique de gaz dits à effets de serre (GES), et notamment du CO_2, est désormais de moins en moins scientifiquement contesté et est considéré par beaucoup comme un enjeu environnemental majeur (IPCC 2007). L'augmentation de la séquestration du carbone par la végétation, particulièrement par le ralentissement du défrichement des forêts tropicales et par des programmes de reforestation de terres agricoles, est souvent évoquée comme solution. L'accent est en effet placé sur les écosystèmes forestiers dont la biomasse et les sols contiennent environ 77% du carbone de la végétation du globe et 42% du carbone des sols de surface, respectivement (Bolin & Sukumar 2000). Toutefois, un changement relativement mineur des habitudes de coupes et de reboisement ne modifiera vraisemblablement pas la séquestration du carbone de manière significative (Karjalainen et al. 2003). Il faudrait un effort massif qui consisterait, entre 1995 et 2050, à éviter la déforestation de 138 millions ha, à promouvoir la régénération naturelle de 217 millions ha de forêts tropicales, et à planter 345 millions ha de forêts, afin de compenser l'équivalent de 12 à 15% des émissions de carbone dues à la combustion d'énergies fossiles et à la déforestation pour la même période (Cannell 1999). Au niveau du Canada, l'installation de peuplements de peupliers faux tremble (*Populus tremuloides* Michx.) en Saskatchewan central sur des champs ou des pâtures permettrait sur 50 ans de séquestrer 30 à 70 tonnes de carbone supplémentaires par hectare (Fitzsimmons et al. 2004), alors que les émissions annuelles d'équivalent carbone du Canada étaient estimées à 197 millions de tonnes en 2000 (Environnement Canada, 2001), soit environ 45 millions de tonnes de carbone de plus que le niveau à atteindre en 2012 pour respecter les objectifs établis par le protocole de Kyoto (McKenney et al. 2004). Très grossièrement, il faudrait donc planter au moins 50 millions d'hectare de peuplier pour atteindre ne serait-ce que les objectifs de Kyoto. Il semble donc irréaliste que la foresterie puisse être l'unique réponse au problème du changement climatique. Elle peut en revanche faire partie de la solution.

Si la surface de terres boisées est primordiale, la productivité des peuplements l'est tout autant : d'une part afin de maximiser la séquestration du carbone pour une surface forestière donnée, et d'autre part parce qu'aucune solution proposée ne saurait faire fi des enjeux économiques. En ce sens, augmenter la productivité des peuplements existants est évidemment un but constant de l'industrie forestière, et maximiser celle des peuplements susceptibles d'être installés pour réduire les émissions globales rendrait cette méthode d'autant plus rentable et donc attractive, notamment si cela doit signifier l'abandon de certaines terres agricoles (McKenney et al. 2004). De plus, une plus grande productivité forestière permet un plus grand usage de produits forestiers, lesquels ont un bilan énergétique beaucoup plus avantageux que leurs alternatives (telles que l'acier ou le béton) dont la production génère d'importants rejets de gaz à effet de serre, souvent d'origine fossile.

Cette étude s'intéresse aux peuplements mixtes (*i.e.* définis ici comme tout peuplement dont aucune essence ne compose plus de 75% de la surface terrière), susceptibles d'être plus productifs que les peuplements monospécifiques (Man & Lieffers 1999; Kelty 2006), comme moyen de maximiser la séquestration du carbone.

0.2. BILAN CARBONE

Bien que pour déterminer les sources et puits de carbone on pense en priorité au carbone contenu dans la biomasse des arbres, et plus particulièrement dans le bois, la quantité de carbone séquestrée dans un peuplement ne se résume pas à la productivité de sa strate arborée. Il est nécessaire pour déterminer ce potentiel d'établir un bilan de carbone pour l'écosystème concerné, c'est-à-dire de mesurer, estimer ou modéliser les flux d'entrée (*e.g.* production photosynthétique nette) et de sortie (*e.g.* respiration hétérotrophe) du carbone, ainsi que les stocks actuels de carbone et la répartition de cet élément dans l'écosystème. Suivant ce principe, il apparaît que les stocks de carbone estimés des sols forestiers (sol minéral et couche morte) sont dans certains cas presque aussi importants que ceux de la biomasse vivante, atteignant par exemple 88 et 98 tC.ha^{-1} respectivement pour les forêts des Appalaches (Liu et al. 2006). Cette tendance est encore renforcée dans les forêts boréales, la lente décomposition due aux basses températures (Falk et al. 2005) induisant un stock de carbone du sol dépassant alors celui de la biomasse vivante, que ce soit en Sibérie (Ito 2005) ou au Manitoba (Martin et al. 2005). Moins actif et moins facilement manipulable que celui de la biomasse vivante, ce large stock de carbone du sol est néanmoins loin d'être négligeable, mais est délicat à estimer, de même que le flux de décomposition (ou respiration hétérotrophe)(de Wit et al. 2006). Notre objectif est de mesurer ces variables en plus du carbone de la biomasse vivante afin de réaliser des bilans carbone comparatifs entre des peuplements mixtes et monospécifiques. Il s'agit d'un projet séparé en trois études distinctes, visant principalement à mesurer et estimer :

- La respiration hétérotrophe et le stock de carbone du sol,
- La biomasse et la croissance racinaire ou souterraine,
- La biomasse et la croissance « aérienne », c'est-à-dire situés au-dessus du sol, des arbres et de la végétation du sous-bois.

La présente étude ne couvre que ce dernier point, à savoir la productivité aérienne des peuplements mixtes comparés aux peuplements monospécifiques.

0.3. L'EFFET CONTROVERSÉ DU MÉLANGE DES ESSENCES FORESTIÈRES

Vandermeer (1989) a proposé deux mécanismes par lesquels les peuplements mixtes pourraient être plus productifs que les peuplements purs : les phénomènes de facilitation entre espèces et la séparation des niches écologiques. On parle de facilitation quand une espèce améliore les conditions du milieu, par exemple en fournissant de l'ombrage aux espèces intolérantes à la pleine lumière pendant leur stade juvénile, ou bien encore en améliorant la biodisponibilité des nutriments dans le sol par une accélération de la décomposition, comme cela a été supposé pour le peuplier faux-tremble (Côté et al. 2000; Prescott et al. 2000). Le concept de la séparation des niches écologiques signifie quant à lui que les divergences dans l'exploitation des ressources (généralement, ressources minérales et lumière) entre différentes espèces amène à une plus large exploitation des ressources du milieu dans les peuplements mixtes, ou autrement dit que la compétition interspécifique est moins forte que la compétition intraspécifique.

Nombreuses sont les études ayant tenté de vérifier la validité de ces théories pour les peuplements forestiers. On peut globalement les classer en deux grandes catégories : celles qui s'attachent aux phénomènes de facilitation, ce qui se traduit dans l'immense majorité des cas par des études sur la nutrition et / ou la décomposition de la litière, et celles qui s'intéressent à la croissance des tiges, donnée qui résulte aussi bien des processus de facilitation que de la séparation des niches écologiques.

0.3.1. Décomposition de la litière et nutrition minérale dans les peuplements mixtes

Le but des études concernant l'effet du mélange des espèces sur la décomposition ou la fertilité du sol est généralement de mettre en évidence un éventuel effet synergique entre les espèces ; autrement dit un effet qui ne soit pas purement additif, mais supérieur (ou inférieur) à ce que l'on pourrait prévoir à partir des données sous peuplements purs de chacune des espèces du mélange. Rothe et Binkley (2001) ont recensé de nombreuses études de ce genre. Il apparaît qu'un tel effet non-additif sur la quantité d'azote foliaire ou minéral survient surtout lorsqu'une des deux espèces du mélange est un fixateur d'azote. En-dehors de ce cas particulier, les concentrations en azote ou phosphore foliaires peuvent bénéficier, pâtir ou rester indifférentes au mélange, sans qu'il soit apparemment possible de relier cette inconstance à une autre variable. La variation de la teneur des feuilles en nutriments n'est toutefois pas nécessairement un indice fiable de la fertilité, un effet positif ne pouvant *a priori* être détecté par ce biais qu'à la condition qu'il existe à l'origine une déficience en nutriments sur les sites étudiés (Rothe et al. 2003). Cette absence d'effet net peut toutefois également s'étendre à la fertilité du sol, peut-être en raison de la difficulté à détecter de telles variations dans les peuplements naturels (*e.g.* à cause de l'hétérogénéité des sols, du drainage, de la végétation de sous-bois concurrente). Ainsi, les études ne montrent généralement pas d'effet du mélange sur la fertilité du sol dans les peuplements naturels, mais au contraire dans des conditions contrôlées, les mélanges ont le plus souvent un effet positif sur la fertilité des sols (Rothe & Binkley 2001).

La décomposition de la litière semble quant à elle plus lente sous les conifères que sous les peupliers faux-tremble, à l'exception des peuplements les plus vieux où la différence s'amenuise (Côté et al. 2000). De même, la couche organique est plus épaisse et acide sous les peuplements d'épinettes que sous une canopée de feuillus tels que des hêtres (Rothe et al. 2002). Mais l'effet facilitateur d'une espèce sur la décomposition ne se résume pas forcément à un simple apport de litière plus facilement décomposable. Godefroid *et al.* (2005) observent que la qualité de l'humus décroît avec l'âge dans les peuplements purs de chênes et de hêtres, mais qu'un mélange des deux espèces, même en petite proportion, permet un maintient de la qualité de l'humus sur le long terme. Dans une revue de littérature, Gartner et Cardon (2004) montrent que 67% des mélanges de litières testés ont une perte de masse non-additive, jusqu'à 65% supérieure au résultat prévu en fonction de la dynamique de la litière de chaque espèce et de la proportion de mélange. De tels effets sont toutefois rares, la majorité des effets additifs se montrant plus modestes. Cela montre que l'effet du mélange de deux espèces sur la décomposition de la matière organique ne peux pas nécessairement être prédit à partir de la vitesse de décomposition de la litière de chaque espèce, et que cet effet est donc extrêmement dépendant de la combinaison d'espèces particulière considérée pour le mélange.

0.3.2. Effet croissance des peuplements mixtes

L'existence d'un éventuel gain de productivité dans les peuplements mixtes est controversée. Selon les espèces considérées et les conditions environnementales, il est possible d'observer des gains, des pertes ou aucune variation de productivité dans les peuplements mixtes par rapport aux peuplements monospécifiques (Brown 1992; Kelty 1992; Kelty 2006). De nombreuses études se sont intéressées à la compétition imposée par un couvert de feuillus intolérants sur des conifères, montrant les gains de croissance de ces derniers lorsque ce couvert est ôté (Jobidon 2000; MacDonald & Thompson 2003; Burgess et al. 2005; Johnstone 2005; Pitt & Bell 2005; Voicu & Comeau 2006). Ces résultats mettent l'emphase sur la compétition pour la lumière, les feuillus intolérants croissant plus vite et dominant généralement rapidement la plupart des conifères dans les premiers stades de succession. D'ailleurs, la réponse de croissance du pin blanc par exemple à une telle suppression de la compétition ne concerne que les individus qui étaient réprimés et non les dominants (Bevilacqua et al. 2005). De plus, la suppression du couvert de feuillus amène une réduction de la densité du peuplement ; il est alors difficile de dire en quoi l'effet positif de cette suppression pour les conifères restants pourrait être différent de celui d'une simple éclaircie dans un peuplement monospécifique. En effet, même si les feuillus intolérants dominent le plus souvent les conifères, ces derniers pourraient en revanche bénéficier des périodes de printemps et d'automne pendant lesquelles leurs compétiteurs sont dépourvus de feuilles (Green 2004).

Quoi qu'il en soit, la difficulté d'étudier la productivité des peuplements mixtes en comparaison avec les peuplements purs réside aussi dans celle de trouver des peuplements en tout point comparables dans la nature. Par exemple, Chen et Klinka (2003) montrent que la biomasse totale de peuplements de pruches (*Tsuga heterophylla (*Raf.) Sarg.) et de thuyas (*Thuja plicata* D.Don ex Lamb.) augmente avec la proportion de pruche dans les peuplements. Malheureusement, ils signalent également une corrélation entre cette proportion et l'âge des peuplements, susceptible de fausser l'interprétation, d'autant plus que la composition spécifique des peuplements ne rend compte que de 14% des variations de la croissance annuelle. La prise en compte de telles covariables est essentielle dans ce genre d'études. Ainsi, les relations de compétition entre le sapin douglas (*Pseudotsga menziesii* (Mirb.) Franco) et le bouleau à papier (*Betula papyrifera* Marsh.) changent d'une zone biogéoclimatique à l'autre (Wang & Kimmins 2002), tandis que Green et Hawkins (2005) montrent une relation négative forte entre la croissance de l'épinette blanche (*Picea glauca* (Moench) Voss) et la densité de bouleau d'un peuplement, mais uniquement sur le versant nord. Le mélange entre le sapin Douglas et la pruche sur la côte pacifique nord-ouest résulte en un gain de croissance pour le Douglas, mais avec une perte de croissance pour la pruche dans des sites océaniques (Amoroso & Turnblom 2006) Cet effet négatif est absent dans des sites plus intérieurs (Erickson et al. 2009). Une étude himalayenne a même trouvé que la compétition interspécifique variait en fonction de l'identité des ectomycorrhizes présentes (Pande et al. 2007).

L'utilisation de plantations expérimentales d'essences à croissance rapide peut être un moyen d'éviter ces biais. De tels mélanges expérimentaux d'acacias (*Acacia mearnsii* de Wild) et d'eucalyptus (*Eucalyptus globulus* ssp. *pseudo-globulus* (Naudin ex Maiden) Kirkpatr.) montrent une plus grande biomasse totale dans les peuplements comportant 50% de chacune des deux espèces par rapport aux peuplements purement monospécifiques (Bauhus et al. 2004). Toutefois, pour encourageants qu'ils soient, de tels résultats ne peuvent être généralisables. Même les plantations d'eucalyptus mélangés avec des fixateurs d'azote ne donnent pas systématiquement des résultats positifs (Forrester et al. 2006). Non-seulement les conditions écologiques jouent-elles un rôle dans les relations interspécifiques, mais Linden (2003) insiste là encore sur l'importance des espèces elles-mêmes, les résultats étant différents dans des mélanges d'épinettes de Norvège et de pins sylvestres, où le pin gagne un peu de croissance individuelle mais sans que l'augmentation globale de volume de bois augmente significativement, et dans des mélanges d'épinettes de Norvège et de bouleaux argentés, dans lesquelles le bouleau croît d'autant mieux que sa présence est faible, semblant indiquer une compétition interspécifique moins forte que la compétition intraspécifique pour ce dernier. La stratification de la canopée en particulier semble augmenter les chances d'obtenir des gains de productivité dans les mélanges en diminuant la compétition interspécifique (Canham et al. 2006; Forrester et al. 2006; Boyden et al. 2009; del Rio & Sterba 2009; Pretzsch & Schutze 2009). Outre les conditions environnementales, la dissimilarité des traits fonctionnels des espèces du mélange (sans doute plus propice à la séparation des niches écologiques), *a priori* plus forte entre des feuillus intolérant de début de succession et des conifères tolérants à l'ombre de fin de succession, semble donc un facteur essentiel à considérer pour prévoir la croissance d'un peuplement.

0.4. L'IMPORTANCE DE LA RÉPONSE DU SOUS-BOIS

La faible quantité de carbone stockée dans la végétation du sous-bois pourrait en faire une quantité négligeable dans un bilan carbone forestier en regard des quantités bien plus importantes situées dans les sols ou la canopée. Ce serait toutefois faire fi du taux de renouvellement de la biomasse de sous-bois, bien plus importante que celle des arbres (Zavitkovski 1976; Yarie 1980). Cela permet au sous-bois non-seulement de contribuer au cycle du carbone d'une manière bien plus importante que ne le laisse présager sa faible biomasse, mais également à accélérer le recyclage des éléments nutritifs et à favoriser ainsi le maintien de la productivité à long terme de la canopée, particulièrement dans les peuplements de conifères, dont le taux de renouvellement annuel est particulièrement faible (Chapin 1983). Inversement, l'accumulation au fil du temps d'une épaisse couche de bryophytes a plutôt tendance à ralentir la décomposition et le cycle des éléments nutritifs (Prescott et al. 2000; Crawford et al. 2003), et ainsi à diminuer la séquestration du carbone dans la canopée tout en l'augmentant dans le sous-bois non-vasculaire et les sols (Lecomte et al. 2006).

Il est donc important d'étudier comment la productivité du sous-bois peut être influencée par la canopée. Cette dernière exerce en effet une forte influence sur les conditions environnementales en sous-bois, notamment la disponibilité de la lumière et des ressources minérales (Riegel et al. 1995). La disponibilité de ces ressources semble généralement augmenter lorsqu'une plus grande proportion de feuillus intolérants à l'ombre tels que le peuplier faux-tremble (*Populus tremuloides*) est présente (Messier et al. 1998; Légaré et al. 2005b), favorisant une plus grande richesse et productivité de la végétation de sous-bois comparés aux peuplements de conifères tolérants à l'ombre (Hart & Chen 2008). Quant à l'hétérogénéité des ressources et la diversification des microhabitats induits par une canopée mixte (Brassard & Chen 2008; Brassard et al. 2008), leur effet sur le sous-bois est débattu et difficile à prévoir (Stevens & Carson 2002; Cardinale et al. 2009).

0.5. MÉTHODE GÉNÉRALE

Les quatre chapitres qui constituent cette thèse émanent tous de mesures et prélèvements effectués sur les mêmes placettes d'échantillonnage, lesquelles sont réparties entre deux zones géographiques distinctes. Sur la ceinture d'argile abitibienne, dans le nord-ouest québécois (Vincent & Hardy 1977; Veillette 1994), nous avons étudié des peuplements matures de première cohorte présentant un mélange « équitable » (proche de 50/50) entre l'épinette noire (*Picea mariana* (Mill.) BSP), un conifère tolérant à l'ombre, et le peuplier faux-tremble, un feuillu intolérant à l'ombre, ainsi que les peuplements monospécifiques dominés par chacune de ces deux espèces. Ces peuplements furent sélectionnés de sorte à limiter autant que possible tout facteur pouvant se confondre avec l'effet de la composition de la canopée : même situation topographique, même drainage, issus du même feu, mêmes caractéristiques de sol minéral. Un dispositif similaire fut mis en place dans le nord-ouest ontarien sur des sols aux textures plus grossières, mais en remplaçant le gradient tremble-épinette noire par un gradient entre le tremble et le pin gris (*Pinus banksiana* Lamb.), un conifère intolérant à l'ombre, et avec une proportion variable d'épinettes noires.

Tous les chapitres étudient donc l'effet du mélange sur les divers stocks et flux de carbone qui furent mesurés à partir de méthodes d'inventaires forestiers. Le premier présente une image instantanée du carbone stocké dans les tiges vivantes au moment de l'échantillonnage. Le deuxième s'intéresse également à la canopée, mais remonte dans le temps afin de révéler comment l'effet du mélange sur cette dernière a évolué au cours de la vie des peuplements. Le troisième chapitre baisse les yeux sur la végétation du sous-bois, estimant à la fois sa biomasse et sa croissance. Le chapitre final, quant à lui, réunit toutes ces données afin de déterminer comment la composition de la canopée influe sur l'ensemble des stocks et flux de carbone situés au-dessus du sol.

CHAPITRE I

MIXED-SPECIES EFFECT ON TREE ABOVEGROUND CARBON POOLS IN THE EAST-CENTRAL BOREAL FORESTS

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1.1. ABSTRACT

This study investigates the potential of mixed forest stands as better aboveground carbon sinks than pure stands. According to the facilitation and niche complementarity hypotheses, we predict higher carbon sequestration in mature boreal mixedwoods. Aboveground carbon contents of black spruce (*Picea mariana* (Mill.) BSP) and trembling aspen (*Populus tremuloides* Michx.) mixtures were investigated in the eastern boreal forest while jack pine (*Pinus banksiana* Lamb.) and trembling aspen were used in the central boreal forest. No carbon gain was found in species mixtures, while nearly pure trembling aspen stands contained the greatest amount of aboveground carbon, black spruce stands had the least and mixtures were intermediate with amounts that could generally be predicted by linear interpolation with stem proportions. These results suggest that for aspen, the potentially detrimental effect of spruce on soils observed in other studies may be offset by greater light availability in mixtures. On the other hand, for black spruce, the potentially beneficial effects of aspen on soils could be offset by greater competition by aspen for nutrients and light. The mixture of jack pine and trembling aspen did not benefit any of these species while inducing a loss in trembling aspen carbon at the stand level.

1.2. RÉSUMÉ

Cette étude s'intéresse au potentiel des peuplements forestiers mixtes en tant que puits de carbone aériens plus efficaces que les peuplements purs. En accord avec les hypothèses de facilitation et de séparation des niches écologiques, nous prédisons une plus grande séquestration du carbone dans les peuplements mixtes. Nous avons donc déterminé les stocks de carbone aériens dans des mélanges d'épinettes noires (*Picea mariana* (Mill.) BSP) et de peupliers faux-tremble (*Populus tremuloides* Michx.) situés dans la forêt boréale de l'Est, tandis que des mélanges de pin gris (*Pinus banksiana* Lamb.) et de peupliers faux-tremble furent plutôt utilisés dans la forêt boréale centrale. Les mélanges d'espèces ne présentaient aucun gain en carbone. Les peuplements dominés par le tremble contenaient la plus grande quantité de carbone aérien, les pessières la plus petite quantité, et les mélanges en contenaient des quantités intermédiaires qui pouvaient généralement être prédites par interpolation linéaire en fonction des proportions de tiges. Ces résultats suggèrent que pour le tremble, l'effet potentiellement néfaste de l'épinette sur les sols peut être compensé par une meilleure disponibilité de la lumière dans les peuplements mixtes. Parallèlement, pour l'épinette noire, l'effet potentiellement bénéfique du peuplier faux-tremble sur les sols pourrait être contrebalancé par une compétition accrue pour la lumière et les nutriments en sa présence. Le mélange de pin gris et de peuplier faux-tremble n'a apporté aucun bénéfice pour aucune des deux espèces tout en induisant une perte en carbone de tremble à l'échelle du peuplement.

1.3. INTRODUCTION

With the increasing attention given to the problem of global climate change, many researchers have focused on vegetation carbon sequestration as part of a possible solution(IPCC 2007). The emphasis has been put on forest ecosystems, which contain nearly 77% of vegetation carbon and 42% of soil carbon in the world (Bolin & Sukumar 2000). Although the main concern is about deforestation in tropical regions, the boreal forest, which contains about 30% of the Earth's phytomass (Bailey 1996), is an important sink in global C balance (Goodale et al. 2002).

Mixedwoods represent half of the Canadian boreal forest (CCFM 2000). While being globally disregarded in forest management, mixedwoods may have many advantages over pure stands, including higher productivity (Man & Lieffers 1999; Johansson 2003; MacDonald & Thompson 2003; Pretzsch 2003), which can translate into higher carbon sequestration. Thus, mixedwoods could contribute to increasing the carbon sink capacity of boreal forests. However, the mixture effect on productivity is controversial. Two mechanisms potentially inducing higher productivity in mixedwoods were proposed by Vandermeer (1989): i) facilitation, *i.e.,* a species promoting the growth or survival of another, mostly by improving abiotic conditions, and ii) niche complementarity, *i.e.,* a better and less competitive use of ecosystem resources between species having distinct functional traits (*e.g.,* a shade-tolerant species growing under an intolerant one). A commonly studied facilitation effect is a higher rate of litter decomposition and thus of nutrient cycling that could be induced by tree mixtures, particularly the admixture of a broadleaf species with a coniferous one (Côté et al. 2000; Prescott et al. 2000). The mixture effect on nutrition and litter decomposition proved largely dependent on the particular species used in the mixture and of the initial soil conditions (Rothe & Binkley 2001; Rothe et al. 2002; Gartner & Cardon 2004; Godefroid et al. 2005). Similarly, the mixture effect on productivity can be positive, negative, or null, depending on the species considered (Brown 1992; Kelty 1992; Chen & Klinka 2003; Lindén & Agestam 2003). Non-overlapping of the functional traits of species could be a factor that determines the outcome of the mixture effect, especially shade tolerance or intolerance (Chen et al. 2003). The mixture effect also depends on the environmental conditions, which can alter it even when the same species are used (Wang & Kimmins 2002; Green & Hawkins 2005).

This study investigating the mixture effect is part of a broader project in which all major carbon pools and fluxes will be estimated in the same stands, but this paper will focus on the carbon pool that is the most dynamic during a forest rotation, that of the living trees. Since the mixture effect can potentially differ depending on component species and abiotic conditions, two kinds of mixtures were studied: i) mature black spruce (*Picea mariana* (Mill.) BSP) and trembling aspen (*Populus tremuloides* Michx.) mixedwoods and their respective single species stands in the Clay Belt of northwestern Québec, and ii) mature jack pine (*Pinus banksiana* Lamb.), trembling aspen, and black spruce mixedwoods and respective pure stands on till deposits in northwestern Ontario. We hypothesized that i) given the potential positive effect of trembling aspen on soil quality (Côté et al. 2000; Prescott et al. 2000; Fenton et al. 2005; Légaré et al. 2005b) and the low shade cast by this shade-intolerant species (Canham et al. 1994; Messier et al. 1998), aspen's presence should have a positive effect on black spruce individual carbon content in mixedwoods, ii) on the other hand, black spruce is always overtopped by trembling aspen. Therefore, there is an anticipated increased light availability for aspen when competing with black spruce, but the adverse effect of black spruce on soil quality (Prescott et al. 2000; Crawford et al. 2003) could have a negative impact on aspen.

Thus, the balance between these two effects could induce a null effect of black spruce on trembling aspen carbon content in mixedwoods, and iii) because trembling aspen and jack pine have similar growth patterns (Longpré et al. 1994) with the latter being not very responsive to differences in soil fertility (Béland & Bergeron 1996), no mixture effect should be observed in aspen-pine mixedwoods. Meanwhile, black spruce could benefit from the higher soil quality induced by aspen and thus sequester more carbon under aspen than under jack pine.

1.4. MATERIALS AND METHODS

1.4.1. Study area

This study took place in two distinct areas of the boreal mixedwood forest region. The first was located in the black spruce – feathermoss forest of western Québec (Bergeron 1996), at the border of the Abitibi-Témiscamingue and Nord du Québec regions (49°08’N to 49°11’N, 78°46’W to 78°53’W). This area is part of the Clay Belt region of Québec and Ontario. This major physiographic region results from deposits left by the proglacial lakes Barlow and Ojibway at the time of their maximum expanse during the Wisconsinian glacial stage (Veillette 1994). The closest meteorological station is located in La Sarre (ca. 30 km south). Average annual temperature is 0.7°C and average annual precipitation totals 889.8 mm (Environment Canada 2007). All study sites were located on subhygric Grey Luvisols (Soil Classification Working Group 1996).

The second study area was located approximately 100 km north of Thunder Bay in northwestern Ontario (49°23’N to 49°36’N, 89°31’W to 89°44’W). Mean annual temperature and total average annual precipitation have been estimated at 0.9°C and 712.8 mm respectively by the BIOSIM model from 1977-2006 climatic data (Régnière & St-Amant 2007). The study was conducted on mesic upland sites whose soils are relatively deep glacial tills belonging to the Brunisolic order (Soil Classification Working Group 1996). Jack pine, trembling aspen, black spruce, and white birch (*Betula papyrifera* Marsh.) occur in this area in mixed dominance with white spruce (*Picea glauca* (Moench) Voss) and balsam fir (*Abies balsamea* (L.) Mill.).

1.4.2. Sampling design

Québec study: Twenty-four sampling plots were established across 8 blocks, located in the same 36 km^2-wide area (maximum distance between blocks: 7 km), dominated by black spruce with patches of aspen. All these stands originated from the same fire that occurred in 1916 (Légaré et al. 2005a). Within each block (numbered from I to VIII), three plots of distinct compositions were selected: pure black spruce, pure trembling aspen, and mixedwoods containing both species (hereafter named BS, TA, and MW, respectively). After measurements, one plot (VIII-BS) proved unsuitable and was therefore discarded from all analyses.

In our study, pure stands contained > 75% of the dominant species in relative basal area, whereas mixedwoods were selected so as to have fewer than 75% of one species in relative basal area (Table 1.1), with stems of different species evenly spread across the stand ("intimate" mixture). All three plots of a given block were separated by a distance of 40-100 m to minimize the variability within each block (complete random block design). We made sure the species proportions were different enough between plots belonging to a same block.

Ontario study: Six composition types were used in the Ontario study: pure jack pine (JP), pure aspen (TA), pine-aspen mixedwoods (MW) with the same selection criteria than in Québec, and the same three overstory types with a black spruce sub-canopy of at least 15% of plot total basal area (respectively denoted JPbs, TAbs, MWbs, see Table 1.1). Each composition type was replicated between two and five times. The study plots were established across an area of approximately 250 km^2. All plots originated from fire with mean breast height age ranging from 59 to 74 years old for pine and aspen and between 51 and 58 years old for black spruce. A completely randomized sampling design was deployed.

Table 1.1 Overstory characteristics of the study plots.

Area	*Composition*	*% Black spruce basal area ± SE*	*% Trembling aspen basal area ± SE*	*% Jack pine basal area ± SE*	*% Other species basal area ± SE**	*Spruce mean breast height age ± SE (yrs)*	*Aspen mean breast height age ± SE (yrs)*	*Pine mean breast height age ± SE (yrs)*	*Total density ± SE (stems/ha)†*	*Number of replicates*
Québec	BS	89.4 ± 4.2	1.8 ± 0.7	-	8.8 ± 4.0	69.5 ± 0.9	-	-	3115 ± 380	7
	MW	33.8 ± 3.6	59.5 ± 3.5	-	6.7 ± 1.6	72.0 ± 0.8	75.8 ± 1.1	-	1578 ± 125	8
	TA	8.9 ± 1.8	88.5 ± 2.6	-	2.6 ± 2.3	69.2 ± 1.4	78.6 ± 1.1	-	1065 ± 105	8
Ontario	JP	7.5 ± 2.0	0.0	83.2 ± 1.9	9.3 ± 1.6	-	-	62.9 ± 1.9	2445 ± 128	4
	JPbs	29.2 ± 3.9	3.6 ± 2.3	64.1 ± 4.9	3.0 ± 1.5	51.9 ± 0.8	-	65.2 ± 0.9	2450 ± 240	3
	MW	6.7 ± 1.4	30.7 ± 7.0	48.2 ± 6.4	14.4 ± 6.1	-	66.2 ± 2.8	62.3 ± 1.9	1300 ± 168	4
	MWbs	26.0 ± 4.8	27.1 ± 3.6	44.0 ± 10.9	2.9 ± 2.5	50.6 ± 3.8	64.6 ± 1.4	68.4 ± 2.0	2463 ± 238	2
	TA	0.0	95.2 ± 1.2	0.7 ± 0.7	4.1 ± 0.9	-	68.7 ± 1.0	-	780 ± 43	5
	TAbs	20.6 ± 3.7	68.8 ± 4.3	3.5 ± 1.9	7.0 ± 1.9	55.8 ± 1.2	65.5 ± 0.9	-	2045 ± 205	4

* Other species consist for the Québec study of jack pine and balsam fir, and for the Ontario study of balsam fir, white spruce, and white birch.

† Total density includes class 1 snags (see text for details).

1.4.3. Sampling and measurements

For both study areas, all sample plots were circular with an area of 400 m^2 with at least a 5 m buffer zone of the same composition. In each plot, all trees > 5 cm DBH (diameter at breast height, 1.3 m) were numbered and measured for species, DBH, and height. Heights were measured using a Vertex clinometer. In order to assess plot density, all snags were also numbered and their decay classes noted in order to identify snags belonging to decay class 1 (*i.e.*, recent snags mostly intact in branches, bark, and top). Mean breast height age was determined by coring a subsample of 20-40 trees in each plot. The cores were then measured and analyzed using a Velmex sliding-stage micrometer and TSAPWin (F. Rinn Engineering Office) software along with COFECHA (Grissino-Mayer 2001). Measurements and sampling took place in June 2006 for the Québec study and in May 2007 for the Ontario study.

1.4.4. Similarity of sites

In order to ensure all sites were of similar quality in each region, we selected stands carefully according to the following criteria. All selected stands were upland sites with no or very little slope. All stands in the same study area had the same moisture regime (mesic in Ontario and subhygric in Québec), and were on the same kind of deposits (clay in Québec and tills in Ontario, see 1.4.1).

Similarity of sites was then validated by soil intrinsic physical and chemical properties: *i.e.*, soil textures, CEC, total N and total C content of the mineral layer at a depth of 35-55 cm (Laganière, unpublished data). No significant differences could be detected between composition types at an error threshold of 0.1 using analyses of variance, except for clay percentage in the Ontario study. However, none of our response variables (individual tree carbon content, total stand carbon content, and height-diameter ratios) appeared to be affected by any of the soil variables. Soil variables had thus no influence on our analyses, confirming that all sampled stands within a study area were comparable.

1.4.5. Data analyses

The aboveground biomass of each tree was estimated from DBH and height with the allometric equations established by Lambert et al. (2005). Carbon was assessed from biomass with the mean carbon content values provided by Lamlom and Savidge (2003): spruces 0.5039 kgC.kg^{-1}, jack pine 0.504 kgC.kg^{-1}, trembling aspen 0.4709 kgC.kg^{-1}, white birch 0.4837 kgC.kg^{-1}, balsam fir 0.5008 kgC.kg^{-1}. Given that no such value were available for black spruce, we used that of white spruce in our calculations.

For each species of interest of the Québec study, differences in carbon content and height-diameter ratio (H-D ratio, potential indicator of competition for light) at the individual tree level were tested among composition types with total stand density as covariants in hierarchical mixed-effect linear models (Pinheiro & Bates 2000) with Block/Composition as the random effect. As class 1 snags can be considered as having been influential on stand growth until recently, they were included in total plot density. Interaction between composition and density was removed when it was insignificant at a threshold of 0.1. Differences in total stand carbon content were tested similarly by summing all individuals within the stand. Tree density without snags was used as a covariant. Comparisons between the individual levels of each factor were processed using Wald's t-tests. Given that we had to discard some improper sampled sites from the analyses, we were unable to retain a balanced design, thus decreasing the statistical power of our tests. To counterbalance this we chose to use a 0.1 error threshold for all of our analyses in order to decrease the risk of making type II errors. This risk could have otherwise been too high particularly in the Ontario study where the number of replicates was lower due to a higher number of composition types.

To test for a positive, negative or neutral effect of mixedwoods on carbon pools at the stand level, observed carbon values in MW plots were compared for each block with expected carbon values. The calculation of the expected carbon values (C_{Exp}) is based on the following: if there is no composition effect on the total stand carbon content, then the carbon content in MW plots should follow the 'additive line' displayed in Fig. 1.1. This corresponds to the C_{Exp} value that appears on the line, and is the null hypothesis. If the observed carbon value in MW for the same proportion of species is significantly higher or lower than C_{Exp}, then we have a positive or negative mixture effect, respectively.

C_{Exp} was calculated as follows:

$$[1]\ C_{Exp} = (\alpha \times pBs_{MW}) + (\beta \times pTa_{MW})$$

with pBs_{MW} being the proportion of spruce density in MW, pTa_{MW} the proportion of aspen density in MW, and α and β having the same meaning as in Fig. 1.1.

As BS and TA plots were not 100% black spruce and 100% trembling aspen respectively, we do not know the α and β values, but they can be derived from the BS and TA plots:

$$[2]\ C_{BS} = (\alpha \times pBs_{BS}) + (\beta \times pTa_{BS})$$

$$[3]\ C_{TA} = (\alpha \times pBs_{TA}) + (\beta \times pTa_{TA})$$

with C_{BS} being the carbon content in BS plot, C_{TA} the carbon content in TA plot, pBs_{BS} the proportion of spruce density in BS plot, pTa_{BS} the proportion of aspen density in BS plot, pBs_{TA} the proportion of spruce density in TA plot and pTa_{TA} the proportion of aspen density in TA plot.

The solution derived from [2] and [3] for α and β is the following:

$$[4]\ \alpha = (C_{BS} \times pTa_{TA} - C_{TA} \times pTa_{BS}) / (pTa_{TA} \times pBs_{BS} - pBs_{TA} \times pTa_{BS})$$

$$[5]\ \beta = (C_{TA} - \alpha \times pBs_{TA}) / pTa_{TA}$$

We computed α and β and then C_{Exp} for each block individually. The expected and observed carbon values were then compared using a paired Student's t- test, with an error threshold of 0.1. The same principle was applied to compare black spruce carbon contents and trembling aspen carbon contents instead of total carbon contents. In these cases, however, the "additive line" was defined by the single-species plot of the considered species (BS plot for spruce and TA plot for aspen) and by a theoretical plot with 0% of the considered species and thus with no carbon of this species, which corresponded to the graphic origin. The species other than aspen and spruce were not included in this analysis. We excluded them from the carbon content and the species density proportion.

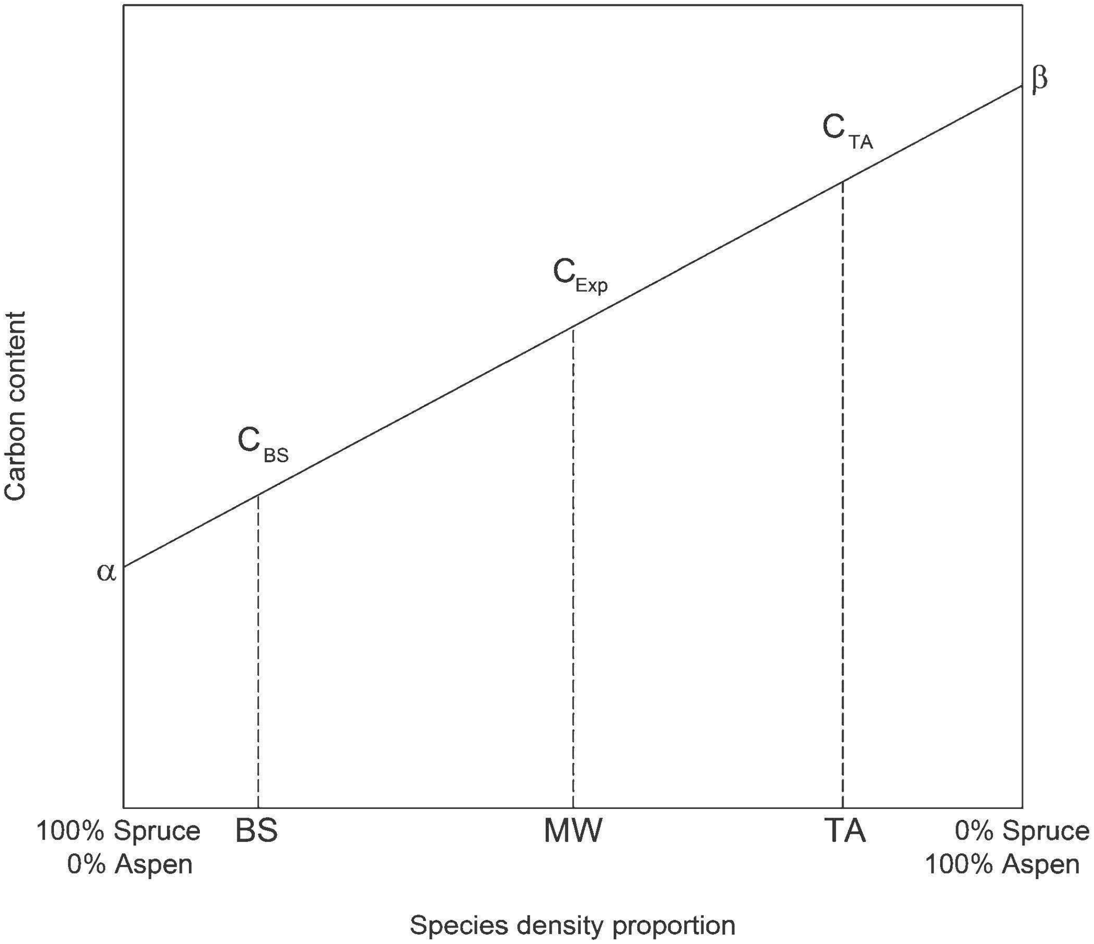

Figure 1.1 Graphical representation of the null hypothesis for stand level carbon comparisons: carbon content in BS, MW or TA plots along species density proportion. C_{BS} and C_{TA} are the carbon content in BS and TA plots, respectively, α and β the carbon content in absolutely pure black spruce and trembling aspen plots respectively. See text for details.

The analyses for the Ontario study were similar to those conducted for the Québec data, except that three species were studied instead of two, and that no random block effect could be included in the mixed linear models. The random effect in this case was thus only the individual plots, to take into account the non-independence of trees within the same plot. Comparisons of expected versus observed values in mixedwoods were also conducted similarly than in the Québec study, but by separately analyzing plots without black spruce sub-canopy (TA-JP means vs. MW) from one side and plots with black spruce (TAbs-JPbs means vs. MWbs) from the other side, studying only pine and aspen responses, and thus reducing black spruce to a binary factor (absence/presence). This was necessary as no black spruce dominated stands could be sampled in the Ontario study. TAbs vs. TA and JPbs vs. JP were also compared, but by using only aspen and pine carbon values and assuming a null amount of carbon of these species in the non-sampled theoretical pure black spruce plot used for expected value calculations. As there was no block here, for each analysis a single value of α and β was computed from all the single-species plots, and then used separately for each MW (or MWbs) plot to compute C_{Exp} values depending on the proportion of each species in the mixed plot. Thus we could generate pairs of observed and expected values to compare in the t-test.

All statistical analyses were performed using R software version 2.6.1 (R Development Core Team, 2007).

1.5. RESULTS

1.5.1. Québec study

1.5.1.1. Individual tree level

Mean individual carbon content of both species decreased with increasing stand density (Fig. 1.2a, Table 1.2). Individual C content of black spruce was higher in BS and MW stands than that in TA stands (Fig. 1.2a, Table 1.2). For trembling aspen, as only a few aspen stems were found in BS plots, its individual responses were compared only between MW and TA plots and showed no difference in mean C content between the two stand types (Fig. 1.2a, Table 1.2).

Mean H-D ratios of both species increased with stand density (Fig. 1.2b, Table 1.2). For black spruce, this increase was lower in BS stands than TA stands with MW stands being intermediate (Fig. 1.2b, Table 1.2). For trembling aspen, H-D ratios were lower in MW than in TA stands (Fig. 1.2b, Table 1.2). Table 1.2 displays the global effects for each variable, rather than the individual comparisons.

1.5.1.2. Stand level

Density had no effect on total carbon content at the stand level, but carbon content differed among three stand types. It was higher in TA and lower in BS, with MW being intermediate (Fig. 1.3, Table 1.2). Comparisons of expected versus observed values in MW plots showed a smaller amount of spruce carbon in MW than expected, whereas aspen C content and total stand C content did not differ between expected and observed values (Fig. 1.4)[a].

1.5.2. Ontario study

1.5.2.1. Individual tree level

Results for each species were compared only for the compositions where they were expected to be found abundantly (*i.e.*, only JPbs, MWbs and TAbs stands for black spruce, TA, TAbs, MW and MWbs for trembling aspen, JP, JPbs, MW and MWbs for jack pine). Black spruce mean carbon content was smaller in MWbs than in TAbs stands (Fig. 1.5a, Table 1.2). Mean carbon content per tree of trembling aspen and jack pine decreased with increasing density. This decrease was stronger for jack pine in MW than in JPbs and MWbs stands. There was no response to composition for trembling aspen (Fig. 1.5a, Table 1.2).

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[a] It appeared after the publication of this chapter that using carbon proportions of each species in MW rather than density is more adequate and leads to more straightforward results: an increase in spruce carbon and a decrease in aspen carbon in MW compared to the expected values, resulting in an overall lower amount of carbon in oberved vs. expected MW. These results are explained by the differences in average density between stand type and its effects on average stem size for each species, and therefore do not change our conclusions. Results for the Ontario study are unaffected.

Table 1.2 Results of analyses of covariance for the mixed linear models

Area	Dependent variable	Fixed effect	F-value	p-value
Québec	Black spruce mean C	Density	31.239	<0.001***
		Composition	7.040	0.01**
	Black spruce mean H-D ratio	Density	36.216	<0.001***
		Composition	0.358	0.708
		Composition x Density	2.826	0.107
	Trembling aspen mean C	Density	4.767	0.072*
		Composition	1.568	0.257
	Trembling aspen mean H-D ratio	Density	5.607	0.056*
		Composition	4.213	0.086*
	Total C	Density	0.007	0.935
		Composition	4.808	0.029*
Ontario	Jack pine mean C	Density	34.531	0.002**
		Composition	1.080	0.437
		Composition x Density	4.104	0.081*
	Jack pine mean H-D ratio	Density	3.272	0.108
		Composition	0.587	0.641
	Black spruce mean C	Density	0.861	0.396
		Composition	3.616	0.107
	Black spruce mean H-D ratio	Density	5.989	0.058*
		Composition	2.556	0.172
	Trembling aspen mean C	Density	3.840	0.079*
		Composition	1.258	0.341
	Trembling aspen mean H-D ratio	Density	0.470	0.509
		Composition	0.213	0.885
	Total C	Density	0.459	0.509
		Composition	1.126	0.388

* $p < 0.1$
** $p < 0.01$
*** $p < 0.001$

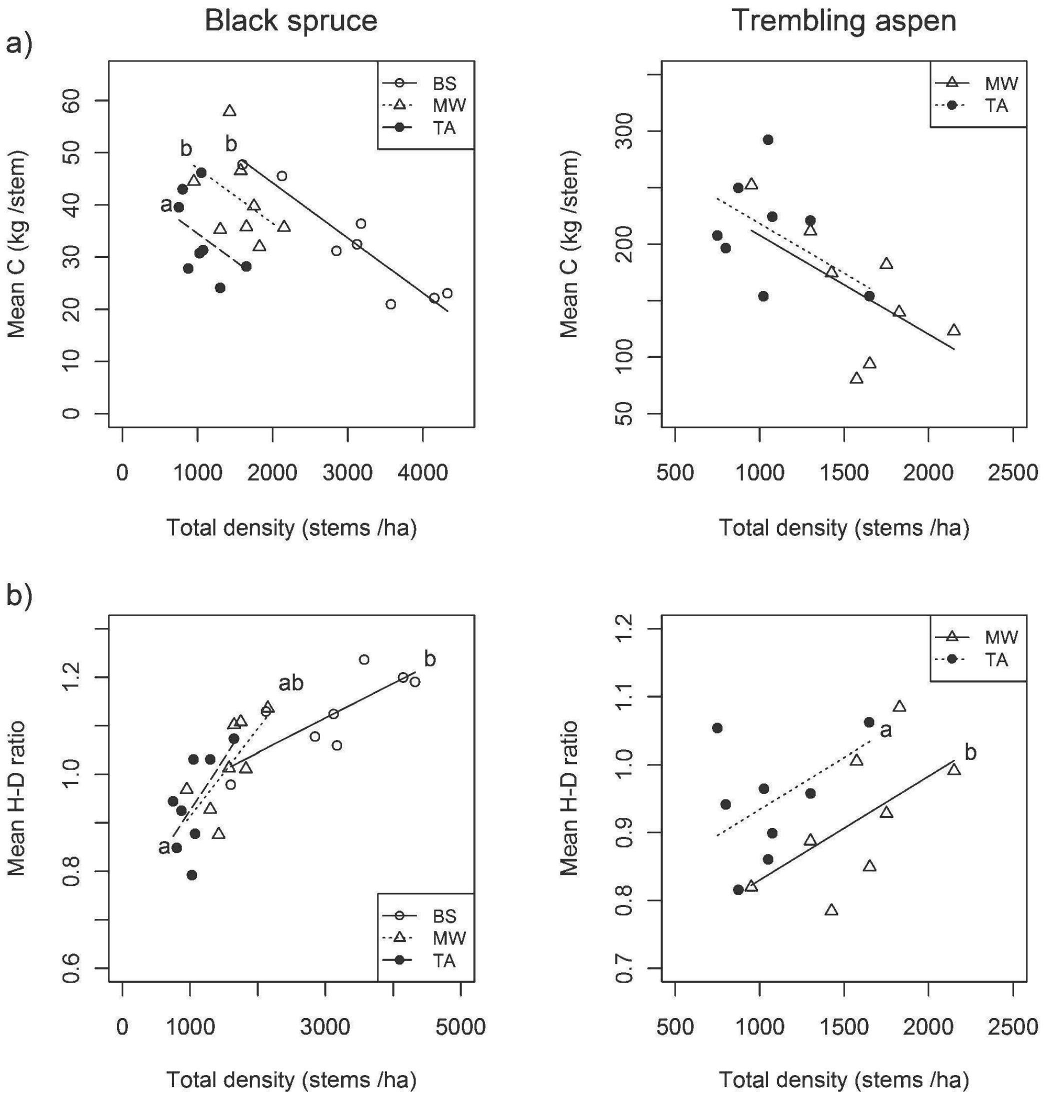

Figure 1.2 a) Mean tree carbon contents and b) mean tree H-D ratios of black spruce and trembling aspen in relation to density and composition, in the Québec study. Letters on the graph show significant differences for the composition type effect or the composition-density interaction effect at α=0.1.

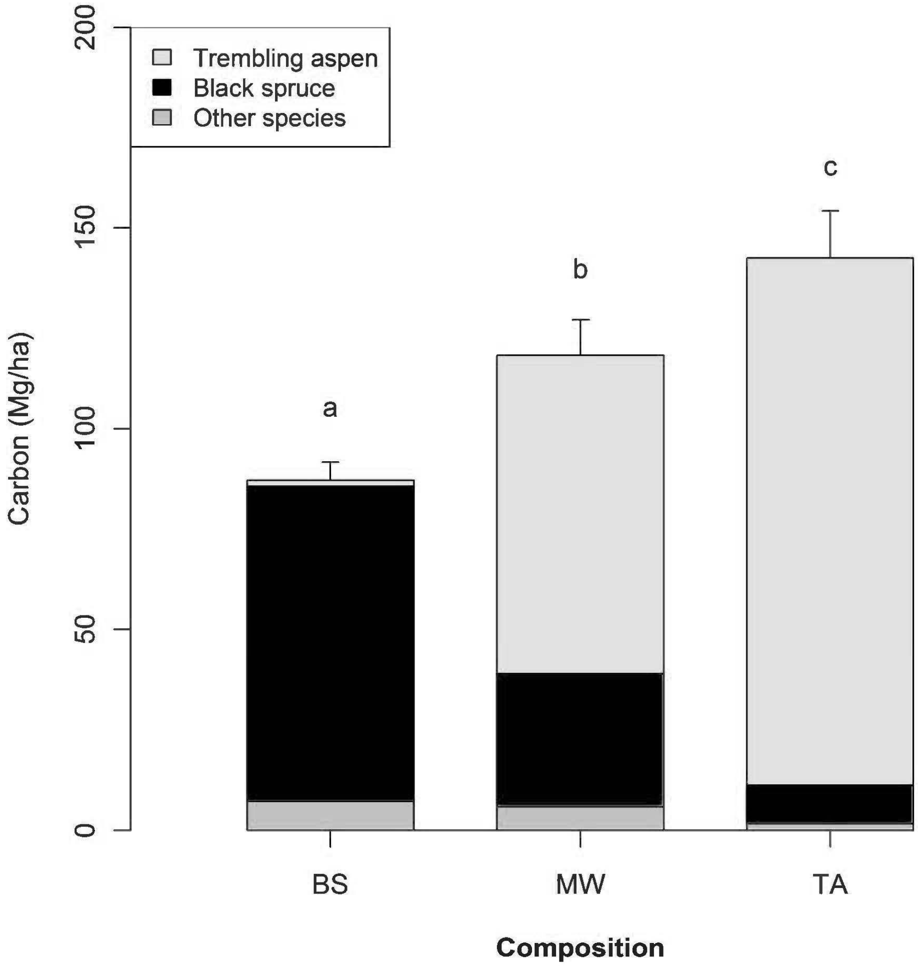

Figure 1.3 Carbon partition between species for each composition at the stand level, for the Québec study. Significant differences are shown by letters for the composition type effect on total stand carbon at α=0.1. Displayed standard errors are calculated from total carbon.

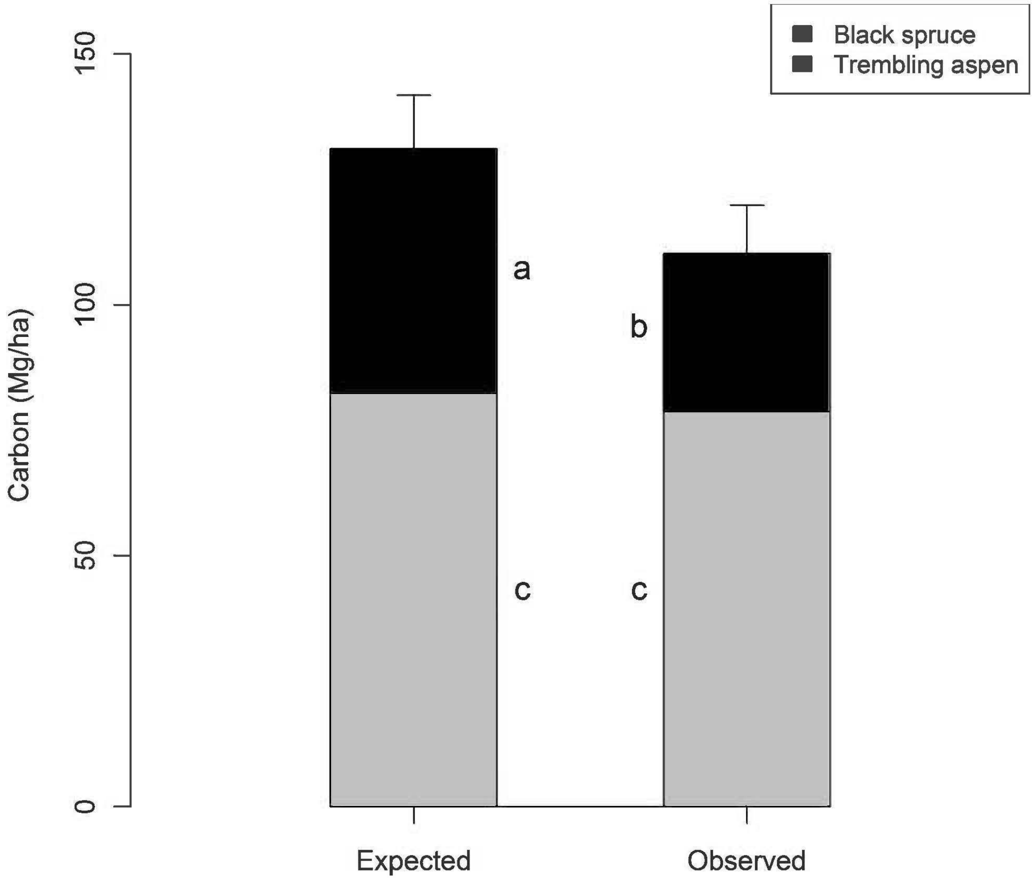

Figure 1.4 Expected and observed carbon values for each species in MW stands of the Québec study. Significant differences are shown separately for each species and at $\alpha=0.1$. Displayed standard errors are calculated from total carbon.

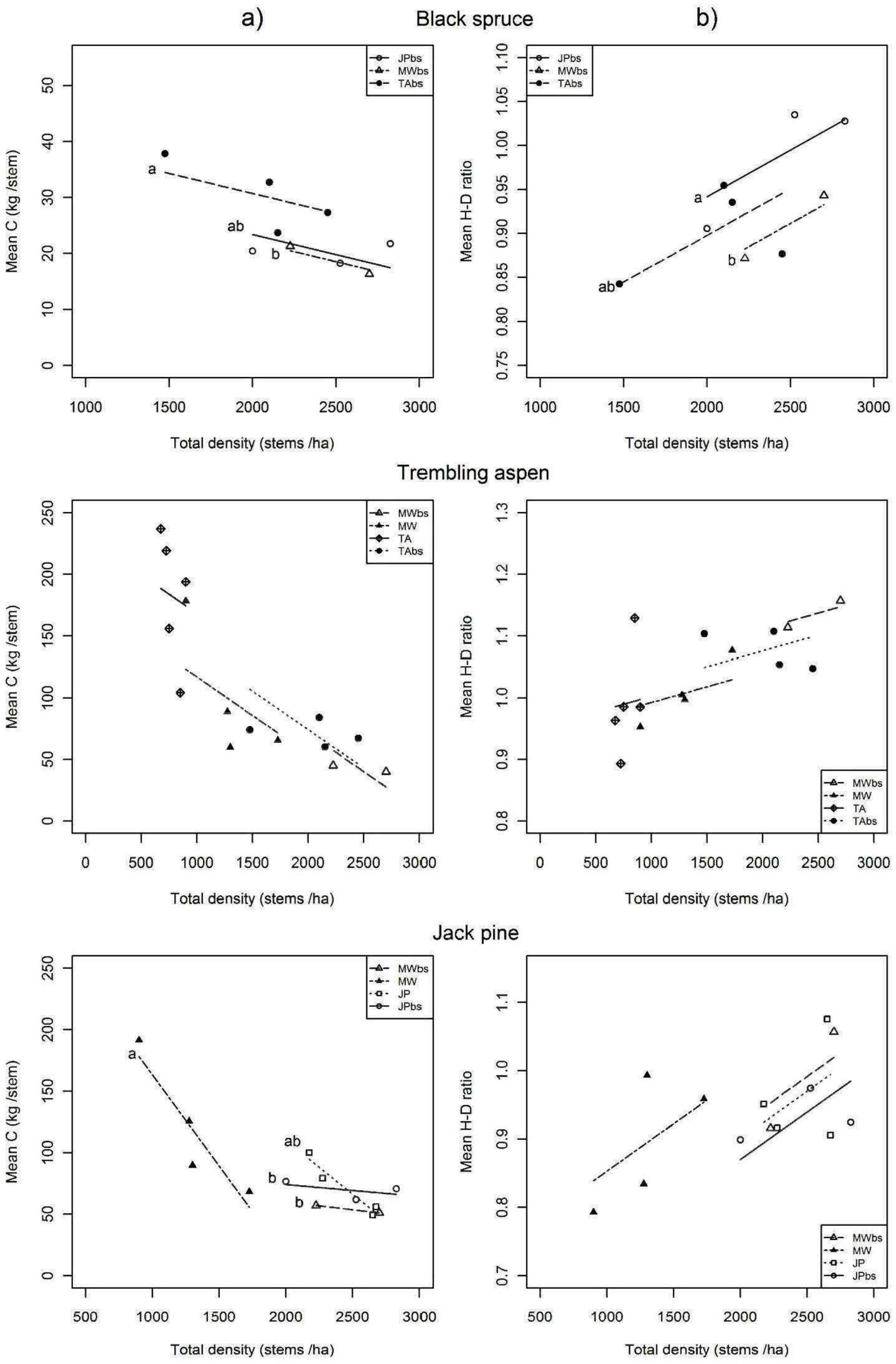
a)
Black spruce
b)
JPbs
MWbs
TAbs
Mean C (kg /stem)
Mean H-D ratio
Total density (stems /ha)
a
ab
b
Trembling aspen
MWbs
MW
TA
TAbs
Jack pine
JP
JPbs
0
10
20
30
40
50
0.75
0.80
0.85
0.90
0.95
1.00
1.05
1.10
1000
1500
2000
2500
3000
50
100
150
200
250
0.8
0.9
1.0
1.1
1.2
1.3
500
0.7

Figure 1.5 (previous page) a) Mean tree carbon contents and b) mean tree H-D ratios of black spruce, jack pine and trembling aspen in relation to density and composition, in the Ontario study. Letters on the graph show significant differences for the composition type effect or the composition-density interaction effect at α=0.1.

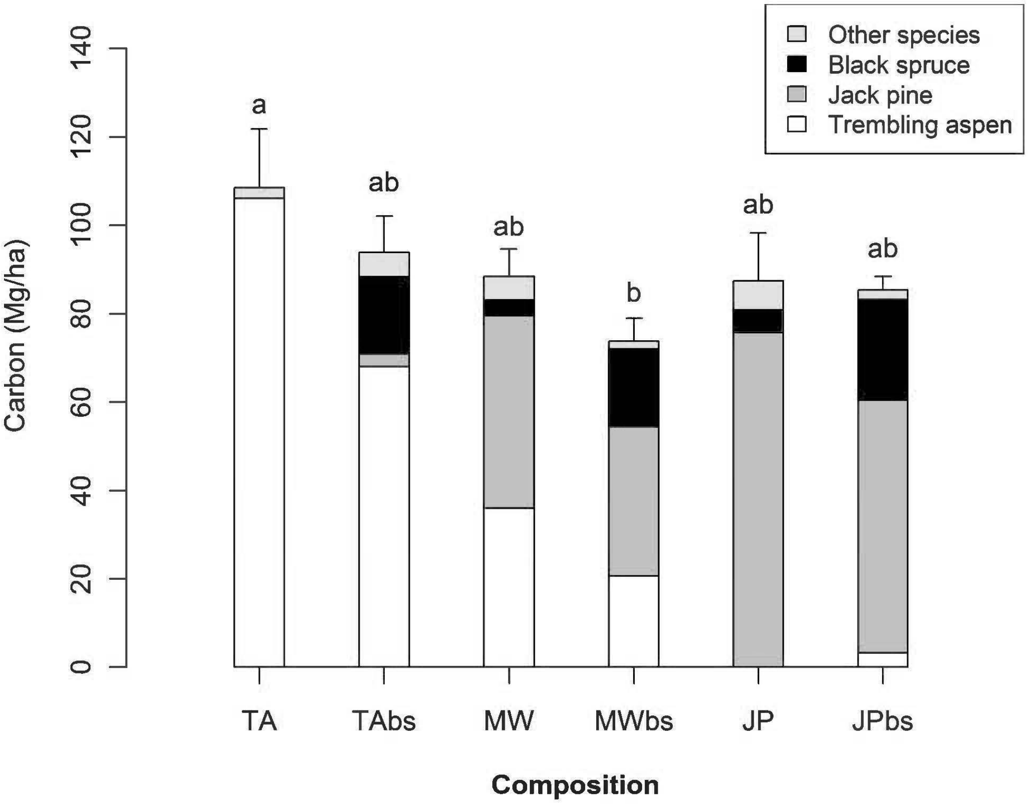

Figure 1.6 Total stand carbon partitioned by species in relation to stand composition type for the Ontario study. Significant differences are shown at α=0.1 Displayed standard errors are calculated from total carbon.

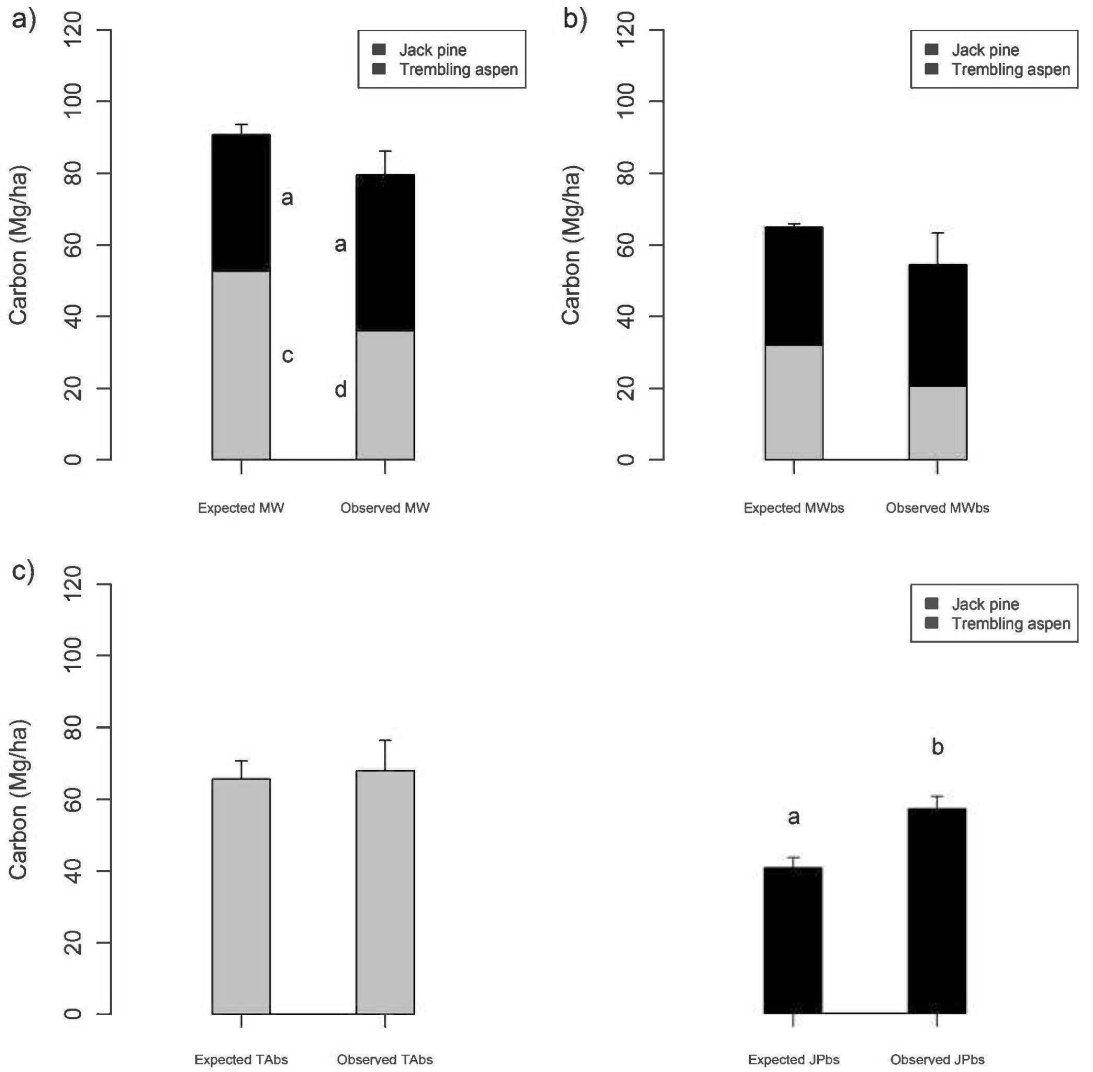

Figure 1.7 Expected and observed total stand carbon of a) jack pine and trembling aspen in MW stands, b) jack pine and trembling aspen in MWbs stands, c) the dominant overstory species in TAbs (*i.e.* trembling aspen) and JPbs (*i.e.* jack pine) stands. Significant differences are shown separately for each species and at α=0.1. Displayed standard errors are calculated from total carbon.

Black spruce mean H-D ratios increased with increasing density (Fig. 1.5b, Table 1.2). These ratios were also smaller in MWbs plots than in JPbs plots (Fig. 1.5b, Table 1.2). Those of jack pine and trembling aspen responded neither to density nor composition (Fig. 1.5b, Table 1.2).

1.5.2.2. Stand level

Total carbon content did not change with density but was lower in MWbs than in TA stands (Fig. 1.6, Table 1.2). The paired t-tests between expected and observed carbon values showed a negative effect for trembling aspen in MW plots, and a positive effect for jack pine in JPbs plots (Fig. 1.7).

1.6. DISCUSSION

Carbon pools in the overstory were highly dependent on forest composition. Trembling aspen dominated stands are the most efficient ones for net carbon accumulation 90 years following fire in the Québec study (142 MgC.ha^{-1}), while black spruce stands are less efficient (87 MgC.ha^{-1}). Given the lower commercial value of trembling aspen, spruce-aspen mixedwood could be considered as a good compromise (118 MgC.ha^{-1}). Perhaps due to the absence of pure black spruce stands, differences in the Ontario study are less pronounced, ranging from 74 MgC.ha^{-1} (MWbs) to 108 MgC.ha^{-1} (TA).

1.6.1. Black spruce and trembling aspen relationships

The accumulation of a thick organic layer in black spruce stands (the paludification process) is slower when aspen is present (Fenton et al. 2005) while the surface soil concentrations of exchangeable cations (K, Ca and Mg) have been shown to increase with aspen presence in black spruce stands (Légaré et al. 2005b). Thus the presence of aspen may favour the development of a warmer and nutrient rich soil that should potentially increase spruce growth (Thiffault & Jobidon 2006). Such a facilitation effect is not observed in our Québec experiment, as black spruce individual carbon pools in mixedwood plots are not different from those in black spruce plots for equivalent densities, and are even lower in trembling aspen plots. Légaré et al. (2004) found, using forest inventory data, a positive effect of aspen on black spruce individual growth only when aspen represents less than 40% of stand basal area. As our MW plots are always beyond this threshold (Table 1.1), the absence of an effect in MW is consistent with the results of Légaré et al. (2004). The following trade-off hypothesis could explain our results: the positive impact of aspen on black spruce due to improved soil conditions is gradually offset as aspen proportion increases. This increasing negative impact could be linked to competition for light, as trembling aspen always overtops black spruce. The fact that the density effect on black spruce H-D ratios is stronger in TA stands could confirm this hypothesis. This result must be interpreted carefully though, for tree morphology is not only driven by competition for light, but also by wind exposure (Holbrook & Putz 1989; Meng et al. 2008). As overtopping from aspen generates both increased shade and shelter from the wind, these two factors potentially explaining the response of H-D ratios to density and composition are, unfortunately, indistinguishable in the Québec study. Increased competition for soil resources could also be an explanation of aspen negative impact on spruce in TA stands.

On the Ontario side, spruce H-D ratios are smaller under a mixed jack pine-trembling aspen canopy than under jack pine (another shade-intolerant, overtopping species). As wind sheltering provided to black spruce is not likely to change between pine or aspen, this suggests that spruce might actually benefit from the leafless periods of aspen, as was hypothesized by some authors (Green 2004). In this case, however, spruce H-D ratios should also be significantly smaller in TAbs plots, which is not the case. This result might then be only an artefact due to the small number of proper MWbs replicates left for analysis (only two instead of four for most of the other composition types). It is thus difficult to tell whether the gain in black spruce individual growth in TAbs plots can be partly attributed to this reduction of shade during the aspen leafless period, and thus to niche separation, or only to the positive effect of aspen on soil conditions compared with jack pine (Longpré et al. 1994). Carbon pools in trembling aspen individual trees do not respond to composition in either the Québec or the Ontario study. Aspen H-D ratios in the Québec study are smaller in MW plots compared with TA plots. This would only confirm the obvious niche separation: aspen trees suffer less from light competition when neighbouring a spruce tree than an aspen tree. This reduced competition, however, is not followed by any increase in carbon content. Considering that trembling aspen is an early-successional species with high resource requirements, another trade-off hypothesis seems likely in this case: the benefit of growing with a less competitive species is offset by the negative impact of black spruce on soil conditions (Légaré et al. 2005b).

Based on the absence of individual responses in mixedwoods from both species, we would expect a purely neutral effect at the stand level (*i.e.*, MW values would be linearly predictable from those of TA and BS plots). This is generally the case except for black spruce, for which values in MW plots are significantly lower than expected from TA and BS plots. This can nevertheless be explained by the strongly reduced density of black spruce in the presence of aspen: one aspen stem occupies a space in a MW stand that would be occupied by several spruce stems in a BS plot. This loss of "growing space" for black spruce in MW accounts for the loss of spruce carbon compared with what was expected. This loss is, however, apparently too weak to be significant when total stand carbon contents (*i.e.,* for all species) are compared.

1.6.2. Trembling aspen and jack pine relationships

Results from the Ontario study showed no effect of jack pine presence on trembling aspen, while the interaction results for jack pine individual carbon contents showed that the density effect on jack pine was stronger in MW plots than in JPbs (and MWbs, but see the remark made previously on these) plots. As pine is in competition with fast-growing aspen in MW and with black spruce in JPbs, this result is not surprising. Although jack pine H-D ratios did not react to composition, these results might suggest that aspen could be a slightly better competitor against pine than pine is against itself. However, this difference was too weak to have an impact at the stand level, as expected and observed values in MW and MWbs are not significantly different for jack pine, which confirms previous results demonstrating the absence of jack pine response to trembling aspen presence (Longpré et al. 1994). This is easily explained by the fact that these two species share the same niche: fast-growing shade-intolerant species with similar growth and space occupancy patterns (Béland et al. 2003), while the broadleaf effect on soil conditions proved non-determinant to jack pine growth compared with competition for light (Longpré et al. 1994; Béland & Bergeron 1996). Interestingly, there was a negative effect on trembling aspen in MW at the stand level that was not statistically detected at the tree level, but which confirmed the tendency that could be observed (see Fig. 1.5). Even though jack pine effect on soil properties is not comparable to that of black spruce (Crawford et al. 2003), it could have made a difference on the low fertility sandy soils of the Ontario study (Ste-Marie et al. 2007).

Finally, the positive effect on jack pine at the stand level in JPbs plots is probably due to the fact that because of the differences in spatial occupancy between pine and spruce, 50% of a stand's density does not represent the same number of stems whether JP or JPbs plots are considered. This result thus only represents a gain in space for jack pine in JPbs plots, similar to the loss of space for black spruce in MW plots in the Québec study.

1.7. CONCLUSION

Our study showed that interspecific interactions vary depending on the considered species. The mixture effect thus seems detrimental when two competitive species are mixed (trembling aspen with jack pine). The adverse effect of black spruce on soil condition likely explains why a more beneficial result has not been observed here when complementary species were mixed (trembling aspen with black spruce). Thus, it may be possible that mixing shade-intolerant species with slow-growing shade-tolerant ones that would not have such a detrimental effect on forest floor properties (*e.g.*, white spruce or balsam fir) could lead to significantly higher carbon pools in mixedwoods for the shade-intolerant species. It must also be remembered that while they contain less spruce carbon, spruce-aspen mixedwoods have a greater amount of total carbon compared with pure black spruce stands, and thus could be a potentially interesting compromise between carbon sequestration and spruce yield.

Previous results from Légaré et al. (2004) also point out the importance of the proportion of the mixture, as black spruce volume was greater at the individual and stand levels when aspen represented between 5 and 40% of stand basal area. This strongly suggests that some specific proportion of tree mixtures may have a positive impact on aboveground carbon sequestration. While in the present case where the potentially beneficial soil effect of trembling aspen in 90-year-old black spruce stands did not seem sufficient to have an impact on black spruce growth, it might, however, in the long term prevent or delay the stands from becoming unproductive as a result of paludification, as documented by Simard et al. (2007) on adjacent sites. On the other hand, the jack pine-black spruce mixture does not seem to have much potential, as the overtopping of spruce by pine may not be counterbalanced by any improvement in soil conditions. The positive long-term effect on carbon sequestration in spruce-aspen mixtures, however, could be counterbalanced by the lower carbon accumulation in the soil organic layer as compared with old paludified black spruce stands. This is why a definitive answer concerning the potential of boreal mixedwoods as carbon sinks will need to consider all pools and fluxes. The information provided by these ongoing studies may also shed light on some of the issues raised in this paper by confirming or refuting the hypotheses proposed to explain our results.

1.8. ACKNOWLEDGMENTS

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CHAPITRE II

EFFECT OF TIME ON COMPETITION AND FACILITATION BETWEEN TREE SPECIES

Xavier Cavard, Yves Bergeron, Han Y.H. Chen et David Paré

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2.1. ABSTRACT

Processes governing tree interspecific interactions, such as facilitation and competition, may vary in strength over time. This study tried to unveil them by performing dendrometrical analyses on black spruce (*Picea mariana* (Mill.) BSP), trembling aspen (*Populus tremuloides* Michx.) and jack pine (*Pinus banksiana* Lamb.) trees from pure and mixed mature boreal forest stands in the Clay Belt of northwestern Quebec and on the tills of northwestern Ontario. We cored 1430 trees and cut 120 for stem analysis across all stand composition types, tree species and study regions. Aspen annual growth rate was initially higher when mixed with conifers, but then progressively decreased over time, probably due to the negative effect of coniferous litters on soil quality, while jack pine growth rate did not differ with black spruce presence throughout all stages of stand development. When mixed with aspen, black spruce showed a contrary response to aspen, i.e., an initial loss in growth possibly due to increased shading but a positive gain later on due to a facilitation effect of aspen litter. In the Quebec region however, both aspen and spruce responses in mixed stands reversed between 37 and 54 years, suggesting that more complex processes such as belowground competition might have been at work on the richer soils of the Clay Belt. Overall, our results demonstrate that interspecific interactions were present and tended to change over time and among species. Our results also suggest that the nature of interspecific interactions may differ with soil nutrient availability.

2.2. INTRODUCTION

Processes governing plant interactions have been the subject of many debates. While competition has been thought to rule plant interactions for decades, the role of facilitative processes has progressively become more recognized (Callaway 1995). It appears that both negative and positive interactions occur between plant species with the balance between them being affected by factors such as plants age or environmental stress (Callaway & Walker 1997; Brooker et al. 2008). Assessing this balance becomes complex in mixed forest stands where trees are large in size and long-lived, and can thus impose a great amount of lasting control on their environmental conditions, while their interactions may vary over time (Filipescu & Comeau 2007).

Two mechanisms have been proposed to be associated with positive interactions (Vandermeer 1989). The first is facilitation, i.e., one species promoting the growth or survival of the others (e.g., improvement of abiotic conditions), and the second is niche complementarity (or niche segregation), i.e., a better or less competitive use of ecosystem resources between species having different functional traits (e.g., a shade-tolerant species growing with an intolerant one). Attempts at confirming these mechanisms unfortunately led to inconsistent results. The hypothesized facilitation effect of litter mixing on nutrition and litter decomposition appears to be dependent on the tree species studied and their growing environments (Rothe & Binkley 2001; Rothe et al. 2002; 2003; Gartner & Cardon 2004). Mixture effect on tree productivity (which may be the outcome of both facilitation and niche complementarity) shows the same dependence on the identity of the tree species in the mixture (Brown 1992; Kelty 1992; Kelty 2006) and environmental conditions (Wang & Kimmins 2002; Green & Hawkins 2005). This variability is not necessarily surprising, as niche complementarity relies on the non-overlapping of functional traits of the tree species in the mixture, particularly for interspecific interactions to be less competitive than intraspecific ones (Chen et al. 2003; Canham et al. 2006; Simard & Vyse 2006).

Mixtures of a shade-tolerant species like black spruce (*Picea mariana* (Mill.) BSP) with a shade-intolerant one like jack pine (*Pinus banksiana* Lamb.) or trembling aspen (*Populus tremuloides* Michx.) could result in niche complementarity because of potential canopy stratification. The outcome could be even more positive in the case of spruce-aspen mixtures due to reduced belowground competition (Strong & La Roi 1983; Brassard et al. in preparation) and the facilitation effect of aspen litter (Côté et al. 2000; Prescott et al. 2000; Fenton et al. 2005; Légaré et al. 2005b). Interspecific interactions between those three tree species, however, appeared to be mostly neutral in terms of the aboveground biomass production 90 years after fire in even mixtures (Chapter I). While neutral interactions between trembling aspen and jack pine have been shown and are not surprising given their similar growth patterns (Longpré et al. 1994), the apparent neutral relationships between black spruce and trembling aspen in even mixtures could be the result of a balance between positive and negative interactions, as hinted by the fact that aspen effect on spruce is positive when spruce is present in a much higher proportion than aspen (Légaré et al. 2004) but negative when aspen dominates the canopy (Chapter I). The positive interactions have been hypothesized to be improved soil conditions for spruce by nutrient-rich aspen litter (Légaré et al. 2005b; Laganière et al. 2009; Laganière et al. 2010) and an interspecific competition lower for aspen than intraspecific competition, due to the smaller stature of black spruce. The negative interactions have been hypothesized to be the adverse effect of black spruce litter on soil productivity (Prescott et al. 2000; Crawford et al. 2003), leading to less available soil resources for aspen, and an interspecific competition greater for black spruce than intraspecific competition, due to the higher stature of aspen.

In this study, we investigated individual tree growth through stand development in single- and mixed-species stands to examine the dynamics of interspecific interactions in the same sampling plots that were used in a previous study (Chapter I). The fact that both canopy stratification and the positive or negative influences of litters on soil productivity are not instant processes led us to the following hypotheses: i) When mixed with trembling aspen, spruce trees may grow more slowly at the early stage of stand development and grow faster at the later stage of stand development; ii) Conversely, when mixed with spruce, aspen may grow faster at first, but more slowly in the later stages of stand development; iii) Finally, relationships between shade-intolerant jack pine and trembling aspen are expected to be mostly neutral, with perhaps a slight decrease in aspen growth in the later stage of mixed stands development (Table 2.1).

Table 2.1 Summary of the hypothesized interspecific interactions: positive (+), neutral (0), or negative (-) as compared with intraspecific interactions.

Effect of / on	Soil productivity*	Light availability*
Black spruce / trembling aspen	0 / -	+ / +
Trembling aspen / black spruce	0 / +	- / 0
Trembling aspen / jack pine	0 / 0	0 / 0
Jack pine / trembling aspen	0 / -	0 / 0
Black spruce / jack pine	0 / 0	+ / +

* early stage development / late stage development.

2.3. MATERIALS AND METHODS

2.3.1. Study areas

This study took place in two areas of the boreal mixedwood forest region. The first was located in the black spruce – feathermoss forest of western Quebec (Bergeron 1996), at the border of the Abitibi-Témiscamingue and Nord-du-Québec regions (49°08'N to 49°11'N, 78°46'W to 78°53'W). This area is part of the Clay Belt region of Quebec and Ontario. This major physiographic region results from deposits left by the proglacial lakes Barlow and Ojibway at the time of their maximum expanse during the Wisconsinian glacial stage (Veillette 1994). The closest meteorological station is located in La Sarre (ca. 30 km south). Average annual temperature is 0.7°C and average annual precipitation totals 889.8 mm (Environment Canada 2007). All study sites were located on subhygric Grey Luvisols (Soil Classification Working Group 1996).

The second study area was located approximately 100 km north of Thunder Bay in northwestern Ontario (49°23'N to 49°36'N, 89°31'W to 89°44'W). Mean annual temperature and total average annual precipitation have been estimated at 0.9°C and 712.8 mm, respectively, by the BIOSIM model based on 1977-2006 climatic data (Régnière & St-Amant 2007). The study was conducted on mesic upland sites whose soils are relatively deep glacial tills belonging to the Brunisolic order (Soil Classification Working Group 1996). Jack pine, trembling aspen, black spruce and white birch (*Betula papyrifera* Marsh.) occur in this area in mixed dominance with white spruce (*Picea glauca* (Moench) Voss) and balsam fir (*Abies balsamea* (L.) Mill.).

2.3.2. Sampling design

In Quebec region, 24 sampling plots were established across 8 blocks, located in the same 36 km^2 wide area (maximum distance between blocks: 7 km) dominated by black spruce with patches of aspen. All these stands originated from the same fire that occurred in 1916 (Légaré et al. 2005a). Within each block (numbered from I to VIII), three plots of distinct compositions were selected: pure black spruce, pure trembling aspen, and mixedwoods containing both species (hereafter named BS, TA, and TAbs, respectively) (Table 2.2). After measurements, one plot (VIII-BS) proved unsuitable for comparison (far more accumulated organic matter than the other BS stands) and was therefore discarded from all analyses.

In the Ontario region, 6 composition types were used: pure jack pine (JP), pure aspen (TA) and pine-aspen mixedwoods (TAJP), with the same selection criteria as in Quebec, and the same three overstory types with a black spruce subcanopy of at least 15% of plot total basal area (respectively denoted JPbs, TAbs and TAJPbs). Each composition type was replicated between two and five times (Table 4). The study plots were established across an area of approximately 250 km^2. All plots originated from fires that occurred in 1918 (H.Y.H. Chen, unpublished data). A completely randomized sampling design was carried out.

Table 2.2 Overstory characteristics of the study plots

Region and composition	No. of replicates	Stand density (stems.ha^{-1})[a]	Stand basal area (m^2.ha^{-1})	Basal area (%)			
				Black spruce	Trembling aspen	Jack pine	Other species[b]
Quebec							
BS	7	3115±380	43.4±2.3	89.4±4.2	1.8±0.7	-	8.8±4.0
TAbs	8	1578±125	52.2±2.7	33.8±3.6	59.5±3.5	-	6.7±1.6
TA	8	1065±105	57.7±3.6	8.9±1.8	88.5±2.6	-	2.6±2.3
Ontario							
JP	4	2445±128	49.4±3.6	7.5±2.0	0.0	83.2±1.9	9.3±1.6
JPbs	3	2450±240	47.6±1.2	29.2±3.9	3.6±2.3	64.1±4.9	3.0±1.5
TAJP	4	1300±168	44.6±2.0	6.7±1.4	30.7±7.0	48.2±6.4	14.4±6.1
TAJPbs	2	2463±238	44.3±1.9	26.0±4.8	27.1±3.6	44.0±10.9	2.9±2.5
TA	5	780±43	43.3±3.8	0.0	95.2±1.2	0.7±0.7	4.1±0.9
TAbs	4	2045±205	53.9±3.3	20.6±3.7	68.8±4.3	3.5±1.9	7.0±1.9

[a] Total density includes class 1 snags (see text for details).

[b] Other species consist of jack pine and balsam fir for the Quebec study, and of balsam fir, white spruce, and white birch for the Ontario study.

In our study, “pure” stands contained > 75% of the dominant species in relative basal area, whereas mixedwoods were selected so as to have fewer than 75% of one species in relative basal area, with stems of different species evenly spread across the stand (“intimate” mixture). All three plots of a given block were separated by a distance of 40-100 m to minimize the variability within each block (complete random block design).

2.3.3. Similarity of site quality

In order to ensure all sites were of similar quality in each region, we selected stands carefully according to the following criteria. All selected stands were upland sites with no or very little slope, had similar ages since fire and were closed-canopy with little damage from windbreaks. All stands in the same study region had the same moisture regime (mesic in Ontario and subhygric in Quebec), and were on the same kind of deposits (clay in Quebec and tills in Ontario, see above).

Similarity of sites was then validated by soil intrinsic physical and chemical properties of the mineral layer at a depth of 35-55 cm, i.e., soil textures, CEC, %N and %C content (J. Laganière, Natural Resources Canada, Québec, QC, Table 2.3). No significant differences could be detected between composition types at an error threshold of 0.1 using analyses of variance, except for clay percentage in the Ontario study. However, none of our response variables (individual tree biomass, height-diameter ratio, height, and annual growth rate) appeared to be affected by any of the mineral soil variables. Variables from the deep mineral soil thus had no influence on our analyses, confirming that they neither affected nor were affected by the vegetation, and that all sampled stands within a study region were comparable.

Forest floor characteristics, i.e., %N, CEC, and total P, K, Ca and Mg, were also measured and analyzed (J. Laganière, Natural Resources Canada, Québec, QC, Table 2.4), as organic layer reflects the most vegetation influence on soil properties. Organic soil characteristics were indeed greatly influenced by canopy composition in both study regions. In Quebec, all of the variables (%N, CEC, total P, K, Ca, Mg) tested with analyses of variance followed by post-hoc Tukey HSD comparisons, were significantly higher in TA and TAbs stands than in BS. None were significantly different between TA and TAbs for an error threshold of 0.05, but %N was marginally higher in TA than in TAbs ($P = 0.087$). In Ontario, %N was higher in TA than in JP and JPbs stands; CEC and total Ca were higher in TA than in all other stand types, and higher in TAbs than in JP and JPbs stands. CEC was also higher in TAJP than in JP and JPbs stands. Total P was higher in TA than in TAJP, JP and JPbs stands. There was an effect of canopy composition on total Mg but no significant differences could be detected in the post-hoc comparisons, while there was no effect at all on total K.

2.3.4. Field measurements

For both study regions, all sample plots were circular with an area of 400 m^2 with at least a 5 m buffer zone of the same composition. In each plot, all trees > 5 cm DBH (diameter at breast height, 1.3 m) were numbered and measured for species, DBH, and height. Height was measured using a Vertex clinometer. In order to assess plot density, all snags were also numbered and their decay classes noted in order to identify snags belonging to decay class 1 (i.e., recent snags mostly intact in branches, bark, and top). All trees in a subsection of each plot were cored at breast height. The size of the subsection depended on overall plot density: 100 m^2 in high-density plots, 200 m^2 in medium-density plots, and 400 m^2 (i.e., all trees) in low-density plots, so that 20-40 cores were taken from each plot. The cores were then measured and analyzed using a Velmex sliding-stage micrometer and the TSAPWin (F. Rinn Engineering Office) and COFECHA (Grissino-Mayer 2001) softwares. Those measurements and sampling took place in June 2006 for the Quebec study and in May 2007 for the Ontario study.

Table 2.3 Characteristics of the mineral soil layer (mean ± 1 SE) of the study plots at a depth of 35-55 cm

Region and	N	C	CEC	Texture (%)		
composition	(%)	(%)	(cmol(+).kg-1)	Sand	Silt	Clay
Quebec						
BS	0.05±0.02	0.74±0.48	10.94±1.29	13.02±3.49	46.61±5.79	40.37±5.47
TAbs	0.03±0.00	0.33±0.05	11.29±1.14	10.33±3.48	45.80±5.27	43.87±4.88
TA	0.06±0.02	0.89±0.43	12.05±0.86	12.32±2.34	42.51±4.35	45.18±4.87
Ontario						
JP	0.06±0.02	0.89±0.32	8.75±1.58	66.5±14.47	30.75±14.41	2.75±0.81
JPbs	0.04±0.01	0.54±0.27	10.33±2.87	59.38±6.18	37.50±6.21	3.13±0.36
TAJP	0.04±0.01	0.53±0.18	13.26±3.23	61.25±9.49	35.63±8.92	3.13±0.63
TAJPbs	0.06±0.02	0.99±0.44	10.91±1.83	63.75±7.52	33.13±7.17	3.13±1.08
TA	0.05±0.01	0.62±0.14	10.09±3.03	48.25±14.38	48.75±14.29	3.00±0.34
TAbs	0.03±0.00	0.49±0.12	13.06±2.67	56.25±4.82	36.50±4.87	7.25±0.68

Table 2.4 Characteristics of the organic soil layer (mean ± 1 SE) of the study plots

Region and composition	N (%)	Total P (mg.g^{-1})	Total K (mg.g^{-1})	Total Ca (mg.g^{-1})	Total Mg (mg.g^{-1})	CEC (cmol(+).kg^{-1})
Quebec						
BS	0.94±0.06a	0.67±0.03a	1.18±0.08a	1.80±0.34a	0.71±0.08a	26.90±1.20a
TAbs	1.43±0.05b	0.97±0.05b	1.68±0.11b	6.78±1.11b	1.81±0.40b	45.59±4.17b
TA	1.61±0.07b	1.02±0.06b	1.79±0.11b	8.99±0.91b	2.12±0.35b	54.92±4.69b
Ontario						
JP	1.04±0.08a	0.57±0.04a	0.74±0.13a	5.00±0.45a	0.94±0.11a	38.28±0.88ab
JPbs	0.99±0.10a	0.47±0.03a	0.68±0.08a	5.03±0.99a	1.11±0.34a	34.51±4.61a
TAJP	1.24±0.16ab	0.60±0.10a	0.81±0.08a	9.94±1.22ab	1.57±0.08a	62.00±6.11c
TAJPbs	1.13±0.07ab	0.66±0.03ab	1.02±0.12a	11.03±2.39ab	1.93±0.48a	61.42±8.70bcd
TA	1.49±0.11b	0.88±0.10b	0.99±0.03a	18.65±2.40c	1.87±0.19a	90.24±7.60e
TAbs	1.24±0.10ab	0.70±0.05ab	0.86±0.09a	11.30±1.40b	1.75±0.26a	66.27±6.11d

Additionally, 60 trees were selected in each study region for stem analysis. They were equally partitioned between species of interest, composition types, and diameter classes (small, medium and large, according to the mean of our sites). They were selected randomly by first encounter method in the buffer zones of two different plots per composition type (i.e. 6 plots in the Quebec region and 12 in the Ontario region), so that damage to the sampling plots would be avoided. Those selected trees were cut in early autumn 2007. Cookies were taken at the heights of 30 cm, 130 cm, and then at each subsequent meter for black spruce or each subsequent two meters for jack pine and trembling aspen, until the top of the tree was reached (diameter size limit = 2 cm). All of these cookies were aged in order to reconstruct axial growth. Radial growth of those taken at breast height (130 cm) was also measured on two radii in the same way as the cores.

2.3.5. Data analyses

The aboveground biomass (stem + branches + bark + foliage) of each cored tree was estimated for each available year from DBH. Biomass of cut trees was calculated for each available year from both DBH and height. In both cases we used the allometric equations established by Lambert et al. (2005). Biomass was expressed in carbon content using the mean carbon content values provided by Lamlom and Savidge (2003): spruces 0.5039 $kgC.kg^{-1}$, jack pine 0.504 $kgC.kg^{-1}$, trembling aspen 0.4709 $kgC.kg^{-1}$. Given that no such value was available for black spruce, we used that of white spruce in our calculations. Annual growth rate (AGR) was the difference in mean stem biomass between two years.

Linear mixed models (Pinheiro & Bates 2000) were used to analyze the data, taking into account their hierarchical organization as the following random factors: Block/Plot/Tree for the Quebec study and Plot/Tree for the Ontario one. An autoregressive correlation matrix was also included in the models to take into account the temporal correlation (i.e. similarity of years close to each other within a tree). Data from each region and for each tree species of interest were processed independently. Heights and height-diameter ratios (H-D ratios) obtained by stem analyses on the cut trees were analyzed with time since fire (TSF), stand composition type, and the interaction between TSF and composition as explanatory variables. As the responses of our dependent variables to TSF were non-linear in most cases, we used linear models by splitting the data into two or three linear or quasi-linear parts that were analyzed separately. The locations of the breakpoints were determined prior to the analyses by performing piecewise regressions on simpler (i.e., non-mixed) models. Total stand density could not be included as a covariate in these models as there were too few replicates from the stem analyses. In this case, we assumed that stand density was a result of stand type and, therefore, the effect of stand type was coupled with stand density for the height and H-D ratio analyses.

AGR was tested in the same way as height and H-D ratio, but including total stand density as a covariate since the cored trees were more numerous and taken from a larger number of stands, which allowed stand density to be tested. We assumed that differences in stand density at 90 years reflected the differences at previous stages of stand development. To ensure that no significant information would be lost by using the cored trees, for which we could not reconstruct past height, we first used the 120 trees cut for stem analyses to compare the biomass estimates calculated from DBH and height with those calculated from DBH only. The comparison was made graphically across all years and for each region, tree species, and composition type. Whenever the patterns between the two estimates were not too different, we analyzed the AGR computed from the cored tree (far more numerous and thus more statistically significant, but derived only from DBH). When those patterns seemed different enough to change the interpretation of the results, however, we used AGR computed from the cut trees (less numerous, but derived from both height and DBH, and thus more individually accurate). In the Quebec study, black spruce biomass estimates calculated without height were underestimated only at the latest stage of stand development regardless of the composition type (Fig. 2.1a), thus still allowing a fair comparison. In the Ontario study, there was no difference between black spruce biomass estimates calculated with or without height (Fig. 2.1c). Trembling aspen biomass estimates from Quebec calculated without height were overestimated at the latest stage of stand development in TA stands (Fig. 2.1b), but this difference was taken into account in the interpretation of our results.

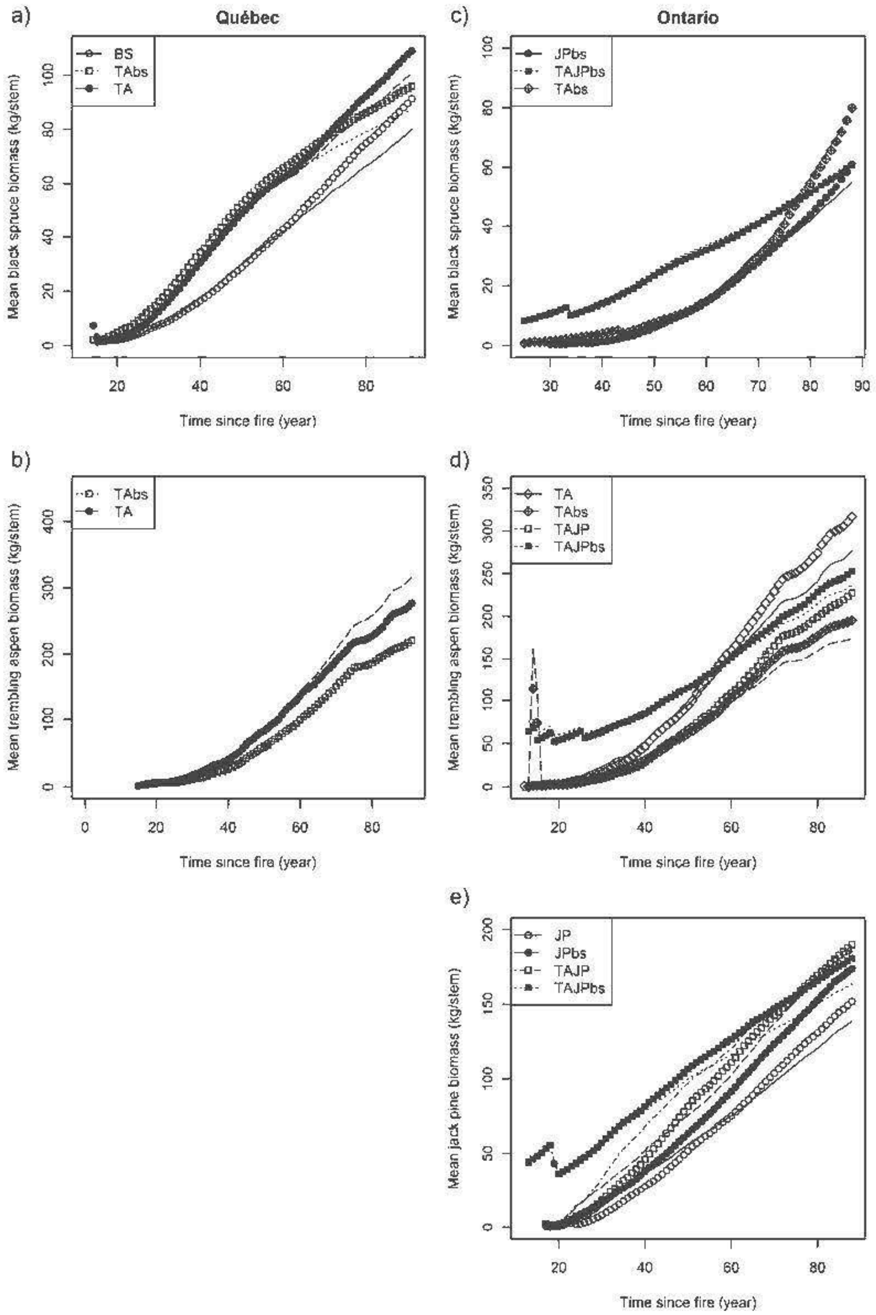

Figure 2.1 Biomass estimates of trees cut for stem analysis in relation to time and stand type for each tree species and study region. Dots, squares and gems stand for biomasses computed from both diameter at breast height (DBH) and height, and lines for estimates computed from DBH only.

Similarly, aspen biomass estimates calculated without height in Ontario were underestimated at the latest stage of stand development, except in TAJP stands (Fig. 2.1d), but this was not deemed problematic as taking these differences into account would not change the patterns of our results. Jack pine biomass estimates calculated without height, on the other hand, were either overestimated, underestimated or accurately estimated compared with biomass estimates calculated from both DBH and height, depending on composition type and time period (Fig. 2.1e). Jack pine annual growth rates were thus analyzed from the stem analyses data rather than from the cores.

All statistical analyses were performed using R software version 2.9.2 (R Development Core Team, 2009) and a significance threshold of 0.05.

2.4. RESULTS

In every case the major significant differences in our models were the interactions between TSF and stand composition type. It is thus the TSF effect (i.e., increase or decrease over time of the response variables, which correspond to the slopes of the lines in the figures) and how it changed with composition type (i.e., significant differences in the TSF effect between composition types) that is described below.

2.4.1. Annual growth rates

There was a negative effect of total stand density on mean AGR in many cases. All of the following results take the density effect into account, and thus correspond to a standardized density between stand types.

In the Quebec study, mean black spruce AGR increased over time, and did so significantly faster in TAbs stands than in the others during the first 37 years of TSF, after which AGR stayed constant in BS, decreased in TAbs and increased in TA stands (Fig. 2.2a). Mean aspen AGR showed a steeper increase in TA than in TAbs stands until the 54th year of TSF, after which it was the opposite: mean AGR increased in TAbs while it decreased in TA stands (Fig. 2.2b).

In the Ontario study, mean black spruce AGR increased similarly across all composition types during the first 57 years, after which it had a higher increase in TAbs than in TAJPbs and JPbs stands (Fig. 2.2c). Mean aspen AGR increase during the first 60 years was the lowest in TAJPbs and TAbs stands, the highest in TA, and intermediate in TAJP stands; AGR decreased in all stand types after 60 years, but it was lower in TA than in TAJP stands (Fig. 2.2d). Mean jack pine AGR increase was lower in TAJPbs than in the other stand types until 45 years, after which it remained stable in JP and JPbs stands and decreased in TAJP stands, while the slope of the decrease in TAJPbs stands was not significantly different from that of any other stand types (Fig. 2.2e).

2.4.2. Heights

In the Quebec study, mean black spruce height growth was at first the highest in TAbs and the lowest in BS stands, with TA being intermediate (Fig. 2.3a). After 54 years of TSF, height growth was significantly higher in BS stands than in TAbs and TA (Fig. 2.3a). Mean trembling aspen height growth was higher in TA stands than in TAbs stands during the first 59 years, after which it was lower in TA than in TAbs stands (Fig. 2.3b).

In the Ontario study, mean black spruce height growth was higher in TAJPbs than in JPbs stands in the first 43 years; it was then the highest in JPbs and the lowest in TAJPbs, with that in TAbs stands being intermediate (Fig. 2.3c). Mean trembling aspen height growth was higher in TA and TAbs than in TAJP and TAJPbs stands during the first 54 years, after which height growth was highest in TA, lowest in TAJPbs, and intermediate in TAJP and TAbs stands (Fig. 2.3d). Mean jack pine height growth was lower in JPbs than in the other stand types in the first 51 years, after which it was lower in JPbs and TAJPbs than in JP and TAJP stands (Fig. 2.3e).

2.4.3. Height-diameter ratios

In the Quebec study, mean black spruce H-D ratio increased over time in BS and TAbs stands but decreased in TA from start of data record to 38 years after fire. Between 38 and 74 years, it increased in all stands, but it did so significantly faster in BS than in the others. After 74 years of TSF, it increased only in BS stands, remaining stable (i.e. no significant TSF effect) in TAbs and TA (Fig. 2.4a). Mean trembling aspen H-D ratio increased over time until the 33rd year of TSF, and it did so faster in TA than in TAbs stands. On the contrary, the increase was steeper in TAbs than in TA stands between 33 and 65 years, after which it decreased in both types of stands, the decrease being stronger in TA than TAbs stands (Fig. 2.4b).

In the Ontario study, mean black spruce H-D ratio decreased over time in TAJPbs and TAbs stands while it increased in JPbs, from start of data record to 52 years after fire. Between 52 and 60 years, it increased in JPbs and TAJPbs but remained stable in TAbs. After the 60th year of TSF, it increased in all stands over time (Fig. 2.4c). There was a marginal difference in the slopes of this increase between JPbs and TAJPbs stands, that of TAJPbs being lower ($P = 0.078$). Mean trembling aspen H-D ratio increased over time in every stand types in the first 41 years, but this increase was lower in TAJPbs and TAbs than in TAJP and TA stands. After 41 years, it significantly decreased over time in all stand types except TA (Fig. 2.4d). Mean jack pine H-D ratio increased over time in all stand types until the 51st year of TSF, the increase being lower in TAJPbs stands than in the others and marginally higher in TAJP stands than in JP and JPbs ($P= 0.065$). Pine H-D ratio decreased over time in all stand types except TAJP after the first 51 years (Fig. 2.4e). The decrease was also marginally lower in TAJPbs than in JP and JPbs stands ($P= 0.082$).

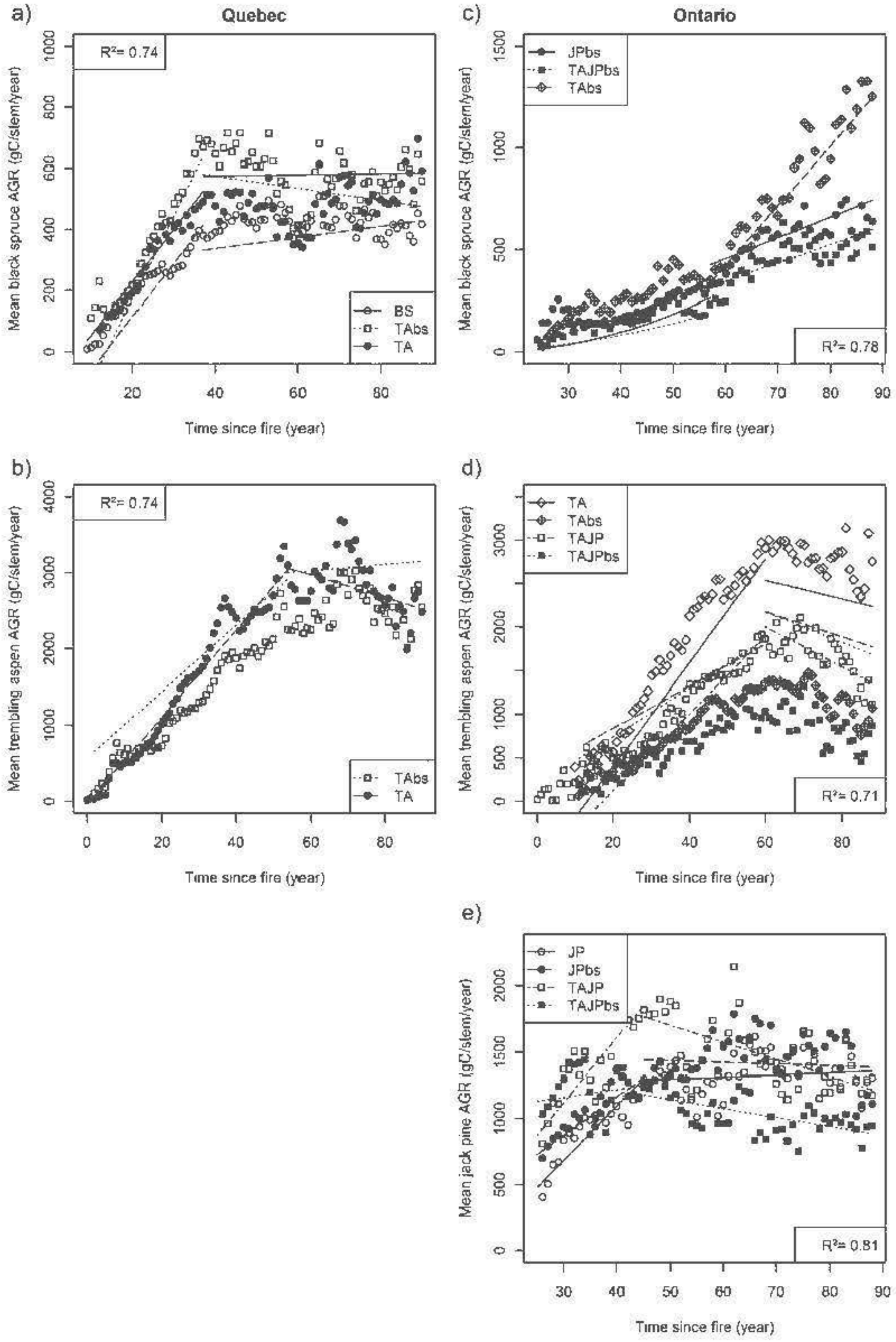

Figure 2.2 (caption follows p55)

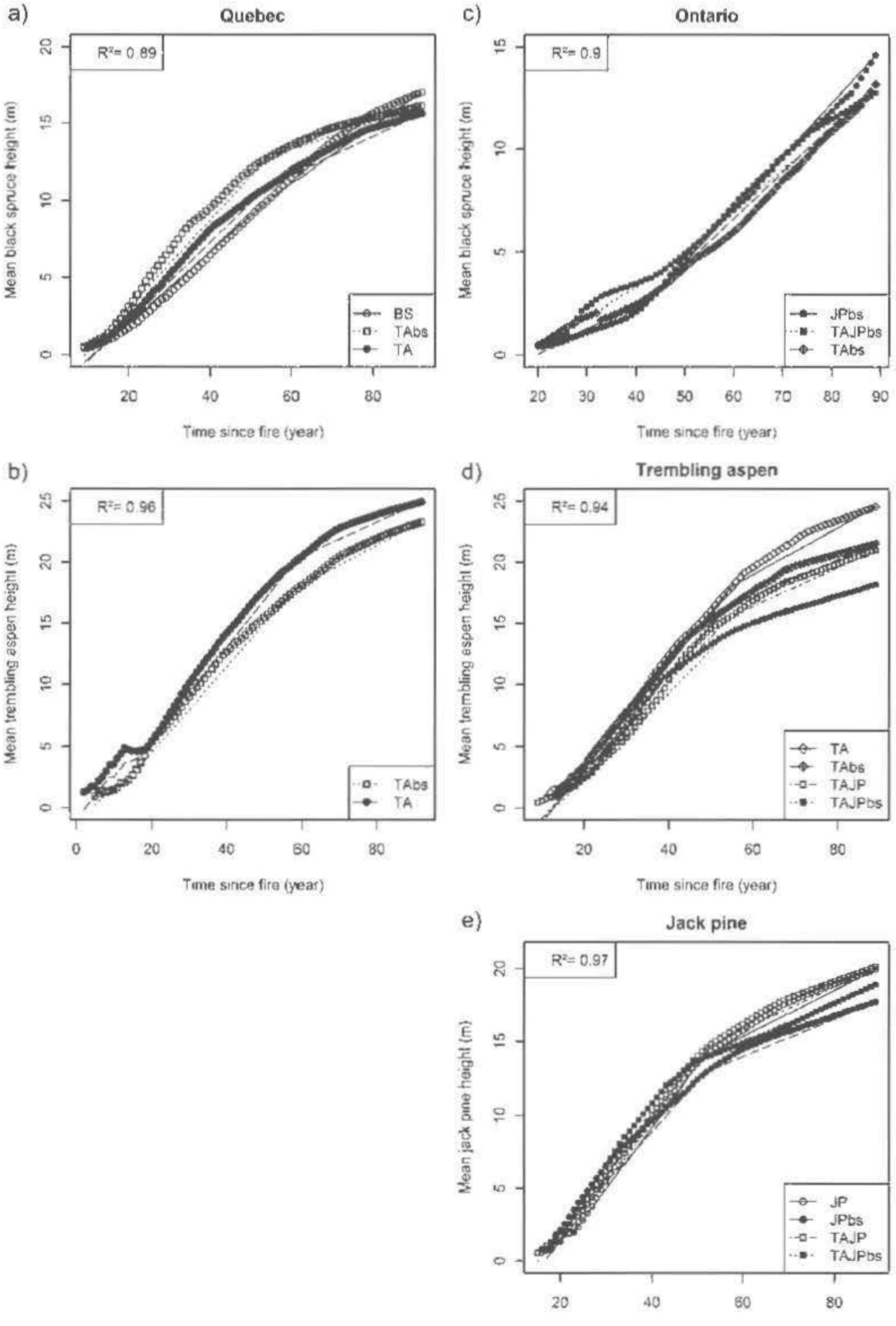

Figure 2.3 (caption follows p55)

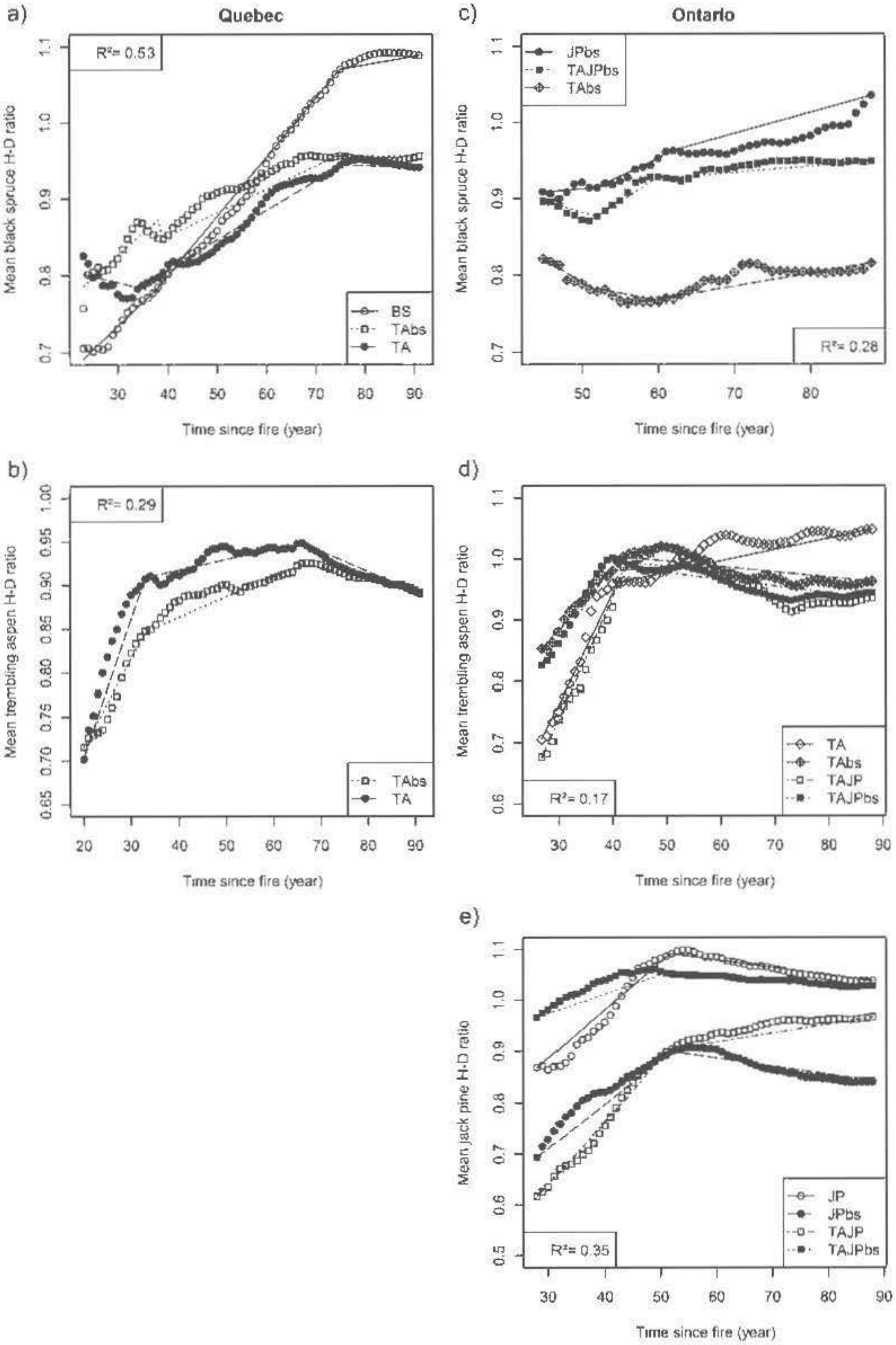

Figure 2.4 (caption follows p55)

Figure 2.2 (p52) Mean individual annual growth rate (AGR) of cored trees in relation to time since fire and stand type. Dots, squares and gems stand for the observed values, and lines for the predicted values. The predicted values of AGR are computed across all stand types for a standardized density while the observed values are not corrected (and thus correspond to the actual densities, which are generally different between stand types), hence the gap between predicted and observed values for some stand types. R^2 is the square of the correlation between observed and non-standardized predicted values.

Figure 2.3 (p53) Mean height of cut trees in relation to time since fire and stand type. Dots, squares and gems stand for the observed values, and lines for the predicted values. R^2 is the square of the correlation between observed and predicted values.

Figure 2.4 (p54) Mean height-diameter (H-D) ratio of cut trees in relation to time since fire and stand type. Dots, squares and gems stand for the observed values, and lines for the predicted values. R^2 is the square of the correlation between observed and predicted values.

2.5. DISCUSSION

2.5.1. Black spruce and trembling aspen relationships

Results from both studies tend to support our hypotheses (Table 2.1) that, at first, aspen could benefit from the reduced aboveground competition due to presence of more spruce and less aspen in the canopy (niche separation), but it became negatively affected by the decrease in fertility generated by spruce litter over time (Prescott et al. 2000; Crawford et al. 2003). Since aspen trees were dominant or codominant stems, their mean height can be treated as site index, and thus as an indicator of soil productivity. The fact that aspen height increase was lower when mixed with black spruce could be a result of inherent site quality, but this is not supported by the absence of differences in mineral soil attributes (Table 2.3). Conversely, the role of spruce in this productivity decrease is supported by the differences in organic soil characteristics (Table 2.4) and the fact that differences in height growth between stand types increased over time (Fig. 2.3b and d).

Spruce growth in the Quebec study may have been lower at first in the presence of aspen due to high top-shading, but then as aspen density decreased due to self-thinning and side-shading from a higher aspen canopy progressively diminished (the canopy became more stratified) the negative competitive effect of aspen on spruce may have lost strength due to niche segregation. Meanwhile, aspen facilitation effect may have gained strength as the positive impact of aspen litter on soil quality increased over time, leading to spruce growth increasing faster in spruce-aspen mixtures (Fig. 2.2a). The diminishing side-shading is demonstrated by spruce H-D ratios that were at first higher when mixed with aspen, but progressively became higher in pure spruce stands (Fig. 2.4a). There were no strong differences in spruce H-D ratios between TA and TAbs stands, and thus probably no difference in shading, which is logical since aspen density was more or less the same between those two stand types. As spruce AGR in TA stands always stayed below that in the other stands, however, higher belowground competition from aspen in the more fertile TA stands might be an explanatory factor.

Spruce response to trembling aspen could not be tested in the Ontario study because of the lack of pure black spruce stands. However, the late increase in AGR under aspen compared with mixed or pine canopies (Fig. 2.2c) confirms that spruce did benefit from facilitation under aspen compared with jack pine (Longpré et al. 1994), and that this effect was not detected in the 2006 biomass values (Chapter I) since it only became perceptible lately. It could still have a major impact on site productivity in the long term. The analyses performed on the forest floor of our stands confirmed that the more conifers there was in a stand, the lower nutrient concentration there was in the organic matter (Table 2.4), which might have had in turn a negative influence on nutrient cycling and availability (Crawford et al. 2003).

However, those trends did not last in the Quebec study. After some time the patterns reversed (Fig. 2.2a and b), thus contradicting our hypotheses. Why did spruce AGR decrease in the late years in TAbs stands and not in BS in spite of the aspen facilitation effect on soil quality? Why did aspen AGR decrease in TA stands and not in TAbs in spite of the spruce impact on soils? We can only make conjectures about this.

For both aspen and spruce, the fact that the stands where individual stems were the biggest (TAbs for spruce and TA for aspen) showed a late decrease in growth could suggest a size-limit effect (i.e., the biggest stems could have grown more slowly in the end because they had more biomass to sustain), but redoing the analyses using only the smallest stems did not change the pattern of our results (not shown). One might also think that for some reason or another, aspen decay began sooner in TA than in TAbs stands, but as aspen snag proportion was not found to be different across stand types (data not shown), nothing supports this hypothesis. This shift in pattern in our Quebec results could also be attributed to some cause external to our stands, such as a change in climatic conditions. The only major climatic variation that could be detected in the area in the past decades, however, was the occurrence of more dry summers in the 1970s than in the surrounding years (Environment Canada 2010). This decrease in precipitation did indeed correspond to a decrease in AGR for the same period (Fig. 2.2a and b), but this was similar across all stand types. Moreover, the decrease in summer rainfall was limited to those years and could thus only explain the periodic AGR variations, not the global trend that can be observed over several decades.

One important aspect to consider is that the results from the Ontario study did not show such a pattern. The main difference between our two study regions that could explain this contrast has to do with soil characteristics, so that the aspen effect on forest floor properties could have been less pronounced on the Quebec clays than on the coarser soils of our Ontario study region (Ste-Marie et al. 2007). The impacts of the spruce and aspen litters on forest floor properties, not being that strong on fine-textured soils, could have reached equilibrium at some point in the Quebec study, after which mixed stands became less positive for spruce and less negative for aspen compared with their respective pure stands. This is partly supported by the fact that in the Quebec study, no significant differences could be detected in organic soil characteristics between TA and TAbs stands, while in Ontario CEC and total Ca were significantly higher in TA than in TAbs stands (Table 2.3). This explanation would mean that the facilitation effect had a much more prevalent role in the poor environment of the Ontario study, which is in accordance with ecological theories stating that as environmental stress (such as resource depletion) increases, facilitation plays a more important role relative to competition, and vice versa (Grime 1977; Callaway et al. 2002; Maestre et al. 2009). Some mixed canopy studies might be interpreted in favor of this theory. Douglas fir (*Pseudotsuga menziesii*) growth benefits from the presence of western hemlock (*Tsuga heterophylla*) without negative side-effects in pacific northwest interior sites (Erickson et al. 2009), but this comes at the price of a decrease in hemlock growth in coastal sites (Amoroso & Turnblom 2006), possibly due to more intense competitive interactions in those more productive stands. Facilitation effects generally seem stronger in mixtures with N-fixing species (Binkley et al. 2003; Bristow et al. 2006), but even then it can be voided in fertilized or intrinsically fertile sites (Moraes de Jesus & Brouard 1989). As hybrid poplar roots tend to avoid occupied soil area (Messier et al. 2009), trembling aspen might also be sensitive to belowground competition and, given that belowground interactions may likely differ according to site fertility, a shift in those interactions may also explain the mid-age shift in spruce and aspen growth responses of spruce in the Quebec study, and its absence in the Ontario study.

2.5.2. Jack pine and trembling aspen relationships

In past studies, jack pine has proven largely insensitive to changes in fertility (Longpré et al. 1994; Béland & Bergeron 1996). Given that there is also no clear niche segregation between trembling aspen and jack pine due to their similar growth patterns, it is thus not surprising that pine did not benefit from aspen presence. What was unexpected, however, was the stronger decrease in pine AGR after 45 years in TAJP stands compared with stands without aspen (Fig. 2.2e). Given that at the same time pine H-D ratio began to increase faster in TAJP than in JP stands (Fig. 2.4e) and that aspen H-D ratio began to decrease in the presence of pine compared with the other stand types (Fig. 2.4d), this loss in pine AGR could mean that aspen may have gained an edge in the aboveground competition against pine, but only in the second half of the stand's life. This effect, however, was not strong enough to have a significant influence on pine biomass in 2006 (Chapter I). Aspen itself did not benefit from this: as we expected, it responded negatively to pine presence (Fig. 2.2d), and particularly in the last years if we take into account that in those years, aspen biomass was overestimated in TAJP compared with the other stand types (Fig. 2.1d). This reinforces jack pine's detrimental effect on soil quality as the most likely explanation to the loss in aspen growth.

2.5.3. Jack pine response to black spruce

Like trembling aspen, jack pine may benefit from a reduction in aboveground competition when mixed with black spruce due to aboveground niche segregation, but unlike trembling aspen it is not a nutrient-demanding species (Longpré et al. 1994; Béland & Bergeron 1996) and thus should not be overly affected by the decrease in soil quality induced by black spruce. Mean pine height, however, began to grow more slowly 51 years after fire when mixed with spruce (Fig. 2.3e). Like that of aspen, it can be treated as a site index and thus means a decrease in soil quality to which pine responded. Unlike aspen, however, differences in pine AGR between JP and JPbs stands seemed constant over time, which means that the late loss in height growth was offset by an increase in radial growth, and that besides this morphological response jack pine growth did not react to black spruce presence. It is possible though that site index may not have the same meaning in mixtures than in pure stands. Pine trees might have reached a lower height when mixed with black spruce not because of lower site quality, but because they did not need to reach such heights to attain dominance in those stands given the lesser stature of spruce. This morphological response could thus be a response to a lower aboveground competition.

2.6. CONCLUSION

We hypothesized after our previous study that the apparent lack of reaction of trees to the presence of other species (Chapter I) was a result of positive and negative effects offsetting each other through stand development, as in the case of Forrester et al. (2007). The dendrometrics presented here have allowed us to show that interspecific interactions varied through stand development. The exact processes by which the species interacted, however, still remain unclear as they proved more complex than we had hypothesized. Trembling aspen reactions to black spruce, notably, appeared different between our two study regions, which could suggest that soil resource availability (negatively or positively affected by the litters of tree species) can influence interspecific relationships between aspen and spruce. It seems quite clear, however, that even though their competitive relationships evolve over time, there was globally no benefit to be obtained from mixing two shade-intolerant species such as trembling aspen and jack pine. Given aspen's high resource requirements, the effect was even worse for this species. It could benefit in the long-term from being mixed with an uncompetitive shade-tolerant species, but only if this species did not have a negative effect on soil quality. Finally, the facilitative effect of aspen litter could have a lasting positive impact on black spruce in low-fertility environments, but it took several decades to become noticeable in tree growth. The complex topic of shifting balance between competition and facilitation over time in mixed forest stands will hopefully be addressed in future studies using permanent sampling plots, which will make it possible to obtain measurements that are out of reach for dendrometrics, such as fine roots measurements at different stages of stand development. Tree mixtures effect has been found to be either positive (Binkley et al. 2003; del Rio & Sterba 2009), neutral (Forrester et al. 2007; Kaitaniemi & Lintunen 2010) or negative (Bolte & Villanueva 2006; Hein & Dhote 2006) across a variety of tree species, stand ages and ecosystems. Stand development is only one of the many factors that need to be studied more deeply in order to be able to predict the outcome of tree mixtures, assuming this is even possible (Huisman & Weissing 2001).

2.7. ACKNOWLEDGMENTS

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CHAPITRE III

MIXED CANOPIES HAVE A NEGATIVE IMPACT ON UNDERSTORY PRODUCTIVITY IN TWO AREAS OF THE EASTERN BOREAL FOREST

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3.1. ABSTRACT

Question: The effect of overstory composition on understory vegetation aboveground dynamics is poorly understood. This study examines the understory biomass, production, and turnover rates of vascular and non-vascular plants along a conifer-broadleaved gradient of resources availability and heterogeneity.

Location: Canadian boreal forests of northwestern Quebec and Ontario.

Methods: We sampled mature stands containing various proportions of black spruce (*Picea mariana* (Mill.) BSP), trembling aspen (*Populus tremuloides* Michx.) and jack pine (*Pinus banksiana* Lamb.). Aboveground biomass of the understory vegetation was assessed through harvesting, annual growth rates were calculated as the differences between biomass in 2007 and 2008 as estimated by allometric relationships, and turnover rates were estimated as net primary production divided by the biomass in 2007.

Results: Higher aspen presence, linked to greater nutrient availability in the forest floor, was generally associated with higher vascular biomass and production in the understory. This effect was less pronounced in sites of high intrinsic fertility. In contrast, bryophyte biomass was positively associated with conifer abundance, particularly in the wet sites of the Quebec study area. Mixed canopies therefore had a negative impact on total understory biomass. Turnover rates did not differ with overstory composition.

Conclusions: While resource availability is a main driver of understory productivity, resources as drivers appear to differ with understory strata, i.e. vascular vs. non-vascular plants. Resource heterogeneity induced by mixed canopy had overall negative effects on understory aboveground productivity, as this productivity seemed to rely on species adapted to the specific conditions induced by a pure canopy.

3.2. INTRODUCTION

The growing recognition of climate change as a major issue of the new century (IPCC 2007) has put a lot of focus on boreal forests, not only because they will likely be heavily affected by these changes (Soja et al. 2007), but also because they could contribute significantly to climate change mitigation. Forest ecosystems in general (Bolin & Sukumar 2000), and boreal forests in particular (Bailey 1996; Goodale et al. 2002), are indeed important contributors to the global carbon cycle. Even though mixedwoods represent half of the Canadian boreal forest (CCFM 2000), not much is known about how the interactions between tree species could affect the carbon balance in boreal forest ecosystems.

Understory vegetation could be considered as negligible in the carbon budget of these ecosystems when compared to the vast amounts of carbon stored in the soils and trees. The limited size of the understory carbon pool is however offset by its high turnover rate, which allows a high annual input of carbon in the understory relative to its total biomass (Zavitkovski 1976; Yarie 1980). The high turnover rate of understory vegetation can play a particularly important role in evergreen forests where the turnover rate of trees is low (Chapin 1983). Higher turnover rates of biomass could mean an increase in carbon accumulation, either by potentially increasing the nutrient cycling rate, and hence long-term productivity, or by increasing soil carbon pools through litter production, depending on the decay properties of the produced litter. It may thus be more crucial to assess the turnover rate of understory vegetation than its production.

While the understory influences the soil nutrient status, it can also be affected by variations in soil conditions and light availability, and such variations can be induced by changes in canopy composition (Riegel et al. 1995). The effect of canopy composition depends on the traits (such as litter properties and shade tolerance/intolerance) of the tree species in a stand. A high abundance of shade-intolerant broadleaved trees such as trembling aspen (*Populus tremuloides* Michx.) in a stand is associated with an increase in both the amount of light reaching the understory (Messier et al. 1998) and higher cation exchange capacity (CEC) of the forest floor (Côté et al. 2000; Prescott et al. 2000; Légaré et al. 2005b). This in turn seems to favour higher vascular plant cover and richness in the understory (Barbier et al. 2008; Hart & Chen 2008). Contrary to vascular plants, bryophytes are hindered by the presence of broadleaved species (Fenton et al. 2005). This negative response of bryophytes to broadleaved overstory can be detrimental as well as beneficial to the carbon budget because a lot of carbon is stored within the bryophytes and organic layers derived from bryophytes, but on the other hand bryophyte accumulation is linked to a decrease in tree growth (Crawford et al. 2003; Simard et al. 2007) and reduces the proportion of productive vascular species in the understory (Kembel & Dale 2006). While it is widely recognized that resource availability has an important influence over vegetation productivity and diversity, stands of mixed overstory tree species could also increase resource heterogeneity and partition in the understory because of their structural diversity in live trees and coarse woody debris (Brassard & Chen 2008; Brassard et al. 2008), but the role of resource heterogeneity is much debated (Stevens & Carson 2002; Cardinale et al. 2009; Bartels & Chen 2010), hence the necessity to assess the understory response to mixed canopy.

This study compared aboveground carbon pools and inputs in the understory, measured as understory biomass and biomass production, beneath pure and mixed tree overstories of the eastern Boreal Shield in Canada. To allow for a better generalization of our results, this study took place in mature black spruce and trembling aspen mixed and pure stands in the Clay Belt of northwestern Quebec, and mature black spruce, trembling aspen and jack pine (*Pinus banksiana* Lamb.) mixed and pure stands on coarse till deposits in northwestern Ontario. Various proportions of these three tree species observed on similar permanent site conditions appear to present an opportunity to test the understory vegetation response to the variation in resource availability in the understory since nutrient mineralization tend to increase with an increasing deciduous overstory (Légaré et al. 2005b). Given that trembling aspen has been shown to have a positive effect on resource availability in the forest floor (Légaré et al. 2005b) and that, on the contrary, deep mineral soil is impervious to changes in vegetation (Augusto et al. 2002; Augusto et al. 2003), analyses were conducted for both the forest floor and mineral soil in order to assess vegetation-induced as well as inherent differences in soil fertility between our stands.

Our objectives were to test that i) understory biomass, growth rates and turnover rates change with a gradient of overstory composition, with higher understory soil resource availability being associated with the presence of trembling aspen. Because the response of understory plants to available resources tends to differ with their life forms or strata (Hart and Chen 2006), we hypothesized responses to overstory composition differ with understory strata, and ii) resource heterogeneity induced by mixed canopies has no effect on understory biomass, growth rates and turnover rates, meaning their values in mixed stands were hypothesized to be intermediate between their values in each corresponding pure stands.

3.3. MATERIALS AND METHODS

3.3.1. Study areas

This study took place in two areas of the boreal mixedwood forest region. The first was located in the black spruce – feathermoss forest of western Quebec (Bergeron 1996), at the border of the Abitibi-Témiscamingue and Nord-du-Québec regions (49°08'N to 49°11'N, 78°46'W to 78°53'W). This area is part of the Clay Belt region of Quebec and Ontario. This region resulted from deposits left by the proglacial Lakes Barlow and Ojibway at the time of their maximum expanse during the Wisconsinian glacial stage (Veillette 1994). The closest meteorological station is located in La Sarre (ca. 30 km south). Average annual temperature is 0.7°C and average annual precipitation totals 889.8 mm (Environment Canada 2007). All study sites were located on subhygric Grey Luvisols (Soil Classification Working Group 1996).

The second study area was located approximately 100 km north of Thunder Bay in northwestern Ontario (49°23'N to 49°36'N, 89°31'W to 89°44'W). The closest meteorological station is located in Thunder Bay (mean annual temperature: 2.6°C; total average annual precipitation: 704.7 mm; Environment Canada 2007). The study was conducted on mesic upland sites whose soils are relatively deep glacial tills belonging to the Brunisolic order (Soil Classification Working Group 1996). Jack pine, trembling aspen, black spruce and white birch (*Betula papyrifera* Britt.) occur in this area in mixed dominance with white spruce (*Picea glauca* (Moench) Voss) and balsam fir (*Abies balsamea* (L.) Mill.).

3.3.2. Sampling design

3.3.2.1. Quebec study

Twenty-four sampling plots were established across eight blocks, located in the same 36 km^2-wide area (maximum distance between blocks: 7 km), dominated by black spruce with patches of aspen. All these stands originated from the same fire that occurred in 1916 (Légaré et al. 2005a). Within each block (numbered from I to VIII), three plots of distinct compositions were selected: black spruce-dominated (75% or more spruce in proportion of basal area), trembling aspen-dominated (75% or more aspen in proportion of basal area), and mixedwoods containing both species in more even proportions (hereafter named BS, TA, and TAbs, respectively), so that the selected stands could have a large degree of variation in trembling aspen and black spruce proportions (Table 3.1). One of the selected plots (VIII-BS) proved to be unsuitable because it had a much thicker layer of accumulated organic matter than the other BS stands, and was therefore discarded from all analyses. All three plots of a given block were separated by a distance of 40-100 m to minimize the variability within each block (complete random block design).

3.3.2.2. Ontario study

Six composition types were used in the Ontario study: jack pine-dominated (JP, 75% or more pine in proportion of basal area), trembling aspen-dominated (TA, 75% or more aspen in proportion of basal area), pine-aspen mixedwoods (TAJP), and the same three overstory types with a black spruce subcanopy (named JPbs, TAbs, and TAJPbs, respectively, with at least 20% spruce in proportion of basal area). Our goal here was to ensure sufficient variation in trembling aspen and jack pine proportions, and to a lesser extent in black spruce proportion (no black spruce dominated stands could be found in upland conditions within the area). Each composition type was replicated between two and five times (Table 3.1). The study plots were established across an area of approximately 250 km^2. A completely randomized sampling design was deployed. All plots originated from fires that occurred in 1918 (Chen, H.Y.H., *unpublished data*).

Table 3.1 Overstory characteristics of the study plots (mean ± 1 SE).

Region	Stand type	Total basal area (m^2 /ha)	Total density (stems /ha)	Number of stands	Species composition by basal area (%)			
					Black spruce	Trembling aspen	Jack pine	Other species[a]
Quebec	BS	43.4 ± 2.3	3115 ± 380	6	89.4 ± 4.2	1.8 ± 0.7	-	8.8 ± 4.0
	TAbs	52.2 ± 2.7	1577.5 ± 127.5	7	33.8 ± 3.6	59.5 ± 3.5	-	6.7 ± 1.6
	TA	57.7 ± 3.6	1065 ± 105	8	8.9 ± 1.8	88.5 ± 2.6	-	2.6 ± 2.3
Ontario	JP	49.4 ± 3.6	2445 ± 127.5	4	7.5 ± 2.0	0	83.2 ± 1.9	9.3 ± 1.6
	JPbs	47.6 ± 1.2	2450 ± 240	3	29.2 ± 3.9	3.6 ± 2.3	64.1 ± 4.9	3.0 ± 1.5
	TAJP	44.6 ± 2.0	1300 ± 167.5	4	6.7 ± 1.4	30.7 ± 7.0	48.2 ± 6.4	14.4 ± 6.1
	TAJPbs	44.3 ± 1.9	2462.5 ± 237.5	2	26.0 ± 4.8	27.1 ± 3.6	44.0 ± 10.9	2.9 ± 2.5
	TA	43.3 ± 3.8	780 ± 42.5	5	0	95.2 ± 1.2	0.7 ± 0.7	4.1 ± 0.9
	TAbs	53.9 ± 3.3	2045 ± 205	4	20.6 ± 3.7	68.8 ± 4.3	3.5 ± 1.9	7.0 ± 1.9

[a] Other species consist of jack pine and balsam fir in the Quebec study, and balsam fir, white spruce and white birch in the Ontario study.

3.3.3. Similarity of sites

In order to ensure that all sites were of similar quality and that canopy composition was the only significant source of variation within each region, we selected stands carefully according to the following criteria. All selected stands were early-successional (all canopy trees were first cohort), mature, closed-canopy, upland sites with no or very little slope and no apparent major disturbance had occurred since the stand-originating fire During plot selection in field, we followed ecological classification approach by using topography and soil texture to ensure all sites in Ontario were mesic and all sites in Quebec were subhygric. Moisture regime class was then confirmed by examination of a soil profile. All stands in the same study area also were on the same type of deposits (clay in Quebec and tills in Ontario), and had the same elapsed time since fire (about 90 years, see above). Shade-intolerant trees (trembling aspen and jack pine) within a stand all had similar heights and always overtopped black spruce trees.

Similarity of sites was then validated by soil intrinsic physical and chemical properties, i.e. soil textures, cationic exchangeable capacity (CEC), and concentrations of total nitrogen (N) and total C of the mineral layer at a depth of 35-55 cm (J. Laganière, Natural Resources Canada, Quebec, Table 3.2), which should be unaffected by vegetation (Augusto et al. 2002; Augusto et al. 2003). Analyses of variance (ANOVA) could not detect any significant differences between canopy types for these variables. Among those variables, only soil mineral CEC was significantly related ($\alpha = 0.1$) to some understory response variables (see below) for the Quebec study plots only and was thus retained as a covariate in those cases. It should however be noted that the trembling aspen proportion of basal area was not correlated to CEC ($R^2 = 0.04$ and 0.03 in Quebec and Ontario, respectively). This CEC effect was thus only due to natural variations within the same type of stands. Thus, canopy composition was not a product of inherent differences in site fertility.

Table 3.2 Characteristics of mineral soil layer (mean ± 1 SE) at a depth of 35-55 cm of the study plots.

Region and composition	N (%)	C (%)	CEC (cmol(+).kg-1)	Textures (%)		
				Sand	Silt	Clay
Quebec						
BS	0.05±0.02	0.74±0.48	10.94±1.29	13.0±3.5	46.6±5.8	40.4±5.5
TAbs	0.03±0.00	0.33±0.05	11.29±1.14	10.3±3.5	45.8±5.3	43.9±4.9
TA	0.06±0.02	0.89±0.43	12.05±0.86	12.3±2.3	42.5±4.4	45.2±4.9
Ontario						
JP	0.06±0.02	0.89±0.32	8.75±1.58	66.5±14.5	30.8±14.4	2.8±0.8
JPbs	0.04±0.01	0.54±0.27	10.33±2.87	59.4±6.2	37.5±6.2	3.1±0.4
TAJP	0.04±0.01	0.53±0.18	13.26±3.23	61.3±9.5	35.6±8.9	3.1±0.6
TAJPbs	0.06±0.02	0.99±0.44	10.91±1.83	63.8±7.5	33.1±7.2	3.1±1.1
TA	0.05±0.01	0.62±0.14	10.09±3.03	48.3±14.4	48.8±14.3	3.0±0.3
TAbs	0.03±0.00	0.49±0.12	13.06±2.67	56.3±4.8	36.5±4.9	7.3±0.7

Table 3.3 Characteristics of organic soil layer (mean ± 1 SE) of the study plots. Different letters indicate significant differences between composition types.

Region and composition	N (%)	Total P (mg.g^{-1})	Total K (mg.g^{-1})	Total Ca (mg.g^{-1})	Total Mg (mg.g^{-1})	CEC (cmol(+).kg^{-1})
Quebec						
BS	0.94±0.06a	0.67±0.03a	1.18±0.08a	1.80±0.34a	0.71±0.08a	26.90±1.20a
TAbs	1.43±0.05b	0.97±0.05b	1.68±0.11b	6.78±1.11b	1.81±0.40b	45.59±4.17b
TA	1.61±0.07b	1.02±0.06b	1.79±0.11b	8.99±0.91b	2.12±0.35b	54.92±4.69b
Ontario						
JP	1.04±0.08a	0.57±0.04a	0.74±0.13a	5.00±0.45a	0.94±0.11a	38.28±0.88ab
JPbs	0.99±0.10a	0.47±0.03a	0.68±0.08a	5.03±0.99a	1.11±0.34a	34.51±4.61a
TAJP	1.24±0.16ab	0.60±0.10a	0.81±0.08a	9.94±1.22ab	1.57±0.08a	62.00±6.11c
TAJPbs	1.13±0.07ab	0.66±0.03ab	1.02±0.12a	11.03±2.39ab	1.93±0.48a	61.42±8.70bcd
TA	1.49±0.11b	0.88±0.10b	0.99±0.03a	18.65±2.40c	1.87±0.19a	90.24±7.60e
TAbs	1.24±0.10ab	0.70±0.05ab	0.86±0.09a	11.30±1.40b	1.75±0.26a	66.27±6.11d

3.3.4. Soil resource availability along the trembling aspen gradient

To assess whether an increasing aspen proportion was correlated with higher soil nutrient availability, organic layer characteristics, i.e., %N, CEC, and total P, K, Ca and Mg, were also measured from five forest floor subsamples per sample plot (J. Laganière, Natural Resources Canada, Sainte Foy, Quebec City, Quebec), as organic layer reflects the most vegetation influence on soil properties. Total C and total N were determined by dry combustion using a LECO CNS 2000 analyzer (LECO Corporation, St. Joseph, Michigan). Total K, Ca and Mg concentrations were determined by atomic absorption spectrophotometry (Perkin Elmer 5100 PC, Boston, Massachusetts) and total P was determined by colorimetry following H_2SO_4/H_2O_2 digestion. CEC was determined by summing exchangeable cations extracted with 0.1 mol/L $BaCl_2$ (Hendershot & Duquette 1986). Cations were determined by atomic absorption spectrophotometry.

3.3.5. Measurements and samplings

For both study regions, all sample plots were circular with an area of 400 m^2 and a buffer zone of at least 5 m. The plot and the buffer zone were relatively uniform in species composition, structure, and site condition. In each plot, three 1 m^2 quadrats were established at 5 m from the plot centre. The location of the first quadrat was determined by randomly selecting a direction. The two others were placed so that the three quadrats were all separated by the same distance.

In each quadrat, all individual understory vascular plants were identified and measured in July and August 2007, with as little disturbance as possible. Understory plants refer to all non-tree plant species plus tree seedlings and saplings with DBH smaller than 5 cm. Grass, lichen and mushroom biomass in our sample plots was negligible and therefore ignored. Main stem length or leaf length was measured, depending on the morphology of the plant species. We attempted to measure a feature of a plant species that would be strongly correlated to its biomass so that its biomass could be easily as well as accurately predicted from the measured morphological feature. All individuals belonging to the same species were measured in the same way. In July and August 2008, all vascular plants in the same quadrats were again identified and measured as in 2007, and their aboveground parts were harvested. Bryophytes were also harvested at this time with all species pooled together. All harvested samples were dried for 48 hours at 65°C and then weighed. Carbon content was considered to be equivalent to half of the dry biomass. This common percentage to all strata probably resulted in a slight overestimation in the carbon content of some of them such as herbs, but should not have a significant influence on the overall results.

3.3.6. Data analyses

In order to evaluate the net biomass increment of the understory (annual growth rate, or AGR) between 2007 and 2008, we established allometric relationships between the weighed biomass and the 2008 total stem or leaf size of all individuals within each quadrat. We pooled species that had similar relationships between biomass and measurements. These relationships allowed us to compute the predicted biomass for 2008 and 2007, and thus the growth between the two years. There were strong linear relationships between measured morphological features and biomass for most species (Table 3.4). In some cases, a square root transformation was needed to achieve linearity. As a result, predicted and measured biomass values at the quadrat level in 2008 were overall highly correlated ($R^2 = 0.66$ and 0.86 in Quebec and Ontario, respectively) (Fig. 3.1).

Table 3.4 Relationships between biomass and measured features at the quadrat level for each species or groups of species sharing a similar morphology. All relationships had a P-value lower than 0.01.

Species or group of species (Marie-Victorin et al. 2002)	**Morphological predictor**	**Biomass transformation**	**R²**
Abies balsamea, Picea mariana	Stem length	Square root	0.62
Acer spicatum	Stem length	Square root	0.93
Amelanchier sp., Alnus crispa, Alnus rugosa, Betula papyrifera, Corylus cornuta	Stem length	None	0.24
Aralia nudicaulis	Leaf size	None	0.92
Aster macrophyllus	Leaf size	None	0.82
Botrychium virginianum, Dryopteris disjuncta, Dryopteris spinulosa, Phegopteris connectilis	Leaf size	None	0.65
Clintonia borealis	Leaf size	None	0.87
Coptis groenlandica, Goodyera repens, Oxalis montana, Viola sp.	Leaf size	None	0.79
Cornus canadensis	Leaf size	None	0.93
Cornus stolonifera	Stem length	Square root	0.92
Diervilla lonicera, Lonicera canadensis	Stem length	None	0.76
Equisetum sp.	Stem length	Square root	0.9
Fragaria virginiana, Rosa sp., Rubus ideus	Stem length	None	0.88
Galium triflorum	Stem length	Square root	0.83
Gaultheria hispidula	Stem length	None	0.8
Kalma angustifolia, Ledum groenlandicum	Stem length	Square root	0.8
Linnaea borealis	Leaf size	None	0.9
Lycopodium annotinum, Lycopodium clavatum, Lycopodium lucidulum	Stem length	Square root	0.57
Lycopodium obscurum	Stem length	None	0.94
Maienthemum canadensis	Leaf size	None	0.81
Petasites palmatus	Leaf size	None	0.97
Populus tremuloides	Stem length	Square root	0.71
Pyrolla sp.	Leaf size	None	0.93
Ribes glandulosum, Rives lacustre, Ribes triste	Stem length	Square root	0.45
Rubus pubescens	Stem length	None	0.88
Streptopus roseus	Stem length	None	0.65
Trientalis borealis	Leaf size	None	0.67
Vaccinium angustifolium, Vaccinium myrtilloides	Stem length	None	0.25
Viburnum edule	Stem length	Square root	0.65

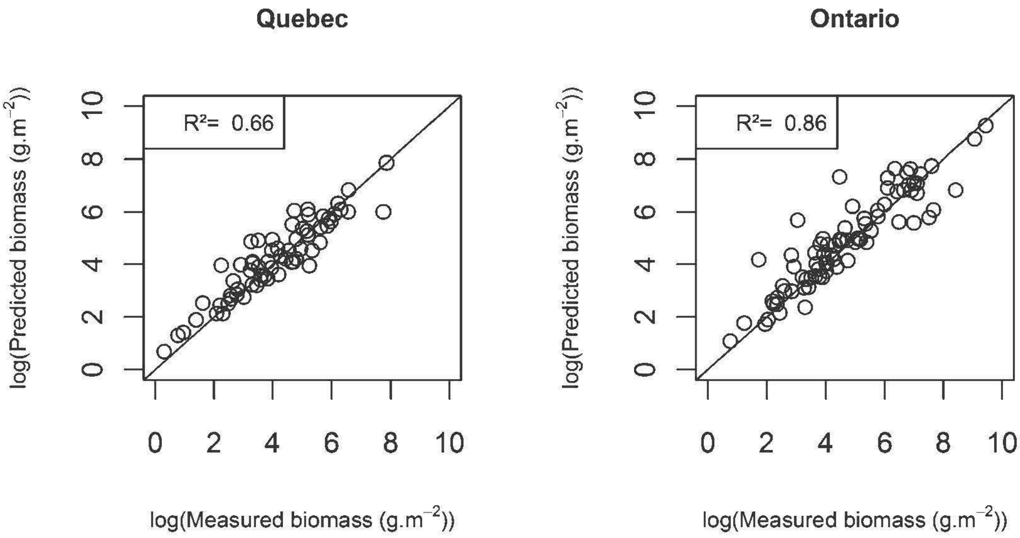

Figure 3.1 Predicted versus measured biomass values at the quadrat level. The log scale is used only for visual clarity.

Understory species were grouped according to the following strata: shrubs (including broadleaf tree saplings), conifer saplings (which were exclusively *P.mariana* and *A.balsamea*), herbs (including ferns), dwarf shrubs (including every ligneous species under 1 m in maximum height), and bryophytes. Biomass and AGR were analyzed for each of these groups. Species life traits and Raunkiær's life forms (Raunkiaer 1934), as found in the TOPIC database (Aubin et al. 2007), were used to compute total aboveground understory production (hereafter named net primary production, or NPP). As we did not measure mortality, we assumed that NPP was equal to AGR plus litter production. For species which do not retain their aboveground parts during winter, NPP was considered equal to their biomass in 2008. For evergreen perennial species, NPP was considered equal to AGR. For deciduous shrubs, NPP was considered equal to AGR plus foliage re-growth, which was estimated to be equivalent to 5% of their biomass in 2007 (Jenkins et al. 2003). For deciduous dwarf shrubs, NPP was considered equal to AGR plus foliage re-growth estimated at 25% of their biomass in 2007 (Mälkonen 1974; Havas & Kubin 1983). Turnover rates of the vascular plants were then computed as percentages of NPP divided by the 2007 biomass.

3.3.7. Statistical analyses

Differences in organic soil variables between composition types were tested with analyses of variance followed by post-hoc Tukey's HSD comparisons. Regression analyses were used to model the effect of the trembling aspen proportion of total basal area on the various biomasses, AGR, NPP and turnover rates of the Quebec study. Both trembling aspen and black spruce proportions were used as predictors in the Ontario study. In the Ontario study, the trembling aspen and jack pine proportions of total basal area were negatively correlated ($R^2 = 0.94$). Hence, choosing the aspen or pine proportion as the main explanatory variable had no major consequences. In the Ontario study, we intended to examine the influence of subcanopy black spruce on understory plants, but the black spruce proportion was more correlated with that of trembling aspen than of jack pine ($R^2 = 0.20$ and 0.05, respectively). To minimize collinearity between the predictors, we used the jack pine and black spruce proportions in multiple regression analyses for the Ontario study. Given the negative correlation between trembling aspen and jack pine proportion ($R^2 = 0.94$), the effect of jack pine proportion presented in the Results section should be considered as inverse to that of trembling aspen proportion. In other words, a decrease in jack pine proportion was equivalent to a similar increase in trembling aspen proportion. When a log transformation was not sufficient to make the residuals follow a normal distribution with low heteroscedasticity, Poisson regressions were used. Piecewise regressions were also used when a break point was apparent (Muggeo 2003; Toms & Lesperance 2003). Effects were considered statistically significant when $p < 0.05$. Tree density had no influence on any attributes of the understory vegetation in our analyses; therefore, it was not included in the final analyses. CEC at a depth of 35-55 cm was retained as a covariate when significant. Interactions between variables were tested and kept when significant at $\alpha = 0.1$. All data and statistical analyses were computed using R software version 2.9.2 (R Development Core Team 2009).

3.4. RESULTS

3.4.1. Nutrient concentrations in the forest floor

In Quebec, all of the variables (%N, CEC, total P, K, Ca, Mg) were significantly higher in TA and TAbs stands than in BS, but not between TA and TAbs for an error threshold of 0.05. %N was marginally higher in TA than in TAbs ($P = 0.087$, Table 3.3).

In Ontario, %N was higher in TA than in JP and JPbs stands; CEC and total Ca were higher in TA than in all other stand types, and higher in TAbs than in JP and JPbs stands. CEC was also higher in TAJP than in JP and JPbs stands. Total P was higher in TA than in TAJP, JP and JPbs stands. There was an effect of canopy composition on total Mg, but no significant differences could be detected through post-hoc comparisons, while there was no effect at all on total K (Table 3.3).

3.4.2. Biomass

In the Quebec study, average aboveground biomass of understory plants was 2.3, 0.8, and 2.0 MgC.ha^{-1} in the BS, TAbs, and TA stands, respectively (Fig. 3.2a). In the Ontario study, the biomass ranged from 0.7 MgC.ha^{-1} in TAJPbs to 9.2 MgC.ha^{-1} in TA stands (Fig. 3.2b).

In the Quebec study, total understory biomass decreased exponentially with an increase in the proportion of trembling aspen until it reached 49.7%, after which it began to increase exponentially (Fig. 3.3a). Total vascular biomass increased with increasing aspen proportion (Fig. 3.3b). The biomass of conifer saplings followed the same pattern as total understory biomass but with a breakpoint located at 45.9% (Fig. 3.3c). The biomass of both shrubs and herbs increased with increasing aspen proportion (Fig. 3.3d and e). Bryophyte biomass followed an exponential decrease with increasing aspen proportion (Fig. 3.3g).

CEC in the Quebec study was positively correlated with the biomass of total vascular plants, conifer saplings, and dwarf shrubs (Fig. 3.3b, c and f). The effect of aspen proportion on the biomass of shrubs was steeper when CEC was lower (Fig. 3.3d).

In the Ontario study, total understory and total vascular biomass decreased with increasing trembling aspen proportion until a breakpoint at around 77%, after which it increased (Fig. 3.4a and b). An increase in black spruce proportion had a negative effect on the total understory and vascular biomass, and it made the effect of trembling aspen proportion on vascular biomass significantly weaker (Fig. 3.4a and b). Conifer sapling biomass decreased with increasing trembling aspen or spruce proportions (Fig. 3.4c), while shrub biomass increased with increasing trembling aspen proportion and decreased with increasing black spruce proportion, the negative effect of black spruce being stronger under high proportions of aspen (Fig. 3.4d). The biomass of herbs linearly increased with an increase in spruce proportion, but only under high proportions of aspen. Spruce proportion also had a negative effect on dwarf shrubs biomass under low proportions of aspen, and a positive effect under high proportions of aspen. In the last two cases, however, the models only accounted for 32% and 28% of the variation in biomass of herbs and dwarf shrubs, respectively (Fig. 3.4e and f). Bryophyte biomass decreased with increasing aspen proportion and increased with increasing black spruce proportion (Fig. 3.4g).

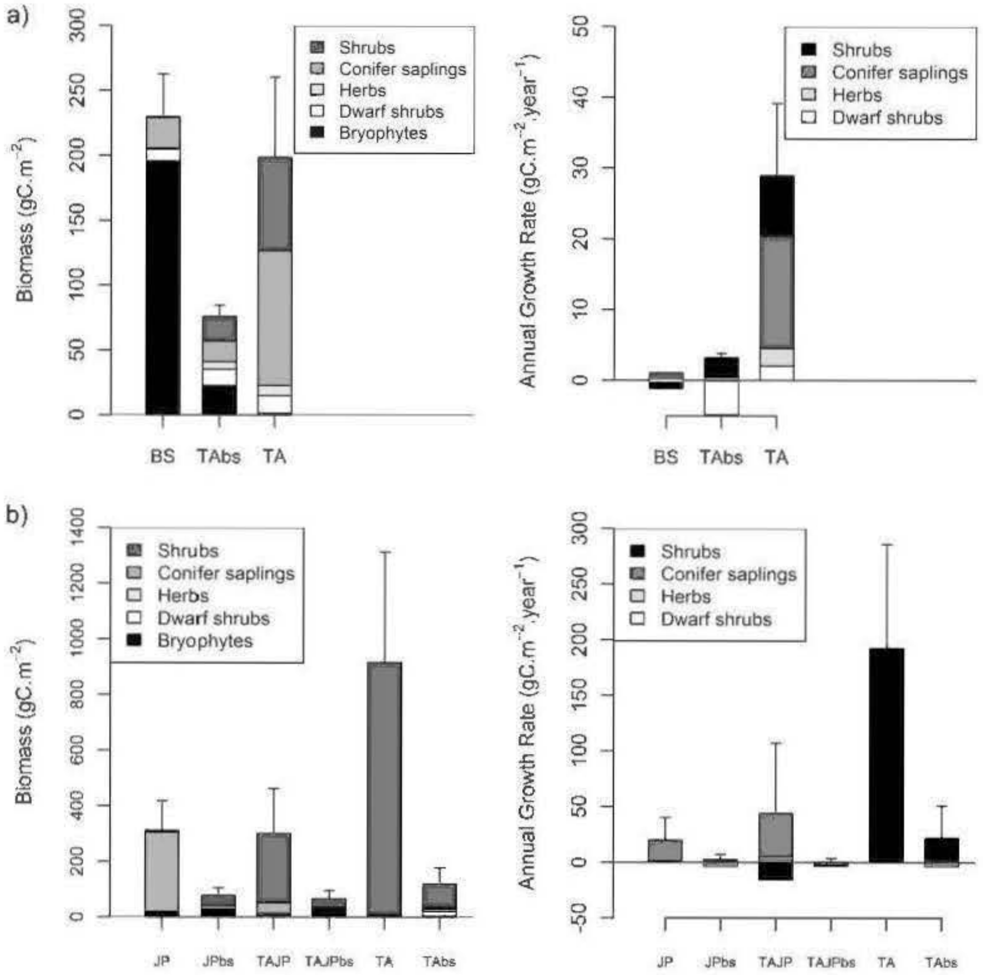

Figure 3.2 Biomass and annual growth rates (AGR) (mean + 1 SE) in relation to stand types for a) the Quebec study and b) the Ontario study. BS = Black spruce, TA = Trembling aspen, JP = Jack pine. Uppercase is for the dominant species of the overstory, lowercase for sub-canopy species.

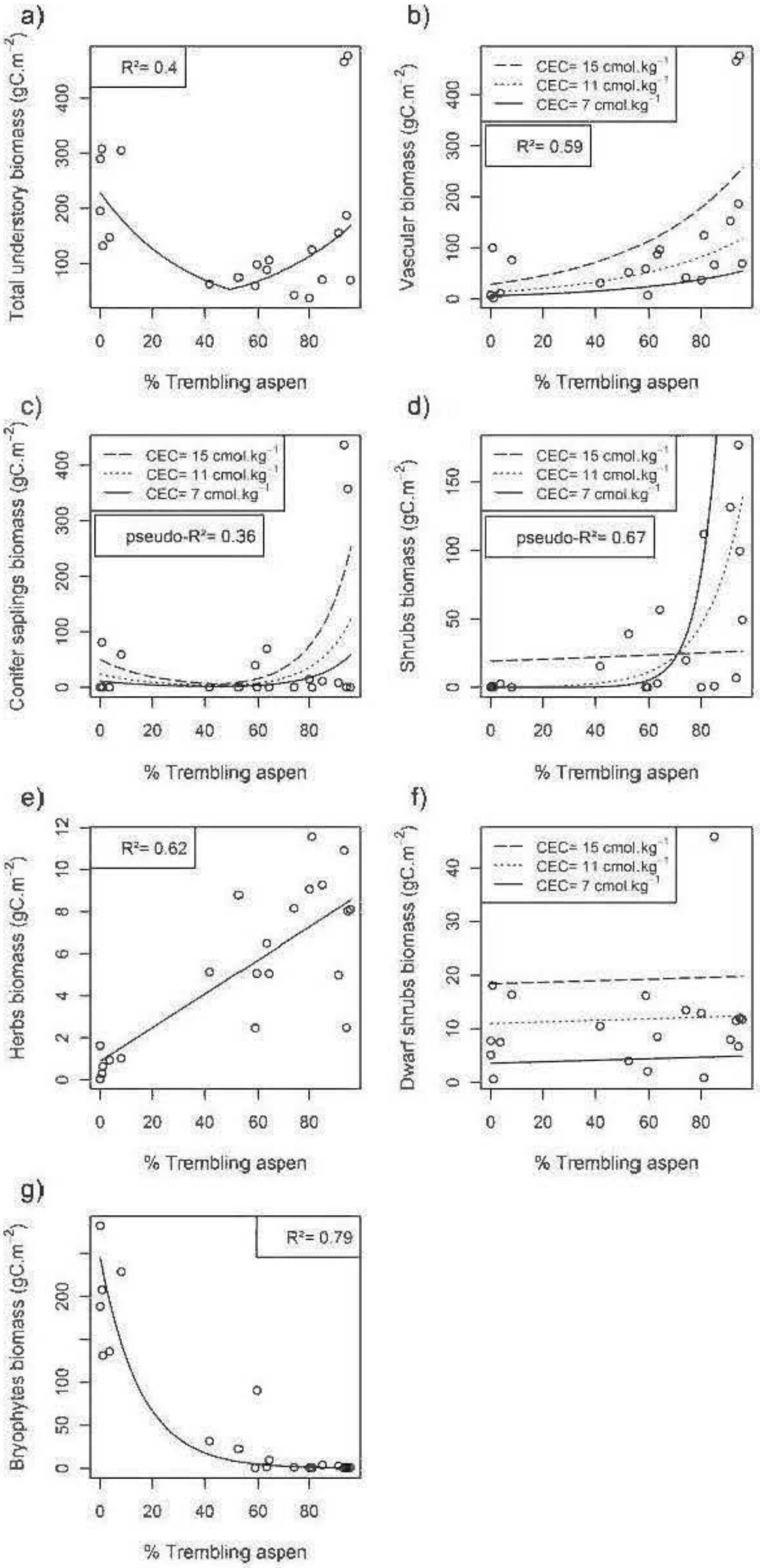

Figure 3.3 Biomass in relation to the trembling aspen proportion of total basal area for the Quebec study. R^2 is displayed when the slope of the effect is significantly different from 0 at α=0.05. Different regression lines show mineral CEC influence when it is significant.

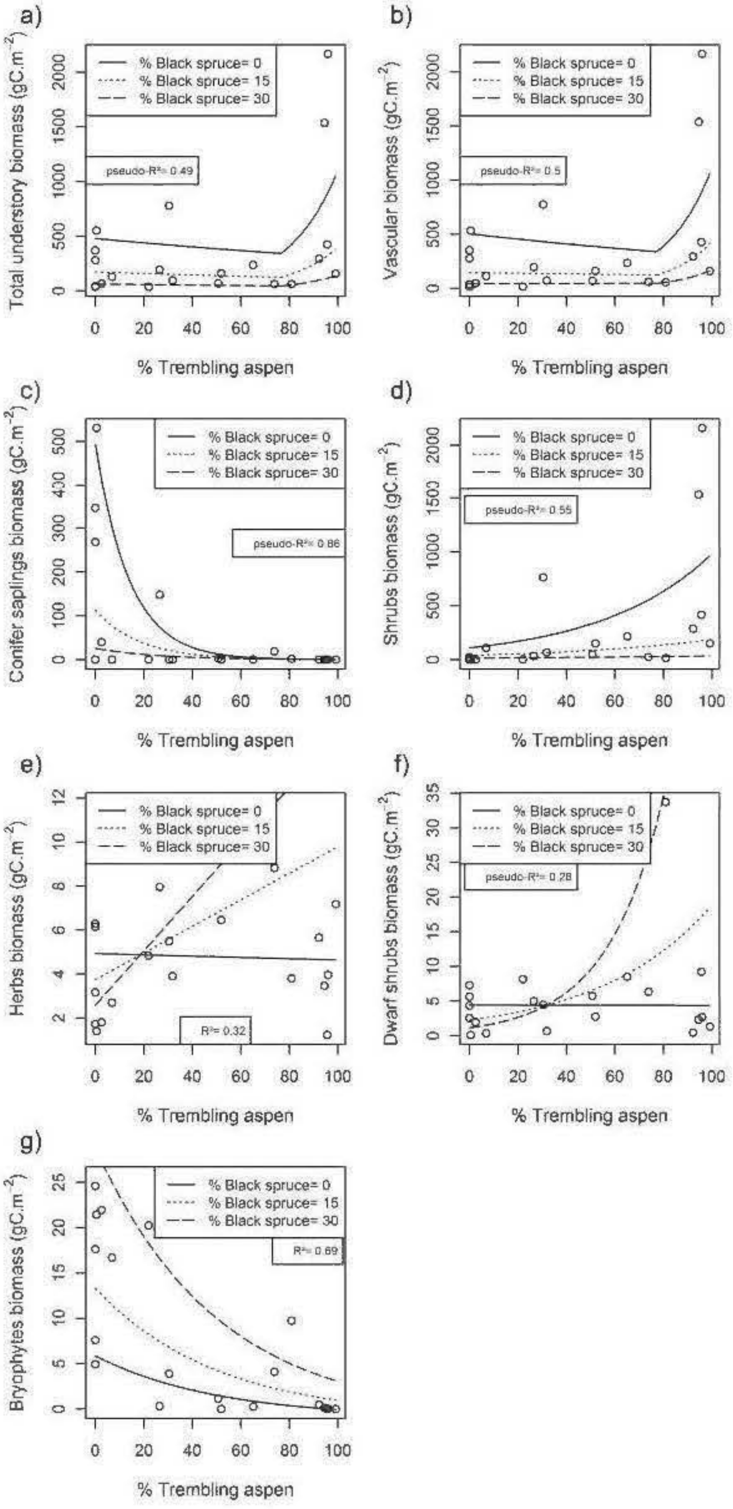

Figure 3.4 Biomass in relation to the jack pine proportion of total basal area for the Ontario study. R^2 is displayed when the slope of the effect is significantly different from 0 at α=0.05. Different regression lines show black spruce proportion influence when it is significant.

3.4.3. Growth and turnover rates

Annual growth rates generally followed the same patterns as those of biomass but with higher variability, resulting in weaker models (Figs. 3.5 and 3.6). In the Quebec study, AGR and NPP responded negatively to CEC when the aspen proportion was low, and positively when the aspen proportion was high (Fig. 3.5a and b). Inversely, AGR of shrubs increased with increasing aspen proportion, and this effect became weaker with increasing CEC (Fig. 3.5c). AGR of herbs also increased with aspen proportion (Fig. 3.5d), whereas the growth rates of conifer saplings and dwarf shrubs did not change with either variable (Fig. 3.5e and f).

In the Ontario study, the NPP of vascular plants and AGR of vascular plants and shrubs increased with increasing aspen proportion. These effects became weaker as the spruce proportion increased (Fig. 3.6a, b and c). AGR of conifer saplings decreased with an increase in aspen proportion, but only when the presence of black spruce was low (Fig. 3.6e). Finally, neither the AGR of herbs nor that of dwarf shrubs responded to any variables (Fig. 3.6d and f). As in the Quebec study, the models' R^2 values (or pseudo-R^2 when Poisson distribution was used) were overall lower than those of the biomass analyses (Fig. 3.6).

Global vascular turnover rate (mean across all vascular strata) ± 1 SE was 11.3 ± 5.2 % in the Quebec study and 17.3 ± 5.8 % in the Ontario study, but it differed strongly among strata (Fig. 3.7). It did not respond to any of the tested variables in either study. The only turnover rates that responded to canopy composition were those of herbs in the Quebec study and dwarf shrubs in the Ontario study, both of which responded negatively to an increase in black spruce proportion. Turnover rates of shrubs were not tested because they were not present enough in coniferous stands. Similarly, turnover rates of conifer saplings were not tested in the Ontario study because they were only present in sufficient numbers in pure pine stands.

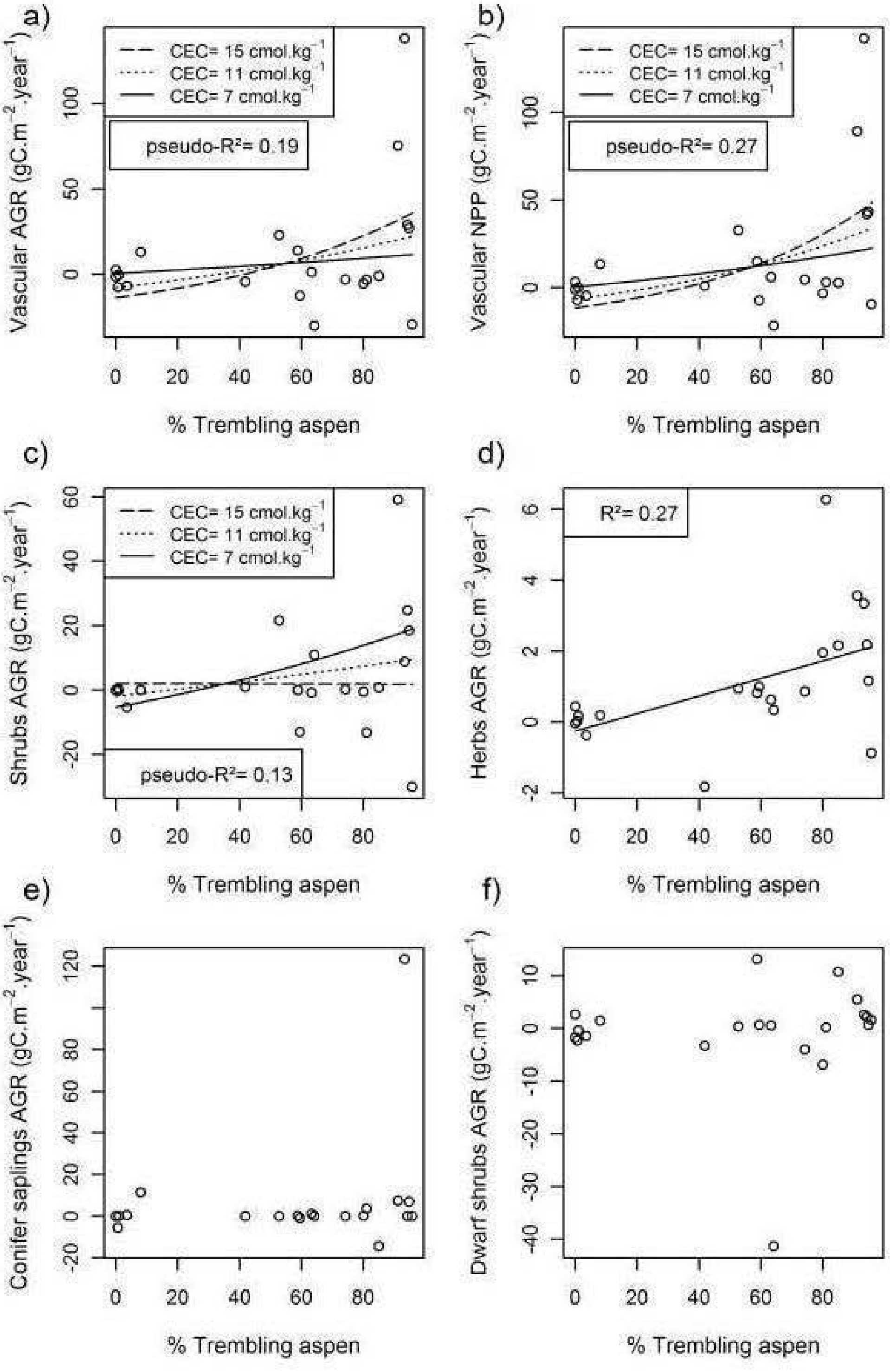

Figure 3.5 Annual growth rates (AGR) and net primary production (NPP) in relation to the trembling aspen proportion of total basal area for the Quebec study. R^2 is displayed when the slope of the effect is significantly different from 0 at α=0.05. Different regression lines show mineral CEC influence when it is significant.

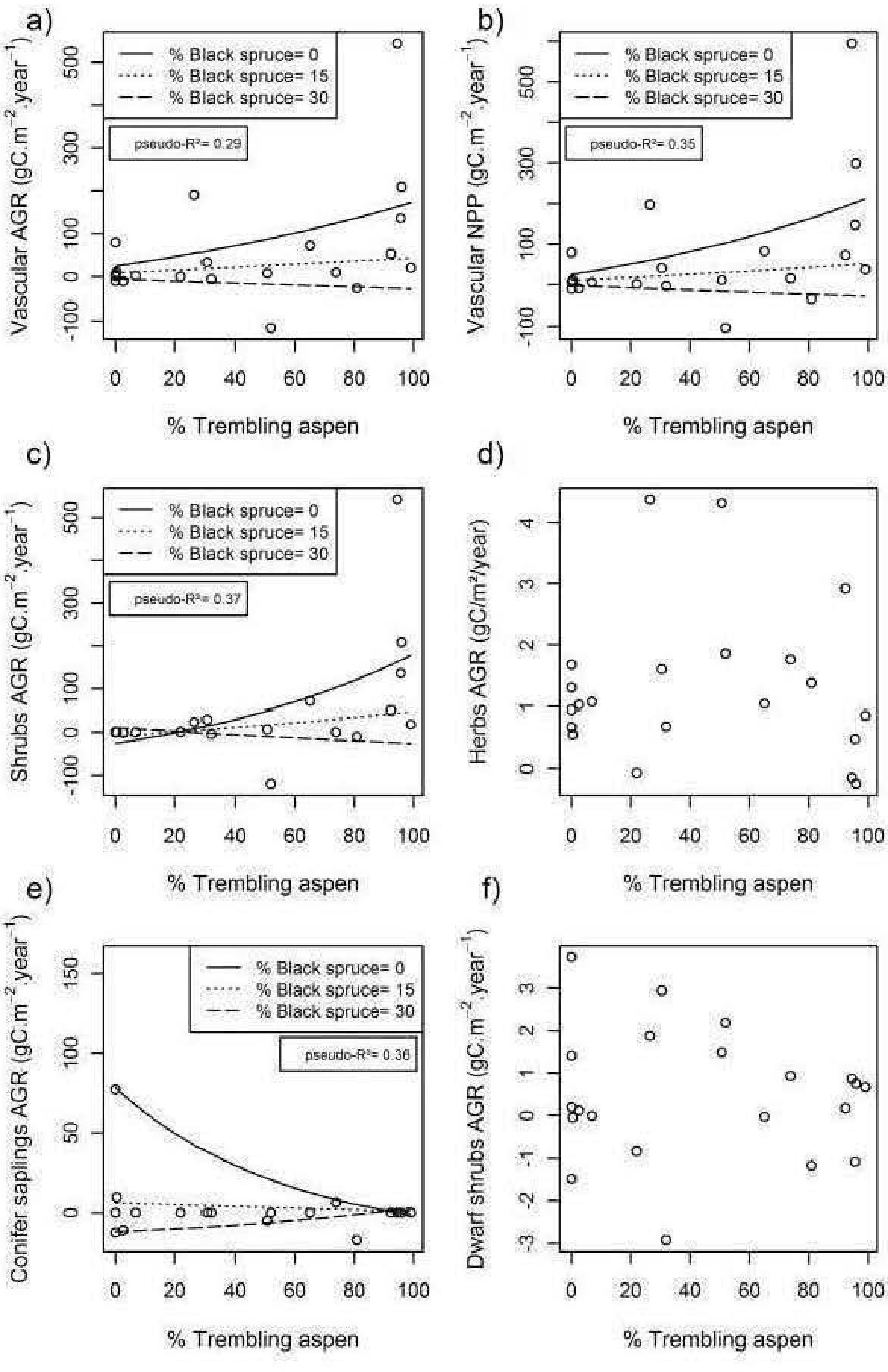

Figure 3.6 Annual growth rates (AGR) and net primary production (NPP) in relation to the jack pine proportion of total basal area for the Ontario study. R² is displayed when the slope of the effect is significantly different from 0 at α=0.05. Different regression lines show black spruce proportion influence when it is significant.

3.5. DISCUSSION

3.5.1. Biomass-measurement relationships

To estimate growth rates, we needed a method to predict the biomass in 2007. We found that using non-destructive morphological measurements for biomass estimation made it possible to obtain a high predictive capability. While the method was time-consuming, the correlation between measured and predicted biomass was better than what can usually be achieved by using percentage cover (Muukkonen et al. 2006). Our predictive models of biomass appear to be adequate for our study.

3.5.2. Biomass

Vascular biomass globally responded positively to an increase in trembling aspen proportion. This result is in accordance with previous work (Hart & Chen 2008) and was expected since tall shrub species such as *Corylus cornuta*, *Alnus* spp. and *Acer spicatum*, which were the major component of the understory vascular biomass (Fig. 5), have high light and nutrient requirements (Haeussler et al. 1990). Based on previous studies (Messier et al. 1998; Légaré et al. 2005b), we hypothesized that the availability of those resources would increase with the increasing presence of aspen. Our study cannot confirm the role of light availability since it was not measured, but suggests that soil resources played an important role for two reasons: first, the organic layers showed much greater nutrient concentrations when aspen was present, confirming the positive impact of aspen litter on soil quality compared with conifers that had been demonstrated in previous studies (Légaré et al. 2005b; Laganière et al. 2009; Laganière et al. 2010); second, in the Quebec study, the aspen effect on vascular biomass (shrubs in particular) was strong where the CEC of the deep mineral soil layer was low, and was weaker where the CEC of the deep mineral soil layer was high. Assuming that mineral soil CEC can be used as a coarse indicator of intrinsic site fertility, a possible explanation for this result is that the effect of aspen on forest floor properties that may be beneficial to some understory species could be less important on richer soils because the nutrient requirements of these shrubs is already met. Also, Ste-Marie et al. (2007) observed a greater effect of aspen on soil nutrient availability in poor sites than in rich ones. In the Ontario study, where the coarser soils are overall poorer, the strong positive effect of aspen proportion on vascular biomass is consistent with the pattern observed for the low CEC sites in the Quebec study.

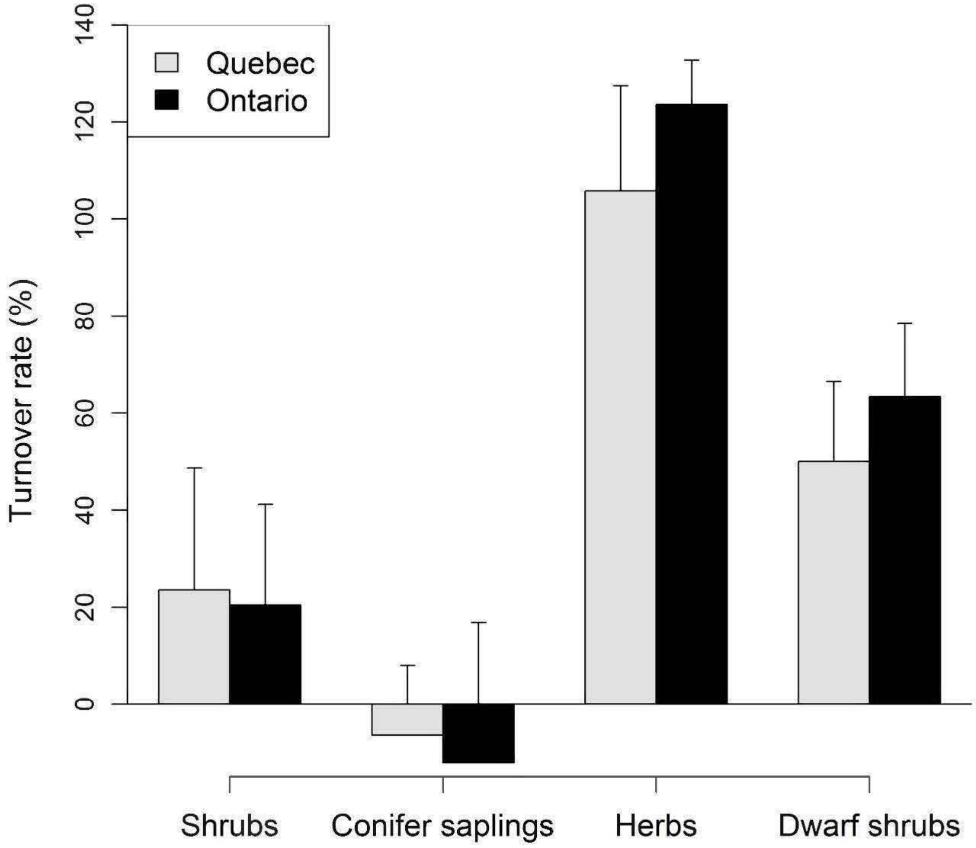

Figure 3.7 Turnover rates (mean + 1 SE) in relation to vascular strata for the Quebec and Ontario studies.

Vascular strata other than tall shrubs showed more complex responses and differed between the two study areas. In Ontario, herbs and dwarf shrubs responded positively to aspen presence only when black spruce was also present. This may be explained by the thick *A. spicatum* layer that cast heavy shade at the ground level in pure trembling aspen stands in the Ontario study. The response of conifer saplings also differed between the two areas. Saplings were favoured by the jack pine overstory in Ontario and decreased with the overstory abundance of black spruce; this might have been a result of higher light availability under pine (Canham et al. 1994; Messier et al. 1998), which benefits tree regeneration. In the Quebec study, however, they reached their lowest abundance in 50/50 aspen-spruce mixedwoods. The surprising result that spruce saplings were more abundant in aspen-dominated stands than in aspen-spruce mixed stands could be explained by the fact that spruce individual growth was inhibited in aspen stands but not in mixedwoods (Cavard et al. 2010). The more abundant saplings found in aspen stands could thus have been suppressed spruce trees, while those in mixedwoods had grown in the intermediate layer of the canopy.

While vascular biomass overall supported the resource availability hypothesis, bryophytes, on the other hand, were favoured in the low resource environments associated with black spruce. This association between bryophytes and spruce canopy has previously been reported (Légaré et al. 2002; Augusto et al. 2003; Fenton et al. 2005). The tolerance of bryophytes to the lack of soil resources can be at least partially explained by their N-fixation ability (DeLuca et al. 2002; Houle et al. 2006). It suggests that total understory biomass could not be predicted exclusively from light and nutrient resources availability. Chemical and physical inhibition by broadleaved litter is the most probable factor to explain the exclusion of bryophytes from mixed and aspen stands (Startsev et al. 2008). It is important to note that bryophytes were a major component of understory biomass in the coniferous stands of the Quebec study (Fig 1a), but not in Ontario (Fig 1b). The main environmental difference that could explain the lower abundance of bryophytes in the Ontario study area is the moisture regime (hygric in Quebec vs. mesic in Ontario). This would suggest that moisture or nutrients leached by hydrologic movement might be a controlling resource for bryophytes, rather than light and soil nutrients availability.

While the responses of vascular and non-vascular plants to resources are known to differ (Hart and Chen 2006), our study shows that those responses were non-linear. Vascular biomass (through tall shrubs) suffers from an exponential decrease with an increasing conifer proportion in the canopy, while bryophytes biomass similarly decreases exponentially with an increasing proportion of aspen. As both bryophytes and shrubs followed this strong exponential decrease when the canopy became more mixed, overstory mixtures appeared to have a negative effect on total understory biomass, contrary to our initial neutral hypothesis. Understory biomass in our stands thus seems to be dominated by specialized species that were hindered by increased resource heterogeneity. Because of the lower presence of bryophytes in the Ontario study, this negative mixture effect was less significant in this area. Conifer saplings rather than bryophytes dominated pine stands understory biomass, but also followed an exponential decrease with increasing aspen proportion. The difference in the global trend of total understory biomass between the two study areas can be explained by the low understory biomass of Ontario pine stands compared with aspen stands, and by the fact that the exponential decrease in shrub biomass was stronger with increasing pine proportion in Ontario than with increasing spruce proportion in Quebec. As a result, the lowest total understory carbon pool predicted by our model for the Ontario area occurred around 20/80 pine-aspen mixtures, instead of 50/50 mixtures as in the Quebec area. This kind of understory specialization leading to lower biomass in mixedwoods has also been observed on different bryophytes species by Carleton (1990). This extreme specialization may be due to the sharply contrasted environmental conditions induced by each tree species in our study. With less different conditions in each type of pure stands, understory species might have coped better with the intermediate conditions of mixed stands.

3.5.3. Carbon dynamics (growth and turnover rates)

AGR and NPP generally followed the same trends as biomass. Since we did not measure the mortality of perennial species, we underestimated net primary production and turnover rates, which explains the presence of some negative values. Those negative values mainly came from the conifer saplings stratum, which represents an important part of the vascular biomass, and thus contributes to the lower overall turnover rates. The lack of mortality data might also contribute to the smaller turnover rates we observed compared with the 34-43% reported by Chapin (1983). Nevertheless, our average understory turnover rates (Fig. 3.7) are higher than those of conifers (2-5% according to Chapin 1983), indicating the importance of understory in the carbon dynamics of boreal forests. The presence of a thick bryophyte layer under black spruce canopies reinforces this conclusion. The bryophyte turnover rate is estimated to represent 24% of their total biomass from similar sites near our Quebec area (N. Fenton, unpublished data), which indicates that not only are bryophytes an important pool, but that they also play a major role in the understory carbon dynamics of black spruce stands in the Clay Belt area. Even though some N fixation activity may be taking place for some moss species (DeLuca et al. 2007; Markham 2009), this mechanism may not be strong enough to counterbalance the positive effect of aspen litter on soil N availability through faster recycling rates (Côté et al. 2000, Table 3.4).

Unfortunately, turnover rates of the different vascular strata did not generally respond to changes in canopy composition, with two exceptions. Given that NPP of annual herbaceous species was calculated from their biomass in 2008, their turnover rates logically have the same positive response to aspen proportion. This effect may be further increased by the fact that the proportion of perennial species among the herbs group was higher in coniferous stands than in deciduous stands (not shown). Similarly, turnover rates of dwarf shrubs in the Ontario study may have responded negatively to an increasing proportion of black spruce because dwarf shrubs found under black spruce consisted mostly of evergreen rather than deciduous species (not shown).

3.6. CONCLUSION

With turnover rates of around 14%, along with carbon pools of up to 9 MgC.ha^{-1}, the understory of eastern boreal forests appears to play a significant role in the carbon budget of these ecosystems. Tree mixtures, and thus resource heterogeneity, had no positive effects on these dynamics as pure stands developed thick layers of specialized species (like bryophytes or tall shrubs), which suffered from the presence of another tree species, so that biomass and annual growth rates reached their lowest values in mixed stands. Vascular biomass seemed to be positively associated with higher soil resources availability attributed to the presence of trembling aspen, particularly in sites of low intrinsic fertility, but the opposite was observed for bryophytes, which were inhibited by aspen and might have been controlled by other resources like moisture or hydrologic movement. Total understory carbon dynamics thus seemed to be driven by resource availability, but the nature of those resources may differ strongly between vascular and non-vascular plants. This was demonstrated with ground-dwelling bryophytes, which were highly productive in the poor soil environments of black spruce stands of the Quebec Clay Belt area. Moreover, competitive exclusion and inhibiting effects such as the one of aspen litter on ground-dwelling mosses appeared to play a major role as well.

3.7. ACKNOWLEDGMENTS

We thank Eric Boucher, Maxime Moncamp and Alexandre Turcotte for field assistance, as well as Brian Brassard, Jérôme Laganière and Stephen Hart for their help in finding the Ontario sites, Isabelle Lamarre, Mark Fox and Samuel Bartels for editing this paper, and anonymous reviewers for their helpful comments. We are also grateful to Tembec Inc. for allowing us access to the Quebec sites and Abitibi Bowater for the Ontario sites. This study was supported by the NSERC-UQAT-UQAM Industrial Chair in Sustainable Forest Management and the Natural Sciences and Engineering Research Council of Canada (strategic grant). This research complies with the current laws of Canada.

CHAPITRE IV

CAN MIXEDWOOD MANAGEMENT INCREASE ABOVEGROUND CARBON SEQUESTRATION IN THE EASTERN BOREAL SHIELD?

Xavier Cavard, Yves Bergeron, Han Y.H. Chen et David Paré

4.1. ABSTRACT

The complex interactions between tree species and their effect on the environmental conditions in the understory make the aboveground dynamics in mixedwoods difficult to predict, while they represent a significant component of the Canadian boreal forest, and hence an major carbon pool. Aboveground overstory and understory carbon pools and net productivity have been measured and estimated in mature pure and mixed stands of black spruce (*Picea mariana* (Mill.) BSP) and trembling aspen (*Populus tremuloides* Michx.) in north-western Quebec, and in pure and mixed stands of black spruce, trembling aspen and jack pine (*Pinus banksiana* Lamb.) in north-western Ontario. Total aboveground carbon pool (TACP) was only weakly affected by the understory, except in pure aspen stands of the Ontario study, and that of mixedwoods was generally intermediate between those of corresponding pure stands. Stands dominated by trembling aspen had the largest aboveground carbon pool in both study areas. Aboveground net primary productivity at 90 years after fire was however strongly influenced by productive layers of specialized understory species that had developed under pure canopies. The mixture effect was thus generally neutral on carbon pools and negative on carbon dynamics 90 years after fire.

4.2. INTRODUCTION

In the present context of global climate change (IPCC 2007), major carbon pools are given increasing attention. This is the case for boreal forests, for not only do they represent a large part of terrestrial phytomass (Bailey 1996; Goodale et al. 2002), but they are also most likely to be affected by climate changes (Soja et al. 2007). Are the boreal ecosystems going to become better or poorer carbon sinks in the future is thus a crucial question, but hardly answerable due to our limited knowledge of their carbon dynamics. A better understanding of the spatial partition of carbon pools and fluxes for instance would allow for management decision that could maximize the carbon sequestration potential of boreal forest stands (Neilson et al. 2007).

One of the biggest gaps in our knowledge that would be invaluable to management decisions concerns mixed forest stands, or mixedwoods. Mixedwoods naturally represent around half of the Canadian boreal forest (CCFM 2000). Still, little is known about how tree species interactions and the diversity of microhabitats they create in the understory would affect carbon dynamics in mixtures. Facilitation (Brooker et al. 2008), competition and niche segregation (*i.e.* a better and less competitive use of resources between species of different functional traits, according to Vandermeer 1989) between tree species can affect their productivity, and hence carbon sequestration (Johnson et al. 2002). Studies on this topic have unfortunately remained inconclusive (Brown 1992; Kelty 1992; Chen & Klinka 2003; Lindén & Agestam 2003). While trees account for the largest share of the aboveground carbon pool in boreal forests, understory vegetation can contribute substantially to the carbon balance of these ecosystems because of its high turnover rate, which allows a high annual input of carbon in the understory relative to its total biomass (Zavitkovski 1976; Yarie 1980). This can be particularly important in evergreen forests where the turnover rate of trees is low (Chapin 1983). Ground-dwelling bryophytes common to boreal forest stands could also offset by their high growth rate (Bisbee et al. 2001) the low-productivity of the sites where they are generally found (Chen et al. 2004).

Previous studies have used forest inventory-like techniques to measure aboveground carbon pools in living trees (cf. Chapter I), aboveground carbon dynamics in trees (cf. Chapter II), and understory aboveground carbon pools and fluxes (cf. Chapter III) in the same mixed and corresponding pure stands of black spruce (*Picea mariana* (Mill.) BSP) and trembling aspen (*Populus tremuloides* Michx.) in the Clay Belt of north-western Quebec, and in mixed and pure stands of black spruce, trembling aspen and jack pine (*Pinus banksiana* Lamb.) on coarse soils of north-western Ontario. The present study aims to use the data from the preceding ones to assess the differences in total aboveground carbon pool (TACP) and aboveground net primary productivity (ANPP) across the different stand composition types. Relationships between the various aboveground carbon pools and fluxes are also investigated. This will allow to test whether TACP and ANPP are higher in mixedwoods than in single-species stands due to synergistic processes, or whether they are mere predictable means of the corresponding pure stands as far as carbon dynamics are concerned.

4.3. MATERIALS AND METHODS

4.3.1. Study areas

This study took place in two areas of the boreal mixedwood forest region. The first was located in the black spruce – feathermoss forest of western Quebec (Bergeron 1996), at the border of the Abitibi-Témiscamingue and Nord du Quebec regions (49°08’N to 49°11’N, 78°46’W to 78°53’W). This area is part of the Clay Belt region of Quebec and Ontario. This major physiographic region results from deposits left by the proglacial lakes Barlow and Ojibway at the time of their maximum expanse during the Wisconsinian glacial stage (Veillette 1994). The closest meteorological station is located in La Sarre (ca. 30 km south). Average annual temperature is 0.7°C and average annual precipitation totals 889.8 mm (Environment Canada 2007). All study sites were located on subhygric Grey Luvisols (Soil Classification Working Group 1996).

The second study area was located approximately 100 km north of Thunder Bay in northwestern Ontario (49°23’N to 49°36’N, 89°31’W to 89°44’W). Mean annual temperature and total average annual precipitation have been estimated at 0.9°C and 712.8 mm respectively by the BIOSIM model from 1977-2006 climatic data (Régnière & St-Amant 2007). The study was conducted on mesic upland sites whose soils are relatively deep glacial tills belonging to the Brunisolic order (Soil Classification Working Group 1996). Jack pine, trembling aspen, black spruce, and white birch (*Betula papyrifera* Marsh.) occur in this area in mixed dominance with white spruce (*Picea glauca* (Moench) Voss) and balsam fir (*Abies balsamea* (L.) Mill.).

4.3.2. Similarity of site quality

In order to ensure all sites were of similar quality in each region, we selected stands carefully according to the following criteria. All selected stands were upland sites with no or very little slope, had similar post-mature ages since fire and were closed-canopy with little damage from windbreaks. All stands in the same study region had the same moisture regime (mesic in Ontario and subhygric in Quebec), and were on the same kind of deposits (clay in Quebec and tills in Ontario, see 4.4.1).

Soil analyses on the deep (35-55cm) mineral soil and on the organic layer were processed, and showed that while deep mineral soil characteristics were very similar within each area and had no relation with overstory productivity, organic soil characteristics on the other hand were greatly influenced by canopy composition, as CEC and total N, P, Mg and Ca were higher with higher proportion of trembling aspen in the canopy. More details can be found in Chapters II and III.

4.3.3. Sampling design

In Quebec region, 24 sampling plots were established across 8 blocks, located in the same 36 km^2-wide area (maximum distance between blocks: 7 km), dominated by black spruce with patches of aspen. All these stands originated from the same fire that occurred in 1916 (Légaré et al. 2005a). Within each block (numbered from I to VIII), three plots of distinct compositions were selected: pure black spruce, pure trembling aspen, and mixedwoods containing both species (hereafter named BS, TA, and TAbs, respectively) (Table 4.1). After measurements, one plot (VIII-BS) proved unsuitable for comparison (far more accumulated organic matter than the other BS stands) and was therefore discarded from all analyses.

In Ontario region, 6 composition types were used in the Ontario study: pure jack pine (JP), pure aspen (TA), pine-aspen mixedwoods (TAJP) with the same selection criteria than in Quebec, and the same three overstory types with a black spruce sub-canopy of at least 15% of plot total basal area (respectively denoted JPbs, TAbs, TAJPbs). Each composition type was replicated between two and five times (Table 4.1). The study plots were established across an area of approximately 250 km^2. All plots originated from fires that occurred in 1918 (Chen, H.Y.H., *personal communication*). A completely randomized sampling design was carried out.

In our study, "pure" stands contained > 75% of the dominant species in relative basal area, whereas mixedwoods were selected so as to have fewer than 75% of one species in relative basal area, with stems of different species evenly spread across the stand ("intimate" mixture). All three plots of a given block were separated by a distance of 40-100 m to minimize the variability within each block (complete random block design).

4.3.4. Field measurements

For both study regions, all sample plots were circular with an area of 400 m^2 with at least a 5 m buffer zone of the same composition. In each plot, all trees > 5 cm DBH (diameter at breast height, 1.3 m) were numbered and measured for species, DBH, and height. Heights were measured using a Vertex clinometer. All snags were also numbered and measured and their decay classes noted according to the following classification: class 1: recent snags mostly intact in branches, bark, and top; class 2: snags showing sign of bark decay, generally no or few branches left; class 3: snags with no bark and branches left; class 4 and 5: stumps of low and high decay state, respectively.

Table 4.1 Overstory characteristics of the study plots.

Region and composition	No. of replicates	Stand density (stems.ha^{-1})[a]	Stand basal area (m².ha^{-1})	Basal area (%) Black spruce	Trembling aspen	Jack pine	Other species[b]
Quebec							
BS	7	3115±380	43.4 ± 2.3	89.4±4.2	1.8±0.7	-	8.8±4.0
TAbs	8	1578±125	52.2 ± 2.7	33.8±3.6	59.5±3.5	-	6.7±1.6
TA	8	1065±105	57.7 ± 3.6	8.9±1.8	88.5±2.6	-	2.6±2.3
Ontario							
JP	4	2445±128	49.4 ± 3.6	7.5±2.0	0.0	83.2±1.9	9.3±1.6
JPbs	3	2450±240	47.6 ± 1.2	29.2±3.9	3.6±2.3	64.1±4.9	3.0±1.5
TAJP	4	1300±168	44.6 ± 2.0	6.7±1.4	30.7±7.0	48.2±6.4	14.4±6.1
TAJPbs	2	2463±238	44.3 ± 1.9	26.0±4.8	27.1±3.6	44.0±10.9	2.9±2.5
TA	5	780±43	43.3 ± 3.8	0.0	95.2±1.2	0.7±0.7	4.1±0.9
TAbs	4	2045±205	53.9 ± 3.3	20.6±3.7	68.8±4.3	3.5±1.9	7.0±1.9

[a] Total density includes class 1 snags (see text for details).

[b] Other species consist for the Quebec study of jack pine and balsam fir, and for the Ontario study of balsam fir, white spruce, and white birch.

All trees in a subsection of each plot were cored at breast-height. The size of the subsection depended on overall plot density: 100 m^2 in high-density plots, 200 m^2 in medium-density plots, and 400 m^2 (thus all trees) in low-density plots, so that 20-40 cores were taken from each plot. The cores were then measured and analyzed using a Velmex sliding-stage micrometer and TSAPWin (F. Rinn Engineering Office) software along with COFECHA (Grissino-Mayer 2001). Those measurements and sampling took place in June 2006 for the Quebec study and in May 2007 for the Ontario study.

Understory vegetation was sampled in 3 quadrates of $1m^2$ each per sampling plot. Non-destructive measurements were taken in July and August 2007 and 2008 to assess annual growth by mean of allometric equations, while biomass was assessed by weighing harvested and dried vegetation in July and August 2008. Understory vegetation was partitioned between the following strata: shrubs (including deciduous tree seedlings), conifer seedlings and saplings, dwarf shrubs (including every ligneous species under 1m height), herbs (including ferns), and bryophytes (cf. Chapter III for details).

4.3.5. Data analyses

Tree biomass was calculated from both DBH and height. In both case we used the allometric equations established by Lambert et al. (2005). Foliage biomass was removed for class 1 snags, foliage and branches biomasses was removed for class 2 and 4, and foliage, branches and bark biomass was removed (leaving only stem biomass) for class 3 and 5. We did not take into account the density loss due to decay. The aboveground biomass of each cored tree was estimated for the last two years before sampling from DBH only. Annual growth rate (AGR) was the differences in stem biomass between those two years (corresponding to 2005 growth season for Quebec and 2006 growth season for Ontario). Tree biomass was expressed in carbon content using the mean carbon content values provided by Lamlom and Savidge (2003): spruces 0.5039 $kgC.kg^{-1}$, jack pine 0.504 $kgC.kg^{-1}$, trembling aspen 0.4709 $kgC.kg^{-1}$. Given that no such value was available for black spruce, we used that of white spruce in our calculations. Understory carbon content was considered to be half of its dry biomass. Total aboveground carbon pool (TACP) was the sum of all overstory (living and dead stem) and understory (all strata) pools at the stand level. Aboveground net primary productivity (ANPP) was defined as the net change in TACP in a year, and was computed as the sum of tree (non-studied species were ignored) and understory annual growth rates (AGR) at the stand level. As bryophytes AGR had not been measured, it was estimated using data coming from stands similar and close to our Quebec sites (Fenton, *unpublished data*).

Differences in carbon pools and fluxes at the stand level between composition types were assessed in the Quebec study by mixed linear models (Pinheiro & Bates 2000) with blocks as a random factor. As there was no block structure in the Ontario study, linear models (equivalent to analyses of variance) were used instead of mixed ones. All statistical analyses were performed using R software version 2.9.2 (R Development Core Team, 2009) and a significance threshold of 0.05.

4.4. RESULTS

4.4.1. Carbon pools

In the Quebec study, TA stands had the highest TACP, BS stands the lowest while TAbs were intermediate (Fig. 4.1a, Table 4.2). There was no significant difference in dead tree carbon pool between stand types (Fig. 4.1a, Table 4.2). Overstory carbon pool was positively correlated to vascular understory carbon pool (r= 0.42) and negatively correlated to bryophytes carbon pool (r= -0.65). Understory of BS, TAbs and TA stands contributed for 2.4%, 0.6% and 1.3% of TACP, respectively.

In the Ontario study, TACP was significantly higher in TA than in JPbs and TAJPbs stands but there was no global effect of composition type (Fig. 4.1b, Table 4.2). There was no significant difference in dead tree carbon pool between stand types (Fig. 4.1b, Table 4.2). Overstory carbon pool was negatively correlated to bryophytes carbon pool (r= -0.39) but not to vascular understory carbon pool (r= 0.10). Understory of JP, JPbs, TAJP, TAJPbs, TA and TAbs stands contributed for 3.3%, 0.86%, 2.87%, 0.79%, 8.00% and 1.35% of TACP, respectively.

Table 4.2 Global effects of stand composition type on carbon pools and fluxes.

Response variable	**Composition F-value**	**Composition P-value**
Quebec study		
Total aboveground carbon pool	10.76	0.003**
Dead overstory carbon pool	0.16	0.852
Aboveground net primary productivity	1.67	0.232
Overstory annual growth rate	10.40	0.003**
Ontario study		
Total aboveground carbon pool	1.83	0.167
Dead overstory carbon pool	1.07	0.417
Aboveground net primary productivity	3.21	0.036*
Overstory annual growth rate	4.54	0.010*

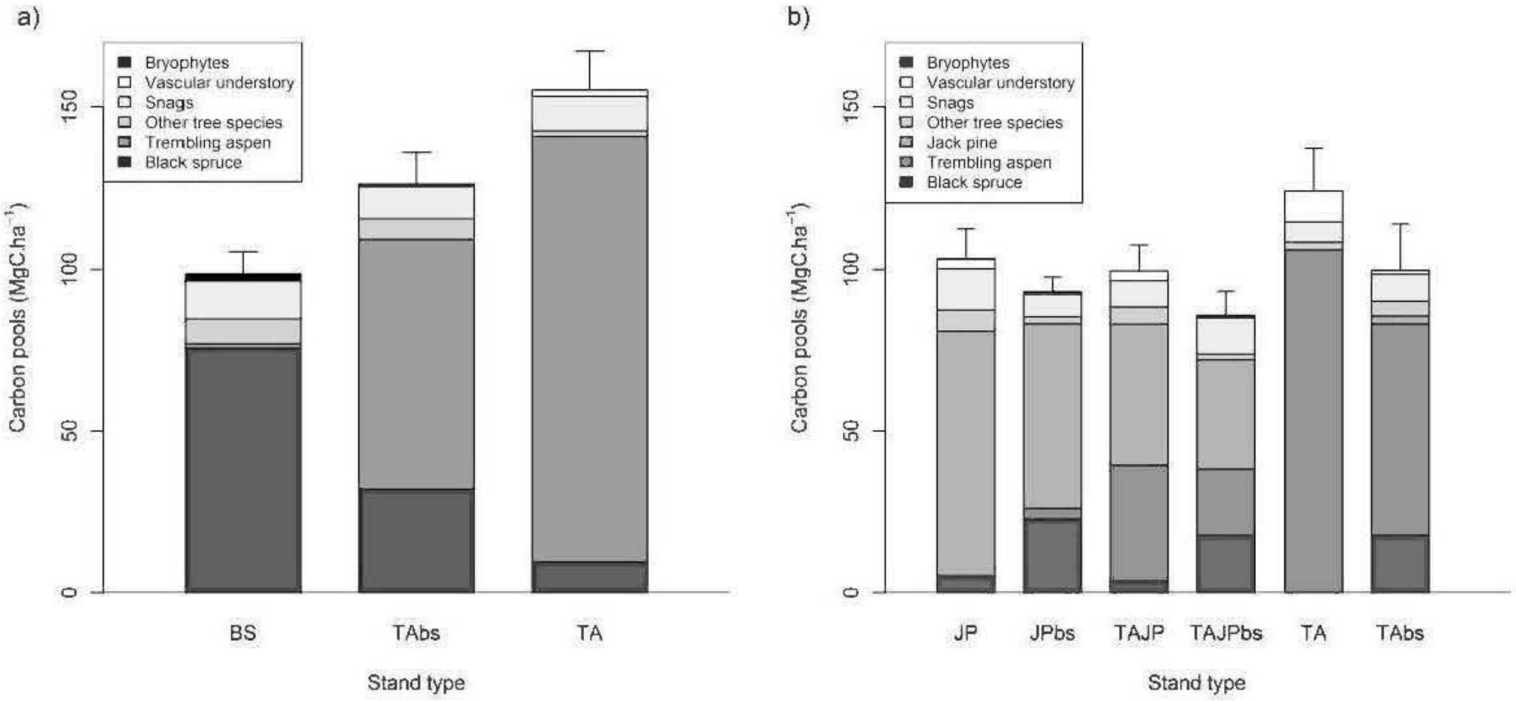

Figure 4.1 Carbon pools partitioned in each stand type of a) the Quebec study and b) the Ontario study. Displayed standard errors are calculated from total aboveground carbon pool (TACP).

4.4.2. Carbon dynamics

In the Quebec study, there was no significant difference in ANPP between stand types, while overstory AGR was highest in TA and TAbs stands than in BS (Fig. 4.2a, Table 4.2). Overstory AGR was not correlated to vascular understory AGR (r= 0.08) but was negatively correlated to bryophytes AGR (r= -0.47). Understory of BS, TAbs and TA stands contributed for 29.1%, 2.2% and 9.6% of ANPP, respectively.

In the Ontario study, ANPP was significantly higher in TA than in all of the other stand types. Overstory AGR was also higher in TA and TAbs than in JP and TAJP stands (Fig. 4.2b, Table 4.2). Overstory AGR was correlated to neither vascular understory AGR (r= -0.05) nor bryophytes AGR (r= -0.08). Understory of JP, JPbs, TAJP, TAJPbs, TA and TAbs stands contributed for 15.90%, 2.71%, 25.64%, 1.94%, 43.72% and 2.50% of ANPP, respectively.

4.5. DISCUSSION

4.5.1. Carbon pools

Given the low contribution of understory and dead tree carbon pools to TACP compared to living stems, TACP response to composition types generally followed the same trends we previously found on tree aboveground carbon pools (cf. Chapter I). This means that the mixture effect on TACP was overall additive: mixtures TACP could be predicted from those of corresponding pure stands. There was one exception to this in the Ontario study: the thick layer of shrubs in TA stands allowed TACP in TA stands to be higher than in stands with high conifer proportion in the canopy, which had the lowest understory biomass (cf. Chapter III).

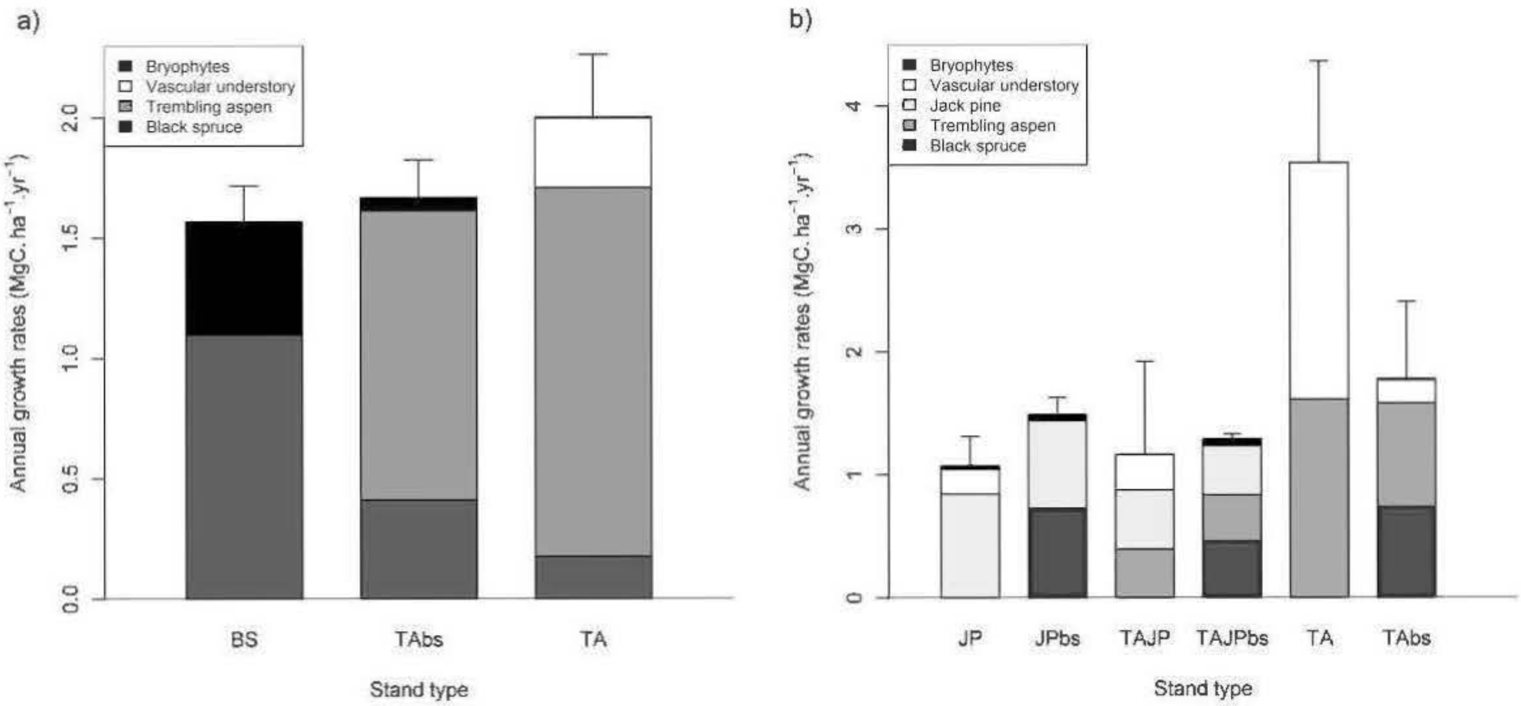

Figure 4.2 Annual growth rates partitioned in each stand type of a) the Quebec study and b) the Ontario study. Displayed standard errors are calculated from aboveground net primary productivity (ANPP).

4.5.2. Carbon dynamics

Unlike global trends of higher long term growth rates in coniferous trees (Cannell 1989), pure black spruce stands in our Quebec study had the lowest tree AGR, 90 years after fire. This may have been due to the accumulation of a thick bryophytes layer under spruces which diminishes soil temperature, slowing down organic matter decomposition and nutrient cycling (Côté et al. 2000; Crawford et al. 2003; Fenton et al. 2005). Understory, however, and particularly bryophytes in BS stands, was far more contributive to ANPP at 90 years after fire than to TACP. Even though this important contribution of bryophytes to carbon dynamics was not measured but merely estimated in this study, it has been shown in previous study on black spruce forests (O'Connell et al. 2003; Bond-Lamberty et al. 2004). Due to the contribution of bryophytes, ANPP was not significantly different between composition types. In some sense, the loss of tree productivity due to the accumulation of bryophytes was offset by its very cause, at least 90 years after fire.

The absence of a significant bryophytes layer even in coniferous stands made the situation very different in the Ontario study. The thick shrub layer under pure aspen stands contributed for almost half of the ANPP, much more than the understory contribution in any other stand type. The presence of even a small amount of conifers in the overstory had thus a dramatic impact on vascular understory biomass and dynamics, as it decreased exponentially with increasing presence of conifers (cf. Chapter III). Because of this non-linear relationship and of the important contribution of understory in carbon dynamics, ANPP in aspen-conifer mixtures was lower than in pure aspen stands but similar than in coniferous stands. This means that the mixture effect on ANPP was negative at 90 years after fire in the Ontario study.

4.6. CONCLUSION

As total aboveground carbon pools were largely dominated by living trees biomass, the mixture effect was mainly additive, that is, total aboveground carbon pools in our study were generally predictable intermediates between those of corresponding pure stands. Carbon dynamics measured as aboveground net primary productivity on the other hand were more influenced by the understory. However, it only altered the trends due to extreme situations where environmental conditions under monospecific canopies allowed the growth of a very dense and specialized understory (bryophytes under black spruce in Quebec and tall shrubs under trembling aspen). These specialized species were strongly and negatively affected by the adjunction of other tree species in the canopy, resulting in ANPP at 90 years after fire in mixedwoods similar to that in the less productive of the corresponding pure stands.

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CONCLUSION GÉNÉRALE

5.1. RÉCAPITULATIF

Nous avons mesuré ou estimé différentes composantes de cycle du carbone dans la partie aérienne de peuplements mixtes et des peuplements purs associés. À la limite entre l'Abitibi et la région de la Baie-James, la comparaison fut effectuée entre des peuplements dominés par l'épinette noire et d'autres dominés par le peuplier faux-tremble, et avec des mélanges entre ces deux essences. Au nord-ouest de l'Ontario, ce furent des peuplements de pins gris et de peupliers faux-tremble, ainsi que leurs mélanges, qui furent comparés, avec une proportion variable d'épinettes noires en sous-canopée.

Les stocks de carbone dans les tiges vivantes 90 ans après feu ont révélé des relations plutôt neutres entre les espèces. Seule la densité variable des différents types de peuplements a globalement une influence sur la biomasse moyenne des tiges, à l'exception de l'épinette noire qui semble avoir perdu de la croissance dans les peuplements largement dominés par le tremble en Abitibi. À l'échelle du peuplement, les stocks de carbone dans les peuplements mixtes ne sont généralement pas très différents de ce qui peut être prédit à partir des peuplements purs associés. Les quelques effets observés à cette échelle peuvent être encore une fois expliquées par les différences de densité entre les types de peuplements. La seule exception est une perte de biomasse pour le tremble à l'échelle du peuplement lorsque mélangé avec le pin gris.

Les analyses dendrochronologiques ont ensuite révélé que les relations entre les espèces ne sont pas neutres mais que les effets positifs et négatifs évoluent et s'annulent au fil du temps. Les analyses de sol semblent confirmer que l'impact bénéfique de la litière de tremble sur le cycle des nutriments est responsable d'un effet positif tardif sur la croissance de l'épinette, tandis que l'évolution de la morphologie de l'épinette indique que l'ombrage dû au tremble, et l'effet négatif qui en résulte, diminue avec le temps. Pour le tremble au contraire, le bénéfice initial d'être mélangé avec l'épinette à croissance lente s'est trouvé être progressivement contrebalancé par l'effet négatif de cette dernière sur les sols. Aucune espèce n'a bénéficié du mélange entre le tremble et le pin gris, mais la croissance du tremble en a plus souffert à long terme en raison encore une fois de l'effet du conifère sur les sols. Seule l'inversion des relations entre le tremble et l'épinette dans les dernières années en Abitibi n'est pas explicable à partir des données disponibles, mais suggère un effet de la fertilité des sols sur l'équilibre entre les phénomènes de facilitation et de compétition.

La végétation de sous-bois quant à elle n'est guère favorisée par les canopées mixtes. Les plantes vasculaires bénéficient des surplus en lumière et en nutriments apportés par le tremble, mais leur productivité (représentée surtout par des arbustes tels que les aulnes ou les érables à épis) chute drastiquement dès lors que la proportion de conifère augmente. Inversement, les bryophytes qui envahissent les sous-bois des pessières ne tolèrent pas que la proportion de tremble dans la canopée augmente un tant soit peu. Ainsi, la biomasse et la croissance du sous-bois des peuplements mixtes est inférieure à celle de chacun des peuplements purs correspondants. Il serait pour l'heure hasardeux d'affirmer si cet effet négatif résulte d'une spécialisation extrême des espèces de sous-bois les plus productives en forêt boréale, ou s'il est plutôt dû aux conditions environnementales très contrastées générées par chacune des espèces d'arbres mélangées.

Finalement, lorsque l'on additionne le carbone du sous-bois avec celui de la canopée, il apparaît que le premier contribue très peu aux stocks de carbone 90 ans après feu comparé au second. Au niveau de l'input de carbone en revanche, mesuré par la productivité aérienne nette, le sous-bois contribue largement plus, particulièrement les bryophytes dans les pessières en Abitibi et les arbustes dans les tremblaies en Ontario. Par conséquent, si l'ensemble des stocks aériens présentent globalement les mêmes résultats que les stocks dans les tiges vivantes, qui en constituent l'essentiel, l'effet négatif des peuplements mixtes sur la productivité du sous-bois par contre fait en sorte que la productivité aérienne dans les mixtes est plus proche de celle du peuplement pur le moins productif que de celle du peuplement pur le plus productif.

5.2. DES RELATIONS INTERSPÉCIFIQUES

Même si elle ne s'est pas révélée aussi efficace que prévue, d'après nos résultats la séparation des niches écologiques semble indéniablement jouer un rôle important dans les relations interspécifiques. Ainsi, le tremble peut évidemment ignorer l'épinette noire en terme de compétition aérienne, tandis que son effet d'ombrage sur cette dernière se réduit fortement avec le temps. Au contraire, le mélange de deux espèces dont les niches écologiques se recoupent largement, le tremble et le pin gris, a résulté en un effet nettement négatif. Le rôle joué ici par la séparation des niches toutefois semble plus d'avoir évité les interactions négatives de prédominer, et donc d'éviter une perte de croissance, plutôt que d'avoir permis une plus grande utilisation des ressources du milieu et donc un gain de productivité à l'échelle du peuplement. Néanmoins, l'adjonction d'épinettes sous les trembles aurait pu théoriquement résulter en un tel gain, n'eût été l'effet des litières des deux espèces (ainsi qu'une éventuelle compétition souterraine).

Les phénomènes de facilitation ne sont évidemment plus à démontrer, mais notre étude rappelle en quoi l'influence des litières est un cas particulier. Un ombrage protégeant des semis d'une lumière ou d'une sécheresse excessive, par exemple, n'impose *a priori* aucune contrepartie négative à l'arbre qui le génère. L'influence de la litière d'une espèce dans un peuplement mixte, au contraire, s'impose toujours au détriment de celle d'une autre litière. Chaque espèce tente en quelque sorte de façonner le milieu d'une manière qui lui est particulière. Par conséquent, si une espèce accélère le cycle des nutriments comparée à l'autre, même si la résultante de l'influence combinée de leurs deux litières n'est pas purement additive, elle ne peut être favorable à l'espèce ayant une litière récalcitrante qu'à la condition d'être défavorable à l'espèce facilitatrice. En d'autres mots, puisque l'influence facilitatrice d'une litière présuppose l'influence négative de l'autre – du moins en comparaison, le bénéfice potentiel pour une espèce ne peut être qu'inversement proportionnel au détriment potentiel pour l'autre (potentiel seulement, car tout dépend ensuite des besoins de chaque espèce et des conditions environnementales). Étant donné que les espèces ayant une litière avec un tel potentiel facilitateur sont plutôt exigeantes en ressources minérales, cette règle semble ne pouvoir être facilement contournée que dans les cas de mélanges avec des espèces fixatrices d'azote (Rothe & Binkley 2001; Kelty 2006).

5.3. RÔLE DES PEUPLEMENTS MIXTES DANS L'AMÉNAGEMENT FORESTIER

On l'a vu, les peuplements qui comportent plusieurs essences mélangées dans des proportions équitables ne connaissent généralement ni gain ni perte de productivité : un mélange équitable tremble-épinette noire par exemple équivaut à peu de chose près, en terme de productivité des tiges, à une moitié de pessière ajoutée à une moitié de tremblaie. Dans les mélange dominés par le tremble en revanche, l'effet sur l'épinette est négatif, alors qu'il a été montré que des plus faibles proportions de tremble dans la pessière (jusqu'à 40% de la surface terrière) résultent en un gain de croissance pour les tiges d'épinette (Légaré et al. 2004). Même sans effet de la composition en tant que telle, la plus faible densité naturelle des mélanges avec le tremble comparée aux pessières génère en elle-même des tiges d'épinettes de plus gros diamètres, ce qui pourrait se révéler précieux. En quelque sorte, les trembles fournissent au minimum l'équivalent d'une « éclaircie gratuite ». Il faut aussi rappeler que leur effet bénéfique sur les sols met du temps à se faire sensible, et pourrait donc bénéficier aux épinettes à plus long terme, après la mort des trembles. Cet effet peut être particulièrement appréciable sur la ceinture d'argile, afin d'éviter l'entourbement et la perte de productivité progressive des pessières, et ce sans avoir à effectuer de coûteuses préparations de terrain visant à perturber les sols en vu de leur « rajeunissement ». Dans des conditions de sol plus pauvres comme celles de notre étude ontarienne, l'effet pourrait même se révéler bénéfique pour la croissance de l'épinette à plus court terme, mais nous n'avons malheureusement pas été en mesure de le tester en raison de l'absence de pessières situées dans des conditions topographiques comparables aux tremblaies dans cette zone.

L'absence d'effet positif net peut paraître décevante, mais seulement si l'on oublie de considérer l'absence de véritable effet négatif. Cela veut dire que l'aménagement forestier pourrait bénéficier sans perte des autres avantages des peuplements mixtes. Ces derniers ont évidemment toute leur place dans l'aménagement écosystémique. Outre de permettre une plus grande concentration de biodiversité grâce à l'adjonction des espèces associées à chaque essence du mélange, et même dans certains cas d'abriter des espèces particulières (Cavard et al. en préparation), les peuplements mixtes peuvent fournir d'autres services de manière naturelle, tels que l'éclaircie ou le rajeunissement des sols mentionnés précédemment pour le mélange tremble-épinette. On devrait probablement songer à les inclure aussi dans l'aménagement intensif. Certains mélanges peuvent en effet offrir une certaine protection contre le feu, et d'autres contre les ravageurs (Koricheva et al. 2006), et constituent donc sans doute la seule alternative aux pesticides contre ce dernier problème, qui touche presque toujours les monocultures.

5.4. RÔLE DES PEUPLEMENTS MIXTES DANS LA SÉQUESTRATION DU CARBONE

Il semble clair que si l'on désire maximiser la séquestration du carbone, les mélanges que nous avons étudié ici ont peu de potentiel comparés aux peuplements purs de la plus productive des espèces (ici, le peuplier faux-tremble), au moins au niveau aérien. On peut dès lors se demander quels mélanges pourraient réussir où ceux-ci ont échoué, en maximisant les interactions positives et en minimisant les négatives. Mélanger un feuillu intolérant à l'ombre avec un conifère tolérant semble avoir du potentiel. Peut-être faudrait-il que la litière du conifère soit plus facilement décomposable que celle de l'épinette noire, et n'ait pas un effet aussi important sur la qualité des sols ? Mais en ce cas, le conifère bénéficierait-il vraiment de l'effet de la litière de tremble ? Peut-être l'échelle temporelle utilisée n'était-elle pas la bonne, et que les effets positifs d'un tel mélange ne se révèleraient qu'à plus long terme, en raison de la faculté du tremble de diminuer l'entourbement et le déclin de productivité observés au fil du temps dans les pessières (Fenton et al. 2005) ? Les études concernant l'effet des mélanges d'espèces sont malheureusement trop souvent obscurcies par de nombreux facteurs non-contrôlés ayant chacun une influence sur les résultats, tels que les conditions climatiques, topographiques et édaphiques. De nombreuses autres recherches, testant séparément l'effet de chacun de ces facteurs pour différents mélanges et à différents stades de développement des peuplements, vont être nécessaires si l'on espère utiliser un jour les peuplements mixtes de manière efficiente, en sachant dans quelles conditions nous pourrions bénéficier des multiples interactions qui se produisent entre les espèces. En ce qui concerne les mélanges particuliers que nous avons testés, la question de leur potentiel en tant que puits de carbone ne saurait trouver de réponse définitive avant que les résultats présentés ici n'aient été combinés avec ceux des études portant sur le carbone racinaire et le carbone du sol.

RÉFÉRENCES

Amoroso, M.M. & E.C. Turnblom 2006. "Comparing productivity of pure and mixed Douglas-fir and western hemlock plantations in the Pacific Northwest". *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere*, vol. 36, no 6, p. 1484-1496.

Aubin, I., S. Gachet, C. Messier & A. Bouchard 2007. "How resilient are northern hardwood forests to human disturbance? An evaluation using a plant functionnal group approach". *Ecoscience*, vol. 14, no 2, p. 259-271.

Augusto, L., J.L. Dupouey & J. Ranger 2003. "Effects of tree species on understory vegetation and environmental conditions in temperate forests". *Annals of Forest Science*, vol. 60, no 8, p. 823-831.

Augusto, L., J. Ranger, D. Binkley & A. Rothe 2002. "Impact of several common tree species of European temperate forests on soil fertility". *Annals of Forest Science*, vol. 59, p. 233-253.

Bailey, R.G. 1996. *Ecosystem geography: from ecoregions to sites*. Springer, New York, USA.

Barbier, S., F. Gosselin & P. Balandier 2008. "Influence of tree species on understory vegetation diversity and mechanisms involved - A critical review for temperate and boreal forests". *Forest Ecology and Management*, vol. 254, no 1, p. 1-15.

Bartels, S.F. & H.Y.H. Chen 2010. "Is understory plant species diversity driven by resource quantity or resource heterogeneity?" *Ecology*, vol. 91, no 7, p. 1931-1938.

Bauhus, J., A.P. van Winden & A.B. Nicotra 2004. "Aboveground interactions and productivity in mixed-species plantations of Acacia mearnsii and Eucalyptus globulus". *Canadian Journal of Forest Research*, vol. 34, no 3, p. 686-694.

Béland, M. & Y. Bergeron 1996. "Height growth of jack pine (*Pinus banksiana*) in relation to site types in boreal forests of Abitibi, Quebec". *Canadian Journal of Forest Research*, vol. 26, no 12, p. 2170-2179.

Béland, M., J.M. Lussier, Y. Bergeron, M.H. Longpré & M. Béland 2003. "Structure, spatial distribution and competition in mixed jack pine (*Pines banksiana*) stands on clay soils of eastern Canada". *Annals of Forest Science*, vol. 60, no 7, p. 609-617.

Bergeron, J.-F. 1996. "Domaine de la pessière noire à mousses". In: *Manuel de foresterie*, pp. 223-238. Les Presses de l'Université Laval, Sainte-Foy, QC, Canada.

Bevilacqua, E., D. Puttock, T. Blake & D. Burgess 2005. "Long-term differential stem growth responses in mature eastern white pine following release from competition". *Canadian Journal of Forest Research*, vol. 35, no 3, p. 511-520.

Binkley, D., R. Senock, S. Bird & T.G. Cole 2003. "Twenty years of stand development in pure and mixed stands of Eucalyptus saligna and nitrogen-fixing Facaltaria moluccana". *Forest Ecology and Management*, vol. 182, no 1-3, p. 93-102.

Bisbee, K.E., S.T. Gower, J.M. Norman & E.V. Nordheim 2001. "Environmental controls on ground cover species composition and productivity in a boreal black spruce forest". *Oecologia*, vol. 129, no 2, p. 261-270.

Bolin, B. & R. Sukumar 2000. "Global perspective." In: Watson, R.T., Noble, I.R., Bolin, B., Ravindranath, N.H., Verardo, D.J. & Dokken, D.J. (eds.) *IPCC special report on land use, land-use change, and forestry*, pp. 23-51. Cambridge University Press, Cambridge, UK.

Bolte, A. & I. Villanueva 2006. "Interspecific competition impacts on the morphology and distribution of fine roots in European beech (Fagus sylvatica L.) and Norway spruce (Picea abies (L.) Karst.)". *European Journal of Forest Research*, vol. 125, no 1, p. 15-26.

Bond-Lamberty, B., C.K. Wang & S.T. Gower 2004. "Net primary production and net ecosystem production of a boreal black spruce wildfire chronosequence". *Global Change Biology*, vol. 10, no 4, p. 473-487.

Boyden, S.B., P.B. Reich, K.J. Puettmann & T.R. Baker 2009. "Effects of density and ontogeny on size and growth ranks of three competing tree species". *Journal of Ecology*, vol. 97, no 2, p. 277-288.

Brassard, B.W. & H.Y.H. Chen 2008. "Effects of forest type and disturbance on diversity of coarse woody debris in boreal forest". *Ecosystems*, vol. 11, no 7, p. 1078-1090.

Brassard, B.W., H.Y.H. Chen, Y. Bergeron & D. Paré *in preparation.* "Niche differentiation drives higher fine root productivity in mixed- than single-species stands".

Brassard, B.W., H.Y.H. Chen, J.R. Wang & P.N. Duinker 2008. "Effects of time since stand-replacing fire and overstory composition on live-tree structural diversity in the boreal forest of central Canada". *Canadian Journal of Forest Research*, vol. 38, no 1, p. 52-62.

Bristow, M., J.K. Vanclay, L. Brooks & M. Hunt 2006. "Growth and species interactions of Eucalyptus pellita in a mixed and monoculture plantation in the humid tropics of north Queensland". *Forest Ecology and Management*, vol. 233, no 2-3, p. 285-294.

Brooker, R.W., F.T. Maestre, R.M. Callaway, C.L. Lortie, L.A. Cavieres, G. Kunstler, P. Liancourt, K. Tielborger, J.M.J. Travis, F. Anthelme, C. Armas, L. Coll, E. Corcket, S. Delzon, E. Forey, Z. Kikvidze, J. Olofsson, F. Pugnaire, C.L. Quiroz, P. Saccone, K. Schiffers, M. Seifan, B. Touzard & R. Michalet 2008. "Facilitation in plant communities: the past, the present, and the future". *Journal of Ecology*, vol. 96, no 1, p. 18-34.

Brown, A.H.F. 1992. "Functioning of mixed-species stands at Gisburn, N.W. England". In: Cannell, M.G.R., Malcolm, D.C. & Robertson, P.A. (eds.) *The ecology of mixed-species stands of trees*, pp. 125-150. Blackwell Scientific Publications, Oxford, UK.

Burgess, D., C. Robinson & S. Wetzel 2005. "Eastern white pine response to release 30 years after partial harvesting in pine mixedwood forests". *Forest Ecology and Management*, vol. 209, no 1-2, p. 117-129.

Callaway, R.M. 1995. "Positive interactions among plants". *Botanical Review*, vol. 61, no 4, p. 306-349.

Callaway, R.M., R.W. Brooker, P. Choler, Z. Kikvidze, C.J. Lortie, R. Michalet, L. Paolini, F.I. Pugnaire, B. Newingham, E.T. Aschehoug, C. Armas, D. Kikodze & B.J. Cook 2002. "Positive interactions among alpine plants increase with stress". *Nature*, vol. 417, p. 844-848.

Callaway, R.M. & L.R. Walker 1997. "Competition and facilitation: A synthetic approach to interactions in plant communities". *Ecology*, vol. 78, no 7, p. 1958-1965.

Canadian Council of Forest Ministers (CCFM) 2000. *National Forestry Database Program*. Available at http://nfdp.ccfm.org/.

Canham, C.D., A.C. Finzi, S.W. Pacala & D.H. Burbank 1994. "Causes and consequences of resource heterogeneity in forests: interspecific variation in light transmission by canopy trees". *Canadian Journal of Forest Research*, vol. 24, no 2, p. 337-349.

Canham, C.D., M.J. Papaik, M. Uriarte, W.H. McWilliams, J.C. Jenkins & M.J. Twery 2006. "Neighborhood analyses of canopy tree competition along environmental gradients in new England forests". *Ecological Applications*, vol. 16, no 2, p. 540-554.

Cannell, M.G.R. 1989. "Physiological basis of wood production: a review". *Scandinavian Journal of Forest Research*, vol. 4, no p. 459-490.

Cannell, M.G.R. 1999. "Growing trees to sequester carbon in the UK: answers to some common questions". *Forestry*, vol. 72, no 3, p. 237-247.

Cardinale, B.J., H. Hillebrand, W.S. Harpole, K. Gross & R. Ptacnik 2009. "Separating the influence of resource 'availability' from resource 'imbalance' on productivity-diversity relationships". *Ecology Letters*, vol. 12, no 6, p. 475-487.

Carleton, T.J. 1990. "Variation in terricolous bryophyte and macrolichen vegetation along primary gradients in Canadian boreal forests". *Journal of Vegetation Science*, vol. 1, p. 585-594.

Cavard, X., Y. Bergeron, H.Y.H. Chen & D. Paré 2010. "Mixed-species effect on tree aboveground carbon pools in the east-central boreal forests". *Canadian Journal of Forest Research*, vol. 40, no 1, p. 37-47.

Cavard, X., S.E. Macdonald, Y. Bergeron & H.Y.H. Chen *in preparation*. "Are mixedwoods important for biodiversity conservation in northern forests?"

Chapin, F.S. 1983. "Nitrogen and phosphorus nutrition and nutrient cycling by evergreen and deciduous understory shrubs in an Alaskan black spruce forest". *Canadian Journal of Forest Research*, vol. 13, no p. 773-781.

Chen, H.Y.H. & K. Klinka 2003. "Aboveground productivity of western hemlock and western redcedar mixed-species stands in southern coastal British Columbia". *Forest Ecology and Management*, vol. 184, no 1-3, p. 55-64.

Chen, H.Y.H., K. Klinka, A.H. Mathey, X. Wang, P. Varga & C. Chourmouzis 2003. "Are mixed-species stands more productive than single-species stands: an empirical test of three forest types in British Columbia and Alberta". *Canadian Journal of Forest Research*, vol. 33, no 7, p. 1227-1237.

Chen, H.Y.H., S. Légaré & Y. Bergeron 2004. "Variation of the understory composition and diversity along a gradient of productivity in Populus tremuloides stands of northern British Columbia, Canada". *Canadian Journal of Botany*, vol. 82, no 9, p. 1314-1323.

Côté, L., S. Brown, D. Paré, J. Fyles & J. Bauhus 2000. "Dynamics of carbon and nitrogen mineralization in relation to stand type, stand age and soil texture in the boreal mixedwood". *Soil Biology & Biochemistry*, vol. 32, no 8-9, p. 1079-1090.

Crawford, R.M.M., C.E. Jeffree & W.G. Rees 2003. "Paludification and forest retreat in northern oceanic environments". *Annals of Botany*, vol. 91, p. 213-226.

de Wit, H.A., T. Palosuo, G. Hylen & J. Liski 2006. "A carbon budget of forest biomass and soils in southeast Norway calculated using a widely applicable method". *Forest Ecology and Management*, vol. 225, no 1-3, p. 15-26.

del Rio, M. & H. Sterba 2009. "Comparing volume growth in pure and mixed stands of Pinus sylvestris and Quercus pyrenaica". *Annals of Forest Science*, vol. 66, no 5, p.

DeLuca, T.H., O. Zackrisson, F. Gentili, A. Sellstedt & M.C. Nilsson 2007. "Ecosystem controls on nitrogen fixation in boreal feather moss communities". *Oecologia*, vol. 152, no 1, p. 121-130.

DeLuca, T.H., O. Zackrisson, M.C. Nilsson & A. Sellstedt 2002. "Quantifying nitrogen-fixation in feather moss carpets of boreal forests". *Nature*, vol. 419, p. 917-920.

Environment Canada 2007. Canadian climate normals 1971-2000. Available at http://climate.weatheroffice.gc.ca/climate_normals/index_e.html.Environment Canada, National Meteorological Service, Downsview, ON.

Environment Canada 2010. Canadian daily climate data. Available at ftp://arcdm20.tor.ec.gc.ca/pub/dist/CDCD/.Environment Canada, National Meteorological Service, Downsview, ON.

Erickson, H.E., C.A. Harrington & D.D. Marshall 2009. "Tree growth at stand and individual scales in two dual-species mixture experiments in southern Washington State, USA". *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere*, vol. 39, no 6, p. 1119-1132.

Falk, M., K.T.P. U, S. Wharton & M. Schroeder 2005. "Is soil respiration a major contributor to the carbon budget within a Pacific Northwest old-growth forest?" *Agricultural and Forest Meteorology*, vol. 135, no 1-4, p. 269-283.

Fenton, N., N. Lecomte, S. Légaré & Y. Bergeron 2005. "Paludification in black spruce (*Picea mariana*) forests of eastern Canada: Potential factors and management implications". *Forest Ecology and Management*, vol. 213, no 1-3, p. 151-159.

Filipescu, C.N. & P.G. Comeau 2007. "Competitive interactions between aspen and white spruce vary with stand age in boreal mixedwoods". *Forest Ecology and Management*, vol. 247, no 1-3, p. 175-184.

Fitzsimmons, M.J., D.J. Pennock, J. Thorpe & Ql 2004. "Effects of deforestation on ecosystem carbon densities in central Saskatchewan, Canada". *Forest Ecology and Management*, vol. 188, no 1-3, p. 349-361.

Forrester, D.I., J. Bauhus, A.L. Cowie, P.A. Mitchell & J. Brockwell 2007. "Productivity of three young mixed-species plantations containing N-2-fixing Acacia and non-N2-fixing Eucalyptus and Pinus trees in southeastern Australia". *Forest Science*, vol. 53, no 3, p. 426-434.

Forrester, D.I., J. Bauhus, A.L. Cowie & J.K. Vanclay 2006. "Mixed-species plantations of Eucalyptus with nitrogen-fixing trees: A review". *Forest Ecology and Management*, vol. 233, no 2-3, p. 211-230.

Gartner, T.B. & Z.G. Cardon 2004. "Decomposition dynamics in mixed-species leaf litter". *Oikos*, vol. 104, no 2, p. 230-246.

Godefroid, S., W. Massant & N. Koedam 2005. "Variation in the herb species response and the humus quality across a 200-year chronosequence of beech and oak plantations in Belgium". *Ecography*, vol. 28, no 2, p. 223-235.

Goodale, C.L., M.J. Apps, R.A. Birdsey, C.B. Field, L.S. Heath, R.A. Houghton, J.C. Jenkins, G.H. Kohlmaier, W. Kurz, S.R. Liu, G.J. Nabuurs, S. Nilsson & A.Z. Shvidenko 2002. "Forest carbon sinks in the Northern Hemisphere". *Ecological Applications*, vol. 12, no 3, p. 891-899.

Green, D.S. 2004. "Describing condition-specific determinants of competition in boreal and sub-boreal mixedwood stands". *Forestry Chronicle*, vol. 80, no 6, p. 736-742.

Green, D.S. & C.D.B. Hawkins 2005. "Competitive interactions in sub-boreal birch-spruce forests differ on opposing slope aspects". *Forest Ecology and Management*, vol. 214, no 1-3, p. 1-10.

Grime, J.P. 1977. "Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory". *American Naturalist*, vol. 111, p. 1169-1194.

Grissino-Mayer, H.D. 2001. "Evaluating crossdating accuracy: a manual and tutorial for the computer program COFECHA". *Tree-Ring Research*, vol. 57, no 2, p. 205-221.

Haeussler, S., K.D. Coates & W.J. Mather 1990. *Autecology of common plants in British Columbia: a literature review*. Forestry Canada & British Columbia Ministry of Forests, Victoria, BC, Canada.

Hart, S.A. & H.Y.H. Chen 2008. "Fire, logging, and overstory affect understory abundance, diversity, and composition in boreal forest". *Ecological Monographs*, vol. 78, no 1, p. 123-140.

Havas, P. & E. Kubin 1983. "Structure, growth and organic matter content in the vegetation cover of an old spruce forest in northern Finland". *Annales Botanici Fennici*, vol. 20, no p. 115-149.

Hein, S. & J.F. Dhote 2006. "Effect of species composition, stand density and site index on the basal area increment of oak trees (Quercus sp.) in mixed stands with beech (Fagus sylvatica L.) in northern France". *Annals of Forest Science*, vol. 63, no 5, p. 457-467.

Hendershot, W.H. & M. Duquette 1986. "A simple barium chloride method for determining cation exchange capacity and exchangeable cations". *Soil Science Society of America Journal*, vol. 50, p. 605-608.

Holbrook, N.M. & F.E. Putz 1989. "Influence of neighbors on tree form - effects of lateral shade and prevention of sway on the allometry of *Liquidambar styraciflua* (sweet gum)". *American Journal of Botany*, vol. 76, no 12, p. 1740-1749.

Houle, D., S.B. Gauthier, S. Paquet, D. Planas & A. Warren 2006. "Identification of two genera of N-2-fixing cyanobacteria growing on three feather moss species in boreal forests of Quebec, Canada". *Canadian Journal of Botany*, vol. 84, no 6, p. 1025-1029.

Huisman, J. & F.J. Weissing 2001. "Fundamental Unpredictability in Multispecies Competition". *The American Naturalist*, vol. 157, no 5, p. 488-494.

IPCC 2007. Climate Change. Fourth IPCC Assessment Report. Intergovernmental Panel on Climate Change, Geneva, Switzerland.

Ito, A. 2005. "Modelling of carbon cycle and fire regime in an east Siberian larch forest". *Ecological Modelling*, vol. 187, no 2-3, p. 121-139.

Jenkins, J.C., D.C. Chojnacky, L.S. Heath & R.A. Birdsey 2003. "National scale biomass estimators for United States tree species". *Forest Science*, vol. 49, no 1, p. 12-35.

Jobidon, R. 2000. "Density-dependent effects of northern hardwood competition on selected environmental resources and young white spruce (Picea glauca) plantation growth, mineral nutrition, and stand structural development - a 5-year study". *Forest Ecology and Management*, vol. 130, no 1-3, p. 77-97.

Johansson, T. 2003. "Mixed stands in Nordic countries - a challenge for the future". *Biomass & Bioenergy*, vol. 24, no 4-5, p. 365-372.

Johnson, D.W., J.D. Knoepp, W.T. Swank, J. Shan, L.A. Morris, D.H. Van Lear & P.R. Kapeluck 2002. "Effects of forest management on soil carbon: results of some long-term resampling studies". *Environmental Pollution*, vol. 116, no p. S201-S208.

Johnstone, J.F. 2005. "Effects of aspen (Populus tremuloides) sucker removal on postfire conifer regeneration in central Alaska". *Canadian Journal of Forest Research*, vol. 35, no 2, p. 483-486.

Kaitaniemi, P. & A. Lintunen 2010. "Neighbor identity and competition influence tree growth in Scots pine, Siberian larch, and silver birch". *Annals of Forest Science*, vol. 67, no 6, *in press*

Karjalainen, T., A. Pussinen, J. Liski, G.J. Nabuurs, T. Eggers, T. Lapvetelainen, T. Kaipainen & Eu 2003. "Scenario analysis of the impacts of forest management and climate change on the European forest sector carbon budget". *Forest Policy and Economics*, vol. 5, no 2, p. 141-155.

Kelty, M.J. 1992. "Comparative productivity of monocultures and mixed-species stands". In: Kelty, M.J., Larson, B.C. & Oliver, C.D. (eds.) *The ecology and silviculture of mixed-species forests*, pp. 125-141. Kluwer Academic Publishers, Dordrecht.

Kelty, M.J. 2006. "The role of species mixtures in plantation forestry". *Forest Ecology and Management*, vol. 233, no 2-3, p. 195-204.

Kembel, S.W. & M.R.T. Dale 2006. "Within-stand spatial structure and relation of boreal canopy and understorey vegetation". *Journal of Vegetation Science*, vol. 17, p. 783-790.

Koricheva, J., H. Vehvilainen, J. Riihimaki, K. Ruohomaki, P. Kaitaniemi & H. Ranta 2006. "Diversification of tree stands as a means to manage pests and diseases in boreal forests: myth or reality?" *Canadian Journal of Forest Research*, vol. 36, no 2, p. 324-336.

Laganière, J., D. Paré & R.L. Bradley 2009. "Linking the abundance of aspen with soil faunal communities and rates of belowground processes within single stands of mixed aspen-black spruce". *Applied Soil Ecology*, vol. 41, no 1, p. 19-28.

Laganière, J., D. Paré & R.L. Bradley 2010. "How does a tree species influence litter decomposition? Separating the relative contribution of litter quality, litter mixing, and forest floor conditions". *Canadian Journal of Forest Research*, vol. 40, no 3, p. 465-475.

Lambert, M.C., C.H. Ung & F. Raulier 2005. "Canadian national tree aboveground biomass equations". *Canadian Journal of Forest Research*, vol. 35, no 8, p. 1996-2018.

Lamlom, S.H. & R.A. Savidge 2003. "A reassessment of carbon content in wood: variation within and between 41 North American species". *Biomass and Bioenergy*, vol. 25, no 4, p. 381-388.

Lecomte, N., M. Simard, N. Fenton & Y. Bergeron 2006. "Fire severity and long-term ecosystem biomass dynamics in coniferous boreal forests of eastern Canada". *Ecosystems*, vol. 9, no 8, p. 1215-1230.

Légaré, S., Y. Bergeron & D. Paré 2002. "Influence of forest composition on understory cover in boreal mixedwood forests of western Quebec". *Silva Fennica*, vol. 36, no 1, p. 353-366.

Légaré, S., Y. Bergeron & D. Paré 2005a. "Effect of aspen (Populus tremuloides) as a companion species on the growth of black spruce (Picea mariana) in the southwestern boreal forest of Quebec". *Forest Ecology and Management*, vol. 208, no 1-3, p. 211-222.

Légaré, S., D. Paré & Y. Bergeron 2004. "The responses of black spruce growth to an increased proportion of aspen in mixed stands". *Canadian Journal of Forest Research*, vol. 34, no 2, p. 405-416.

Légaré, S., D. Paré & Y. Bergeron 2005b. "Influence of aspen on forest floor properties in black spruce-dominated stands". *Plant and Soil*, vol. 275, no 1-2, p. 207-220.

Lindén, M. 2003. "Increment and yield in mixed stands with Norway spruce in southern Sweden". *Acta Universitatis Agriculturae Sueciae Silvestria*, vol. 260

Lindén, M. & E. Agestam 2003. "Increment and yield in mixed and monoculture stands of *Pinus sylvestris* and *Picea abies* based on an experiment in southern Sweden". *Scandinavian Journal of Forest Research*, vol. 18, no 2, p. 155-162.

Liu, J.X., S.G. Liu, T.R. Loveland & Da 2006. "Temporal evolution of carbon budgets of the Appalachian forests in the US from 1972 to 2000". *Forest Ecology and Management*, vol. 222, no 1-3, p. 191-201.

Longpré, M.H., Y. Bergeron, D. Paré & M. Béland 1994. "Effect of companion species on the growth of jack pine (*Pinus banksiana*)". *Canadian Journal of Forest Research*, vol. 24, no 9, p. 1846-1853.

MacDonald, G.B. & D.J. Thompson 2003. "Responses of planted conifers and natural hardwood regeneration to harvesting, scalping, and weeding on a boreal mixedwood site". *Forest Ecology and Management*, vol. 182, no 1-3, p. 213-230.

Maestre, F.T., R.M. Callaway, F. Valladares & C.J. Lortie 2009. "Refining the stress-gradient hypothesis for competition and facilitation in plant communities". *Journal of Ecology*, vol. 97, no 2, p. 199-205.

Mälkonen, E. 1974. "Annual primary production and nutrient cycle in some Scots pine stands". *Communicationes Instituti Forestalis Fenniae*, vol. 84, p. 1-87.

Man, R.Z. & V.J. Lieffers 1999. "Are mixtures of aspen and white spruce more productive than single species stands?" *Forestry Chronicle*, vol. 75, no 3, p. 505-513.
Marie-Victorin, E. Rouleau & L. Brouillet 2002. *Flore Laurentienne*. 3rd edition. Gaëtan Morin.

Markham, J.H. 2009. "Variation in moss-associated nitrogen fixation in boreal forest stands". *Oecologia*, vol. 161, no 2, p. 353-359.

Martin, J.L., S.T. Gower, J. Plaut, B. Holmes & Fg 2005. "Carbon pools in a boreal mixedwood logging chronosequence". *Global Change Biology*, vol. 11, p. 1883-1894.

McKenney, D.W., D. Yemshanov, G. Fox, E. Ramlal & Tr 2004. "Cost estimates for carbon sequestration from fast growing poplar plantations in Canada". *Forest Policy and Economics*, vol. 6, no 3-4, p. 345-358.

Meng, S.X., S.M. Huang, V.J. Lieffers, T. Nunifu & Y.Q. Yang 2008. "Wind speed and crown class influence the height-diameter relationship of lodgepole pine: Nonlinear mixed effects modeling". *Forest Ecology and Management*, vol. 256, no 4, p. 570-577.

Messier, C., L. Coll, A. Poitras-Lariviere, N. Bélanger & J. Brisson 2009. "Resource and non-resource root competition effects of grasses on early- versus late-successional trees". *Journal of Ecology*, vol. 97, no 3, p. 548-554.

Messier, C., S. Parent & Y. Bergeron 1998. "Effects of overstory and understory vegetation on the understory light environment in mixed boreal forests". *Journal of Vegetation Science*, vol. 9, no 4, p. 511-520.

Moraes de Jesus, R. & J.S. Brouard 1989. "Eucalyptus-Leucaena mixture experiment. I. Growth and yield". *International Tree Crops Journal*, vol. 5, p. 257-269.

Muggeo, V.M.R. 2003. "Estimating regression models with unknown break-points". *Statistics in Medicine*, vol. 22, p. 3055-3071.

Muukkonen, P., R. Mäkipää, R. Laiho, K. Minkkinen, H. Vasander & L. Finér 2006. "Relationship between biomass and percentage cover in understorey vegetation of boreal coniferous forests". *Silva Fennica*, vol. 40, no 2, p. 231-245.

Neilson, E.T., D.A. MacLean, F.R. Meng & P.A. Arp 2007. "Spatial distribution of carbon in natural and managed stands in an industrial forest in New Brunswick, Canada". *Forest Ecology and Management*, vol. 253, no 1-3, p. 148-160.

O'Connell, K.E.B., S.T. Gower & J.M. Norman 2003. "Comparison of net primary production and light-use dynamics of two boreal black spruce forest communities". *Ecosystems*, vol. 6, no 3, p. 236-247.

Pande, V., U.T. Palni & S.P. Singh 2007. "Effect of ectomycorrhizal fungal species on the competitive outcome of two major forest species". *Current Science*, vol. 92, no 1, p. 80-84.

Pinheiro, J.C. & D.M. Bates 2000. *Mixed-effects models in S and S-PLUS.* Springer Verlag, New York.

Pitt, D.G. & F.W. Bell 2005. "Juvenile response to conifer release alternatives on aspen-white spruce boreal mixedwood sites., Part I: Stand structure and composition". *Forestry Chronicle*, vol. 81, no 4, p. 538-547.

Prescott, C.E., L.M. Zabek, C.L. Staley & R. Kabzems 2000. "Decomposition of broadleaf and needle litter in forests of British Columbia: influences of litter type, forest type, and litter mixtures". *Canadian Journal of Forest Research*, vol. 30, no 11, p. 1742-1750.

Pretzsch, H. 2003. "Diversity and productivity of forests". *Allgemeine Forst Und Jagdzeitung*, vol. 174, no 5-6, p. 88-98.

Pretzsch, H. & G. Schutze 2009. "Transgressive overyielding in mixed compared with pure stands of Norway spruce and European beech in Central Europe: evidence on stand level and explanation on individual tree level". *European Journal of Forest Research*, vol. 128, no 2, p. 183-204.

Raunkiaer, C. 1934. *The life forms of plants and statistical plant geography.* Clarendon Press, Copenhagen, Denmark.

Régnière, J. & R. St-Amant 2007. "Stochastic simulation of daily air temperature and precipitation from monthly normals in North America north of Mexico." *International Journal of Biometeorology*, vol. 51, no p. 415-430.

Riegel, G.M., R.F. Miller & W.C. Krueger 1995. "The effects of aboveground and belowground competition on understory species composition in a *Pinus ponderosa* forest". *Forest Science*, vol. 41, no 4, p. 864-889.

Rothe, A. & D. Binkley 2001. "Nutritional interactions in mixed species forests: a synthesis". *Canadian Journal of Forest Research*, vol. 31, no 11, p. 1855-1870.

Rothe, A., J. Ewald & D.E. Hibbs 2003. "Do admixed broadleaves improve foliar nutrient status of conifer tree crops?" *Forest Ecology and Management*, vol. 172, no 2-3, p. 327-338.

Rothe, A., K. Kreutzer & H. Kuchenhoff 2002. "Influence of tree species composition on soil and soil solution properties in two mixed spruce-beech stands with contrasting history in Southern Germany". *Plant and Soil*, vol. 240, no 1, p. 47-56.

Simard, M., N. Lecomte, Y. Bergeron, P.Y. Bernier & D. Paré 2007. "Forest productivity decline caused by successional paludification of boreal soils". *Ecological Applications*, vol. 17, no 6, p. 1619-1637.

Simard, S. & A. Vyse 2006. "Trade-offs between competition and facilitation: a case study of vegetation management in the interior cedar-hemlock forests of southern British Columbia". *Canadian Journal of Forest Research*, vol. 36, no 10, p. 2486-2496.

Soil Classification Working Group 1996. *The Canadian system of soil classification.* 2nd. Agriculture and Agri-Food Canada Publication 1646, Ottawa, ON, Canada.

Soja, A.J., N.M. Tchebakova, N.H.F. French, M.D. Flannigan, H.H. Shugart, B.J. Stocks, A.I. Sukhinin, E.I. Parfenova, F.S. Chapin & P.W. Stackhouse 2007. "Climate-induced boreal forest change: Predictions versus current observations". *Global and Planetary Change*, vol. 56, no 3-4, p. 274-296.

Startsev, N., V.J. Lieffers & S.M. Landhäusser 2008. "Effects of leaf litter on the growth of boreal feather mosses: Implication for forest floor development". *Journal of Vegetation Science*, vol. 19, no 2, p. 253-260.

Ste-Marie, C., D. Paré & D. Gagnon 2007. "The contrasting effects of aspen and jack pine on soil nutritional properties depend on parent material". *Ecosystems*, vol. 10, no 8, p. 1299-1310.

Stevens, M.H.H. & W.P. Carson 2002. "Resource quantity, not resource heterogeneity, maintains plant diversity". *Ecology Letters*, vol. 5, no 3, p. 420-426.

Strong, W.L. & G.H. La Roi 1983. "Root-system morphology of common boreal forest trees in Alberta, Canada". *Canadian Journal of Forest Research*, vol. 13, p. 1164-1173.

Thiffault, N. & R. Jobidon 2006. "How to shift unproductive Kalmia angustifolia - Rhododendron groenlandicum heath to productive conifer plantation". *Canadian Journal of Forest Research*, vol. 36, no 10, p. 2364-2376.

Toms, J.D. & M.L. Lesperance 2003. "Piecewise regression: A tool for identifying ecological thresholds". *Ecology*, vol. 84, no 8, p. 2034-2041.

Vandermeer, J. 1989. *The ecology of intercropping*. Cambridge University Press, Cambridge, UK.

Veillette, J.J. 1994. "Evolution and paleohydrology of glacial Lakes Barlow and Ojibway". *Quaternary Science Reviews*, vol. 13, no 9-10, p. 945-971.

Vincent, J.-S. & L. Hardy 1977. "L'évolution et l'extension des lacs glaciaires Barlow et Ojibway en territoire québécois". *Géographie physique et Quaternaire*, vol. 31, no p. 357-372.

Voicu, M.F. & P.G. Comeau 2006. "Microclimatic and spruce growth gradients adjacent to young aspen stands". *Forest Ecology and Management*, vol. 221, no 1-3, p. 13-26.

Wang, J.R. & J.P. Kimmins 2002. "Height growth and competitive relationship between paper birch and Douglas-fir in coast and interior of British Columbia". *Forest Ecology and Management*, vol. 165, no 1-3, p. 285-293.

Yarie, J. 1980. "The role of understory vegetation in the nutrient cycle of forested ecosystems in the Mountain Hemlock Biogeoclimatic Zone". *Ecology*, vol. 61, no 6, p. 1498-1514.

Zavitkovski, J. 1976. "Ground vegetation biomass, production, and efficiency of energy utilization in some northern Wisconsin forest ecosystems". *Ecology*, vol. 57, no 4, p. 694-706.