UNIVERSITÉ DU QUÉBEC EN ABITIBI-TÉMISCAMINGUE

LES FACTEURS ÉCOLOGIQUES ET LES MÉCANISMES EXPLIQUANT LA LOCALISATION DE L'ÉCOTONE SAPINIÈRE/PESSIÈRE DANS L'OUEST DU QUÉBEC

THÈSE
PRÉSENTÉE
COMME EXIGENCE PARTIELLE
DU DOCTORAT EN SCIENCES DE L'ENVIRONNEMENT

PAR
YASSINE MESSAOUD

DECEMBRE 2007

La Bibliothèque
Cégep - Université
Abitibi-Témiscamingue

BIBLIOTHÈQUE
Cégep de l'Abitibi-Témiscamingue
Université du Québec en Abitibi-Témiscamingue

Mise en garde

La bibliothèque du Cégep de l'Abitibi-Témiscamingue et de l'Université du Québec en Abitibi-Témiscamingue a obtenu l'autorisation de l'auteur de ce document afin de diffuser, dans un but non lucratif, une copie de son œuvre dans Depositum, site d'archives numériques, gratuit et accessible à tous.

L'auteur conserve néanmoins ses droits de propriété intellectuelle, dont son droit d'auteur, sur cette œuvre. Il est donc interdit de reproduire ou de publier en totalité ou en partie ce document sans l'autorisation de l'auteur.

À la mémoire de mon Père, décédé avant la soumission de cette thèse, qui a suivi ce projet depuis le début,

Ma mère,

Mes frères Fouzi et Shukry,

Mon oncle Mourad et ma Tante Anneli,

Ma cousine Yasmina alias Snövit.

REMERCIEMENTS

Je voudrais avant tout remercier mon directeur de thèse Yves Bergeron pour son encadrement et ses conseils qui m'ont été indispensables tout au long du projet et qui le seront dans mon avenir scientifique. J'ai appris beaucoup de choses sous sa direction et j'ai beaucoup apprécié sa patience et son humanisme. Je remercie aussi Alain Leduc et Hugo Asselin qui m'ont suivi à tour de rôle tout au long de ce projet par leurs conseils au niveau des statistiques et des corrections des articles.

Je remercie aussi Jean-Pierre Saucier ainsi qu'à Pierre Grondin du Ministère des Ressources Naturelles du Québec pour les données d'inventaire écologique et leur aide pour la réalisation du premier chapitre. Je remercie également les personnes qui m'ont aidé en forêt soit Martin Simard, Benoît St-Vincent, Mark Purdon, Fateh Sadi et aux autres assistants de terrain. Merci aussi à Natasha Roudeix pour son aide au labo. Je tiens à remercier Danielle Charron et Marie-Hélène Longpré pour la logistique de terrain. Merci beaucoup à Patricia Wood, Ronnie Drever, Erol Yilmaz et Nicole Fenton pour la révision de l'anglais.

Pour finir, je remercie également les autres personnes qui m'ont aidé de manière directe et indirecte à réaliser ce travail.

AVANT-PROPOS

Cette thèse a été rédigée sous la forme de 4 articles scientifiques en anglais, et comporte un résumé, une introduction et une conclusion générale rédigés en français. Pour satisfaire aux exigences du jury de cette thèse, permettez-moi d'éclaircir le rôle des deux co-auteurs Alain Leduc et Hugo Asselin à la réalisation des différents chapitres. Dans tous les cas le design sur le terrain, les analyses et la rédaction ont été effectuées par moi-même sous la direction et les conseils de Yves Bergeron.

Chapitre 1: La contribution d'Alain Leduc a été dans la gestion des données et dans le domaine statistique ainsi que la révision du manuscrit. Les données proviennent de l'inventaire écologique du Ministère des Ressources Naturelles du Québec. Cet article a été publié dans la revue scientifique Global Ecology and Biogeography.

Chapitre 2, 3 et 4: La contribution de Hugo Asselin a suivi de très prêt l'évolution de ces trois articles et a grandement contribué à la qualité de l'anglais. Les données de ces trois chapitres proviennent des quatre sites d'étude. Le chapitre 2 a été publié dans la revue scientifique American Journal of Botany. Le chapitre 3 a été soumis à la revue Forest Ecology and Management. Enfin dans le chapitre 4, des données de l'inventaire dendrométrique des placettes temporaires du Ministère des Ressources Naturelles du Québec ont été ajoutées à celles de nos 4 sites d'étude. L'article a été soumis à la revue Canadian Journal of Forest Research.

TABLE DES MATIÈRES

LISTE DES TABLEAUX

LISTE DES FIGURES

LISTE DES ANNEXES

RÉSUMÉ DE LA THÈSE

La localisation d'un 'écotone' entre deux types de végétation a souvent été attribuée au climat. Dans cet écotone, les espèces atteignant leur limite nordique deviennent plus sensibles aux conditions climatiques. La zone circumboréale traversant les hautes latitudes du continent nord-américain et eurasiatique atteint sa limite sud à *ca* 60°N en Scandinavie, alors qu'elle atteint son point le plus au sud au monde (à la même altitude) à *ca* 48°N au nord-est américain (ouest Québec-est Ontario). Au Québec, cette zone est subdivisée en deux principaux types de forêt continue; dans sa partie sud la forêt mixte dominée par le sapin baumier (*Abies balsamae*), l'épinette blanche (*Picea glauca*) ainsi que le bouleau blanc (*Betula papyrifera*), communément appelée le sous-domaine bioclimatique de la sapinière à bouleau blanc de l'ouest. Dans la partie nord la forêt coniférienne est dominée par l'épinette noire (*Picea mariana*), nommée le sous-domaine bioclimatique de la pessière à mousse de l'ouest. L'écotone entre ces deux types de forêt est caractérisé par un changement de dominance d'espèces et non à la limite nordique de distribution du sapin baumier. Notre objectif était donc de savoir si la localisation de cet écotone était également conditionnée par le climat. L'étude a été subdivisée en deux parties principales : la première portait sur la mise en évidence des facteurs écologiques contrôlant la limite nordique de cette forêt mixte (chapitre I). La seconde portait sur la comparaison de la performance (chapitre II : Reproduction, chapitre III : Régénération et chapitre IV : Croissance) de ces trois principales espèces de conifère de part et d'autre de l'écotone.

Dans le chapitre I, des données de 5023 placettes provenant de l'inventaire écologique du Ministère des Ressources Naturelles du Québec (MRNQ), distribuées au niveau des deux types de forêt ont été utilisées pour mettre en évidence les variables abiotiques et biotiques en relation avec la présence ou l'absence des sapinières à différentes échelles; locale et paysage. Dans les autres chapitres, des données de terrain ont été puisées dans quatre sites situés le long d'un gradient latitudinal traversant l'écotone. Ces données ont été complémentées par des données de l'inventaire dendrométrique du même Ministère

Tous les résultats obtenus indiquent qu'au total, les facteurs écologiques utilisés dans notre étude expliquent 34-42% la limite nordique de la forêt mixte. Cette limite est en partie expliquée par la rareté des conditions écologiques favorisant la présence de cette forêt. De plus, les populations de sapinière dans la pessière à mousse sont incapables de saturer tous les rares sites propices. Cependant subsistent des sapinières sur des sites non propices (phénomène de débordement), quoique moins abondantes dans la pessière que dans la sapinière. Ces résultats nous amènent à supposer que l'histoire postglaciaire et à un second degré les perturbations par les feux pourraient être des facteurs déterminant expliquant la distribution actuelle des sapinières. Cependant, la limite sapinière/pessière est due à la faible capacité reproductive du sapin baumier et de l'épinette blanche dans la forêt coniférienne. La production de cônes de ces deux espèces était plus faible, alors que celle de l'épinette noire était plus régulière. Le pourcentage de graines pleines et le taux de germination de celles-ci étaient également plus faibles pour le sapin dans la forêt coniférienne sauf dans les années de paisson pleine (forte production de cônes). La fréquence de production de cônes de sapin était plus faible dans la forêt coniférienne, alors qu'elle était similaire pour l'épinette noire.

En plus, la densité de régénération (semis et gaulis) du sapin était en général plus faible et le taux de mortalité plus élevé dans la forêt coniférienne.
Cependant, la croissance en hauteur du sapin et de l'épinette blanche est similaire dans les deux types de forêt. Les conditions des sites i.e. les types de dépôts de surface ont un effet plus grand que le climat. Les bonnes conditions de sol i.e. sol sablonneux dans la forêt coniférienne permettent au sapin et à l'épinette blanche, une fois établis, d'avoir une croissance en hauteur similaire à celle de l'épinette noire, espèce dominante.

L'écotone entre la forêt mixte et coniférienne, caractérisé par le changement de dominance, reflète bien l'effet direct (capacité reproductive et de régénération) et indirect (conditions écologiques, croissance en hauteur) des conditions climatiques sur la présence et la dynamique de cette forêt mixte.

INTRODUCTION GÉNÉRALE

La distribution géographique des zones de végétation a longtemps été attribuée de façon *majeure au* climat et à une échelle plus réduite, aux conditions édaphiques (Whittaker, 1970; Ritchie & Hare, 1971; Walter, 1973; Larsen, 1980; Arris & Eagleson, 1989; Woodward et al., 1994). En zone boréale, les feux et les épidémies d'insectes sont les principales perturbations naturelles (Sirois, 2000; Bergeron et al., 2004). Celles-ci peuvent influencer grandement la présence et/ou l'abondance des espèces forestières composant cette zone (Hogg, 1994; Hogg & Schwarz, 1997; Capuccino, 1998; Fig. 0.1). À noter qu'en plus, tous ces facteurs peuvent interagir entre eux d'une part, et, d'autre part, la végétation va également influencer sur certains de ces facteurs à l'échelle d'un écosystème forestier (Figure 0.1).

Climat

Les températures, les précipitations et dans certaines conditions le vent sont les principaux facteurs climatiques limitant le recrutement et la croissance des principales espèces composant une zone de végétation donnée et par conséquent l'abondance de celles-ci (Barnosky, 1987 ; Huntley & Webb, 1989 ; Burns & Honkala, 1990; Hofgaard et al., 1991; Kullman, 1996 ; Hogg &t Schwarz, 1997). En effet, durant l'Holocène, l'évolution et la migration des espèces vers les hautes latitudes et altitudes ont été tributaires du réchauffement climatique qui a eu lieu durant cette période (Ritchie, 1987 ; Richard, 1993).

En Amérique du nord, la limite sud de la zone boréale dominée par les conifères descend en latitude depuis l'Alaska jusqu'à l'Est canadien et atteint son minimum (*ca* 48°N) au niveau de l'est canadien plus précisément entre l'est de l'Ontario et l'ouest du Québec correspondant à la région de l'Abitibi. Excepté les zones montagneuses, c'est dans cette région que cette forêt atteint sa limite le plus au sud au monde (Pouliot, 1994). La forêt mixte quant à elle est située dans cette région entre le 47° et le 49° (Bérard, 1996). Dans l'ouest québécois, les précipitations ne semblent pas influencer globalement la répartition des zones de végétation puisque celles-ci sont assez abondantes et plus ou moins bien réparties durant la saison de végétation, mais bien les températures. Celles-ci diminuent au fur et à mesure qu'on se dirige vers les latitudes et les altitudes élevées (Damman, 1979 ; Bergeron et al., 1985 ; Loehle, 2000). Ce gradient de température décroissant et donc la diminution des degrés jours est généralement responsable de la diminution de l'abondance des espèces plus thermophiles et de la diminution de la richesse spécifique (Nikolov & Helmisaari, 1992 ; Payette, 1993).

Les espèces appartenant aux régions plus au sud supportent peu des températures basses et requièrent un nombre de degré jour élevé. Dans les régions plus au sud, leur taux de croissance en hauteur était plus élevé que celles appartenant aux régions plus nordiques (Loehle, 2000). Ces dernières même en augmentant leur taux de croissance en hauteur dans des conditions plus chaudes ne pourront pas rivaliser avec celui des espèces plus thermophiles, ce qui les défavoriseraient et deviennent rares, voire éliminées de la zone de végétation sous-jacente. Par contre, dans des régions plus froides où la saison de croissance est plus courte avec des risques de gel plus fréquents pendant la saison de croissance, toutes les espèces ont tendance à avoir une croissance plus lente et sont souvent endommagées par le froid et surtout par le gel (Raitio, 1987; Langvall & Orlander, 2001; Langvall et al., 2001).

La différence est que les espèces nordiques sont plus adaptées à ces conditions que les espèces plus thermophiles et donc peuvent donc mieux survivre aux dommages dus au froid que les espèces plus thermophiles, ce qui leur permet (espèces nordiques) d'optimiser leur croissance même dans ces conditions. Les espèces plus thermophiles sont moins résistantes au froid et donc seront beaucoup moins abondantes. En effet, ces espèces connaissent une forte réduction de croissance, par une plus forte mortalité et des dommages causés par le froid. En plus, ces espèces connaissent une faible ou une absence de production de graines assurant le maintien de l'espèce. Tout ceci implique une plus faible compétitivité par rapport aux espèces plus adaptées à ces conditions. Il apparaît dans ce cas qu'il existe un gradient de tolérance au froid (Stohlgren & Bachand, 1997; Loehle, 1998). En effet, il a été démontré qu'en absence de déficit hydrique, la performance (production de cônes et de graines, croissance) d'une espèce semblait être dépendante principalement des températures durant la saison de croissance (Zasada, 1971; Zasada et al., 1978 ; Black &t Bliss, 1980 ; Payette et al., 1985 ; Kullman, 1986 ; Colombo, 1998; Sirois et al., 1999 et Sirois, 2000).

Ceci pourrait être le ou un des principaux facteurs limitant la distribution d'une ou de plusieurs espèces à l'échelle d'un paysage et limiter ainsi son expansion. Dans une même région, certaines espèces comme le pin rouge (*Pinus resinosa*) sont caractérisées par une faible production de graines par rapport à d'autres espèces (Van Wagner, 1971; Burns & Honkala, 1990). Leur répartition géographique semblerait donc être plus sensible aux basses températures, tout en tenant compte de leur tolérance à l'ombre. Dans des régions où la topographie prédomine, la végétation des sommets de collines ou des coteaux est plus thermophile en matière de composition floristique que celle de bas de pente. Cela s'explique par la présence d'un drainage d'air froid qui a pour conséquence de maintenir un microclimat plus frais et une présence de période plus importante de gel et donc une saison de croissance plus courte. En effet, en étudiant la régénération des principales espèces arborescentes au niveau d'une transition entre la forêt mixte et la forêt feuillue dominée par l'érable à sucre en Ontario, Barras & Kellman (1998) signalent que la régénération de l'érable à sucre (*Acer saccharum*) était abondante au niveau de ces deux types de forêt et que la présence de cette transition abrupte entre les deux communautés était due aux basses températures qui règnent au niveau des bas de pente.

À la transition entre deux zones de végétation, les espèces deviennent plus sensibles au climat (Brubaker, 1986 ; Hogg & Schwarz, 1997 ; Houle &t Filion, 1993; Loehle, 2000). Étant donné que le climat est variable dans l'espace et le temps, ce dernier peut induire une modification de la zone de végétation (Payette et al., 1985). Cela implique une régression ou une avancée de cette zone vers le sud ou plus vers le nord selon qu'on se dirige vers un climat plus froid ou plus chaud. Il est très probable que les premiers principaux signes des changements climatiques pourraient se manifester plus au niveau des limites des zones de végétation. Beaucoup d'études ont été réalisées au niveau des transitions entre la forêt boréale/toundra (Payette & Filion, 1985 ; Rupp, et al. 2000 et 2001 ; Lavoie & Payette, 1994; Sirois, 1997) ou à la limite des arbres dans l'étage alpin (Rocheford & Peterson, 1992 ; Earle, 1993 ; Pellat, 2000 ; Luckman, 2000). La plupart de ces auteurs n'ont de façon globale perçue aucun signe de déplacement de la végétation vers des latitudes ou des altitudes plus élevées. Payette & Filion (1985) ont par contre trouvé que le déplacement altitudinal de la limite des arbres s'est effectué de 100 m au cours des 100 dernières années, alors que la limite latitudinale n'a pas connu de variation. Ces milieux sont considérés comme étant des conditions extrêmes. D'autres facteurs comme le vent, les avalanches ou le substrat (e.g. épaisseur du sol) peuvent être dans ces conditions des facteurs limitant au déplacement de la forêt vers la toundra arctique ou alpine, ce qui ne semble ne pas être des régions indicatrices d'un éventuel changement climatique (Loehle, 2000). En effet, certains écotones ne sont pas en équilibre avec le climat local (Weisberg & Baker, 1995 ; Paulsen et al., 2000). Peu d'études ont été effectuées au niveau d'une transition entre deux types de forêt. Dans ces milieux, et en absence de perturbations majeures, ces écotones seraient plus sensibles aux fluctuations climatiques qu'à l'intérieur d'une zone de végétation et pourraient donc plus nous renseigner sur l'impact des changements climatiques sur la performance des espèces, et donc du déplacement de la zone de forêt mixte (sapinière à bouleau blanc) vers la zone de forêt boréale (pessière à mousse). Il faudra cependant tenir compte des conditions locales (conditions édaphiques, topographie) qui pourraient masquer l'effet du climat (Bergeron et al., 1985).

Perturbations naturelles

Dans la forêt boréale, outre le climat, les perturbations, telles que les feux et les dommages causés par les insectes, sont très étendues et sont souvent responsables de la structure de la végétation et de la répartition des espèces qui la compose (Bergeron et al., 1985). De façon générale, les dommages causés par les insectes comme la tordeuse des bourgeons d'épinette affectent plus les peuplements matures et surannés de conifères notamment les sapinières et influent donc la structure de la forêt plus que la distribution dans le cas où la régénération préétablie serait abondante. Ceci induit un remplacement de ces arbres matures par des gaulis de la même espèce et permet ainsi un feedback positif dans le cas où cette régénération serait abondante (MacLean, 1980 et 1984 ; Bergeron et al., 1995). Par contre, cela pourrait affecter négativement la distribution d'une espèce, voire sa disparition, à sa limite nord de répartition géographique. Par exemple, Payette & Filion (1985) signalent que l'épinette blanche, au nord du Québec, est confinée dans des sites particuliers et que la régénération préétablie est beaucoup plus faible. Ceci est dû à la faible présence des arbres adultes et la faible production de graines à cause des basses températures (Lavoie & Payette, 1994 ; Weisberg & Baker, 1995 ; Sirois, 1997). Dans la forêt boréale, caractérisée par la présence très importante des conifères, l'épidémie de tordeuse des bourgeons d'épinette semble être beaucoup plus répandue et dévastatrice que dans la zone de végétation sous-jacente, dominée par la sapinière à bouleau blanc, caractérisée par la présence d'un nombre important de feuillus (bouleaux, peupliers) au sein même des peuplements de sapin. Cette mixture permet d'atténuer de façon significative les dommages causés par ces insectes (Bergeron et al., 1995): Ces peuplements mixtes semblent abriter des insectes prédateurs contrôlant aussi les populations de la tordeuse (Capuccino et al., 1998).

Les régimes des feux, de par leur nature, leur fréquence et leur extension sont souvent responsables de la distribution des espèces (Bergeron & Gagnon, 1987). Par exemple, les cycles des feux peuvent favoriser certaines espèces comme le pin gris (*Pinus banksiana*) et l'épinette noire (*Picea mariana*), plus adaptés aux courts cycles des feux, au détriment des autres espèces comme le sapin baumier (*Abies balsamea*) et le thuya occidental (*Thuja occidentalis* ; Greene & Johnson, 2000). En effet, ces espèces ainsi que l'épinette blanche (*Picea glauca*) pourraient ne pas bien être adaptés aux grands feux de la forêt boréale, vu l'étendue des distances par rapport aux semenciers préservées des feux, cédant ainsi la place à l'épinette noire et au pin gris plus avantagés par leurs cônes sérotineux qui leur permet de réenvahir les sites même s'ils sont éliminés par le feu (Galipeau et al., 1997). De leur côté, Payette & Filion (1985) indiquent que les fluctuations de la limite des arbres dans le nord québécois, au cours de l'Holocène, furent de faible amplitude malgré un réchauffement du climat. Ils suggèrent que les régimes des feux pourraient être les principales causes de l'absence d'établissement de l'épinette blanche dans la toundra. Bergeron &t Brisson (1994) signalent que les régimes des feux caractérisés par leur intensité élevée et leur étendue, sont plus responsables de la limite nord de la répartition géographique du pin rouge que les faibles températures. Ils suggèrent que la limite nord de la distribution géographique de cette espèce dans la forêt boréale pourrait être plus au nord en l'absence des feux dévastateurs. En effet, ils mentionnent sa présence près des rivages des lacs, qui sont des sites plus ou moins protégés par ces feux. Cependant, cette espèce est favorisée par des feux de surface de faible intensité.

Conditions édaphiques

La limite d'une espèce ou d'une zone de végétation peut aussi s'expliquer par les conditions édaphiques. Par exemple, l'absence d'habitats propices à une espèce ou à un groupe d'espèces e.g. absence de sites mésiques propices au sapin baumier dans la zone de la pessière à mousses pourrait aussi être la cause de la limite nordique de répartition géographique (Bakusis & Hansen, 1965 ; Bergeron & Dubuc, 1989). En effet, il a été démontré que la présence de sphaignes implique une augmentation de l'humidité et une acidification du sol, ce qui limiterait l'établissement du sapin baumier (Ammari, 2001). Sirois (1997) a mentionné que le marcottage du sapin baumier à sa limite nord de répartition géographique était favorisé par la présence de mousses (et non de la sphaigne) au niveau du sol.

Effet indirect du climat

Plusieurs auteurs ont pu démontrer que le climat agit aussi bien sur les régimes de perturbation que sur les conditions édaphiques (fertilité, humidité, pH; Fig.0.1). Par exemple, le ralentissement de la décomposition de la matière organique est souvent dû aux faibles températures du sol ainsi qu'aux pluies froides durant la saison de végétation favorisant ainsi l'accumulation de la litière (représentée dans ce cas surtout par les aiguilles) voire l'acidification du sol ; ce qui semble empêcher l'installation de certaines espèces non tolérantes aux faibles pH (Fowells, 1965 ; Paré & Bergeron, 1996 ; Béland & Bergeron, 1993). Les fluctuations climatiques agissent directement sur les régimes des perturbations. Dans l'est de l'Amérique du nord et ce depuis le petit Âge Glaciaire, le passage d'un climat froid et sec vers un climat plus tempéré et plus humide semble diminuer la fréquence et l'étendue des feux, ce qui pourrait influencer grandement la distribution des espèces et la structure du paysage (Bergeron et Archambault, 1993; Flannigan & Bergeron, 1998; Dale et al., 2000), en favorisant par exemple la migration de certaines espèces, e.g. pin rouge, vers le nord (Flannigan et al., 1998).

Concernant les perturbations dues aux insectes, il semble qu'un climat plus sec favorise l'extension des dommages probablement due à la plus grande sensibilité de certaines espèces végétales au stress hydrique et donc de leur vulnérabilité à l'égard des attaques d'insectes (Morin & Laprise, 1997).

Objectif

Notre étude s'inscrit dans le cadre de la dynamique de la limite nordique de la forêt mixte dans la zone boréale de l'ouest du Québec. Si cette limite ne traduit pas la limite nordique de distribution de l'espèce dominante, le sapin baumier, alors on suppose que cette limite pourrait être plus au nord qu'elle ne l'est actuellement. On a remarqué par exemple qu'après une coupe forestière ou un feu de forêt, plusieurs espèces appartenant à la forêt mixte e.g. bouleau à papier et le peuplier faux tremble ont tendance à occuper selon les conditions la pessière située plus au nord (Harvey & Bergeron, 1989). Cependant, cette conversion ne fait pas l'unanimité. Par exemple, Brumelis & Carleton (1988) ont montré qu'après une coupe forestière, cette conversion de la pessière vers une forêt mixte composée de sapin baumier (*Abies balsamea*) et de feuillus e.g. peupliers faux tremble (*Populus tremuloides*) et bouleaux blancs (*Betula papyrifera*) ne se faisait que dans des sites où l'accumulation de la matière organique est plus faible et donc des milieux moins acides et bien drainés où la décomposition de la matière organique est plus ou moins rapide, ce qui implique des sites riches. On peut donc dire que la présence de conifères de la forêt mixte contenant du sapin et de l'épinette blanche (*Picea glauca*) Voss) est positivement corrélée aux feuillus de jeunes stades successionnels comme le bouleau et le peuplier faux tremble. Cette présence est expliquée, d'une part, par la fertilité du site et, d'autre part, par à une protection plus ou moins importante contre les épidémies de tordeuses des bourgeons d'épinette et les feux (voir plus haut). Cependant, certains auteurs mentionnent qu'une litière importante composée de peuplier faux tremble et de bouleau blanc ne semble pas être un substrat idéal pour l'émergence des semis de sapin (Simard et al., 1998 and 2003; Parent et al., 2006).

De son côté, Gagnon (1989) a trouvé que la limite abrupte entre deux types de peuplement (pessière, forêt feuillus dominé par le peuplier faux tremble) se maintenait et ce malgré le passage d'un feu intense et la présence de sites propices à la migration des feuillus dans la pessière. L'auteur suggère que ce phénomène est lié à la composition forestière avant l'arrivée du feu. En plus, il demeure incertain si cette conversion de la pessière en forêt mixte est permanente ou si l'épinette noire pourrait réenvahir avec succès les sites.

Le but de cette étude est de documenter les raisons de la localisation de la limite nordique de la forêt mixte à une si faible latitude (*ca* 49°N). Pour cela, notre étude sera divisée en deux principales parties : les facteurs écologiques expliquant la localisation de l'écotone forêt mixte/forêt coniférienne (chapitre I) et l'étude des mécanismes (reproduction, régénération et croissance en hauteur; chapitres II, III et IV respectivement) des principales espèces dominant les deux types de forêt. Dans notre cas, il s'agira de comparer la performance de trois espèces arborescentes de fin de succession, à savoir le sapin baumier, l'épinette blanche dominant dans la forêt mixte et l'épinette noire dominant dans la forêt coniférienne (*Picea mariana*).

Dans le chapitre I, il s'agira d'utiliser les données de l'inventaire écologique du troisième décennal distribuées dans les deux sous-domaines bioclimatiques (Figure 0.2). Nos deux hypothèses sont que (1) les sites propices à l'établissement et au développement des sapinières sont moins abondants dans la pessière, et (2) que ces sapinières localisées dans la pessière sont non seulement moins abondantes, mais en plus sont incapables de saturer les rares sites propices dans ce type de forêt.

Dans le chapitre II, on étudiera les différents traits de la reproduction sexuée du sapin et des deux épinettes et de les comparer entre les deux types de forêt. Quatre sites d'étude ont été choisis (deux dans la forêt mixte et deux dans la forêt coniférienne; Figure 0.3). On s'attend à ce que la capacité reproductive du sapin et de l'épinette blanche soit plus faible dans la forêt coniférienne, alors que celle de l'épinette noire est plus constante.

Dans le chapitre III et IV on étudiera d'une part la régénération du sapin et dans le dernier chapitre la croissance en hauteur des trois espèces dominant de part et d'autre de l'écotone au niveau des mêmes sites d'étude. Dans le dernier chapitre, des données de l'inventaire dendrométrique des placettes temporaires du Ministère des Ressources Naturelles du Québec ont été également utilisées (Figure 0.3). On s'attend à ce que cette régénération soit plus faible dans la forêt coniférienne et que la croissance du sapin et de l'épinette blanche diminue graduellement en se dirigeant vers le nord, alors qu'elle demeure constante pour l'épinette noire au niveau des deux types de forêt.

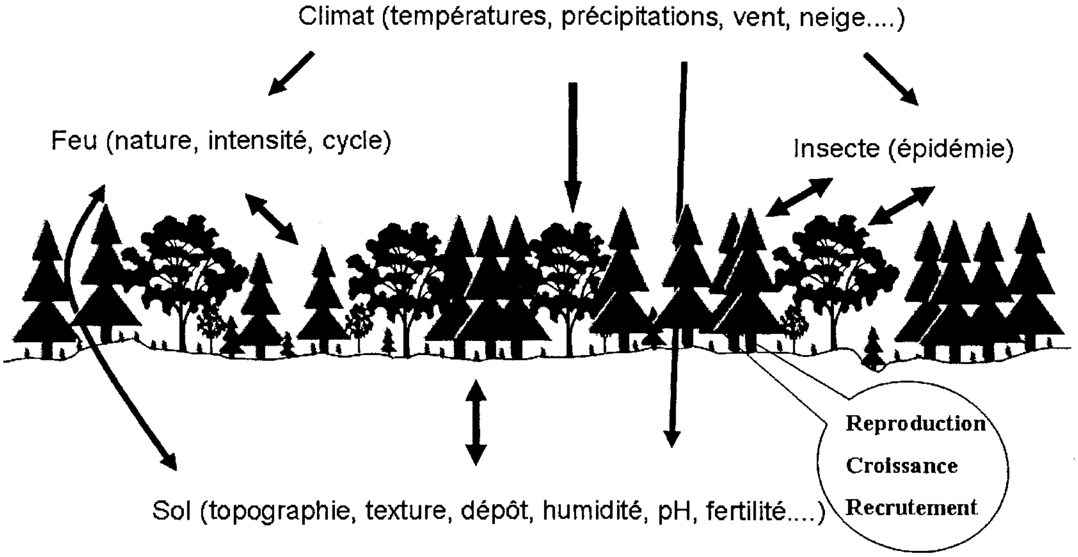


Figure 0.1. Exemple des principaux facteurs écologiques pouvant influencer sur la distribution et la dynamique (les mécanismes) de la forêt mixte (sapinière à bouleau blanc) dans la zone boréale.

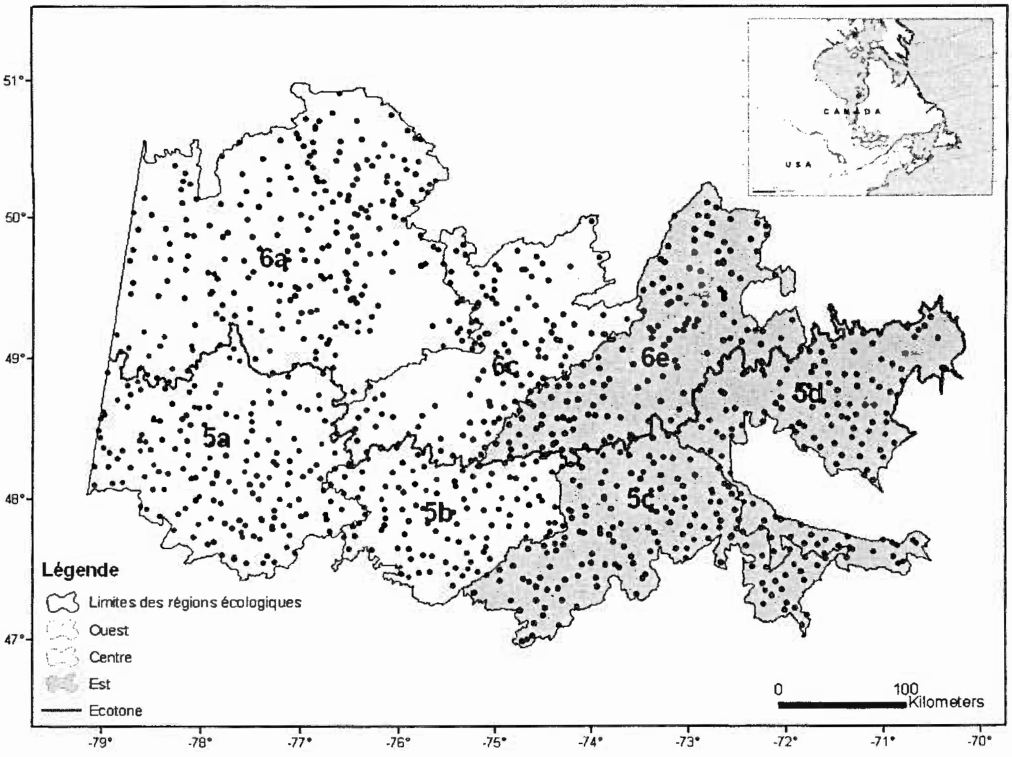


Figure 0.2. Distribution des placettes temporaires de l'inventaire écologique du Ministère des Ressources Naturelles du Québec (MRNQ), utilisées dans le chapitre I (le trait gras rouge indique l'écotone entre le sous-domaine de la sapinière à bouleau blanc et la pessière à mousse). Les différentes couleurs indiquent les secteurs.

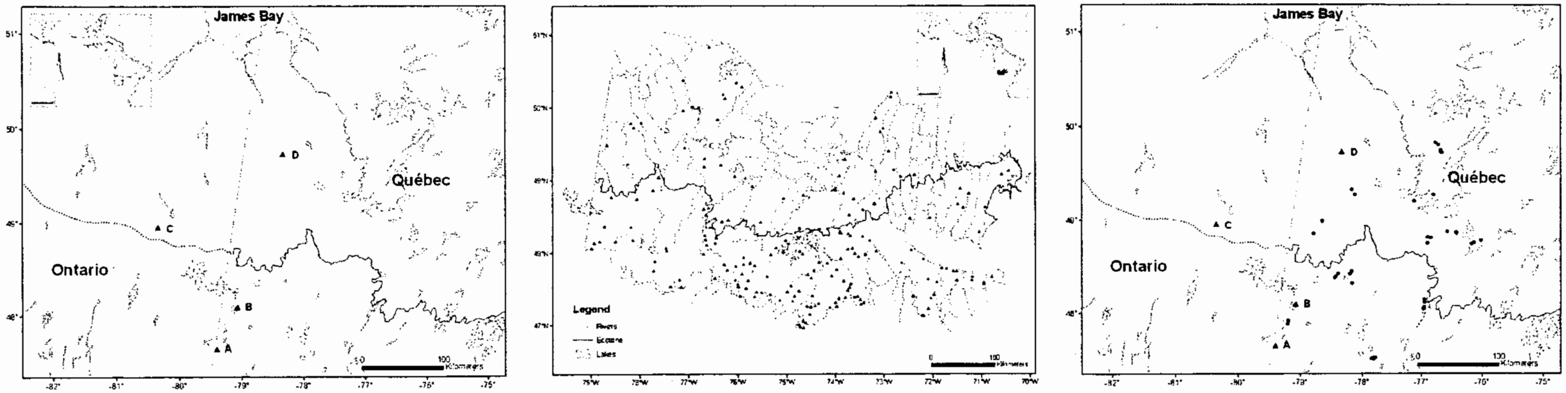


Figure 0.3. Région d'étude montrant les quatre sites (A: lake Montalais, B: lake Duparquet, C: Cochrane, D: Maskouchis). Le trait plein rouge indique la localisation de l'écotone entre la forêt mixte et la forêt coniférienne dans l'ouest du Québec et les traits pointillés rouge montrent les limites des régions écologiques 5a (forêt mixte) et 6a (forêt coniférienne). Les placettes du MRNQ utilisées dans le chapitre IV sont représentées par des triangles blancs (sapin baumier), cercles blancs (épinette blanche), et cercles gris (épinette noire).

CHAPITRE I

Ecological factors explaining the location of the boundary between the mixedwood and coniferous bioclimatic zones in the boreal biome of eastern North America

Yassine Messaoud[1*], Yves Bergeron[1,2] and Alain Leduc[2]

[1]Chaire industrielle CRSNG-UQAT-UQAM en aménagement forestier durable, Université du Québec en Abitibi-Témiscamingue, C.P. 700, Rouyn-Noranda, Québec, J9X 5E4, Canada

[2] Groupe de Recherche en Écologie Forestière inter-universitaire and Département des sciences biologiques, Université du Québec à Montréal, C.P. 8888, Succ. Centre-Ville, Montréal, Québec, H3C 3P8, Canada

*corresponding author: yassine.messaoud@uqat.ca

Article publié en 2007 dans Global Ecology and Biogeography, volume 16, pp. 90-102

1.1. Abstract

Aim : Climate is often regarded as the primary control determining the location of an ecotone between two vegetation zones. However, other ecological factors may also be important, especially when the northern limit of the dominant species of a vegetation zone extends further than the limit of the zone itself. This study aimed to identify the ecological variables explaining the transition between two zones within the boreal biome in Quebec (Eastern Canada): the southern mixedwood forests dominated by balsam fir (*Abies balsamea*) and white birch (*Betula papyrifera*), and the northern coniferous forests dominated by black spruce (*Picea mariana*).

Location: Quebec (Eastern Canada).

Methods: Data from 5023 sampling plots from the ecological inventory of the Québec Ministry of Natural Resources distributed throughout the two bioclimatic zones were used in logistic regressions to determine the relationships between the presence or absence of balsam fir stands and different abiotic and biotic variables, at both stand and landscape scales.

Results: The presence of balsam fir stands was negatively related to the thick organic horizons, coarse xeric deposits and low positions on the slope, whereas stands were favoured by high elevations, steep slopes and moderate drainage. These results defined the suitable conditions for balsam fir stand development. In the coniferous zone these suitable conditions were less abundant. Furthermore, the saturation level of suitable sites was lower, as well as the incidence of balsam fir stands in unsuitable sites (overflow). Balsam fir stands were mostly located near lakes and rivers. All significant variables at both the stand and landscape scales explained between 34 and 42 % of the location of the potential northern distribution limit of the mixedwood zone.

Main conclusions: Our results suggest the important role of historical factors related to postglacial vegetation and past disturbances in determining the relative abundance of balsam fir in both zones of the boreal biome.

Keywords: Boreal biome, coniferous forest, eastern North America, ecological factors, logistic regression, mixedwood forest, northern distribution limit, scale

1.2. Résumé

But: Le climat est souvent considéré comme le facteur déterminant la localisation d'un écotone entre deux zones de végétation. Cependant, d'autres facteurs écologiques peuvent également être importants, particulièrement quand la limite nordique des espèces dominantes d'une zone de végétation s'étend plus loin que la limite de la zone elle-même. Cette étude vise à identifier les variables écologiques expliquant la transition entre deux zones dans le biome boréal au Québec (Est du Canada) : au sud, la forêt mixte est dominée par le sapin baumier (*Abies balsamea*) et le bouleau blanc (*Betula papyrifera*) appelée communément la sapinière, et au nord la forêt coniférienne dominée par l'épinette noire (*Picea Mariana*) nommée pessière.

Localisation: Québec (Est Canada).

Méthodes: Des données de 5023 placettes d'échantillonnage de l'inventaire écologique du ministère des ressources naturelles du Québec (MRNQ) distribuées dans deux zones bioclimatiques ont été utilisées dans des régressions logistiques pour déterminer les relations entre la présence (ou l'absence) des populations de sapinière et les différentes variables abiotiques et biotiques, à l'échelle locale et du paysage.

Résultats: La présence de la sapinière a été négativement liée aux horizons organiques épais, aux dépôts grossiers et au bas de pente, tandis que leur présence a été favorisée par des altitudes élevées, des pentes raides avec un drainage modéré. Ces résultats définissent bel et bien les habitats propices pour l'établissement et le développement des populations de sapinière. Dans la zone coniférienne, ces habitats propices étaient moins abondants. En plus, le niveau de saturation de ces habitats était plus bas, comme l'incidence des populations de sapinière sur des habitats non propices (débordement). Ces populations étaient pour la plupart du temps situées près des lacs et des fleuves. Toutes les variables significatives à l'échelle locale et du paysage expliquent seulement 34 à 42 % de la localisation de la limite nordique potentielle de distribution de cette forêt mixte.

Conclusion générale: Nos résultats suggèrent le rôle important des facteurs historiques rapportés à la végétation postglaciaire et à un second degré les perturbations (feux) sur l'abondance relative de cette forêt mixte dans les deux zones du biome boréal.

Mots-clés: Biome boréal, forêt coniférienne, Nord-est américain, Facteurs écologiques, Régression logistique, Forêt mixte, Limite nordique de distribution, Échelle.

1.3. Introduction

In North America, the southern limit of the continuous boreal biome, dominated by coniferous species such as black spruce (*Picea mariana* (Mill.) B.S.P.), white spruce (*Picea glauca* (Moench) Voss), and balsam fir (*Abies balsamea* (L.) Mill.), decreases in latitude from Alaska eastwards (Fowells, 1965; Burns & Honkala, 1990) and reaches its lowest latitude (*ca* 48° N) in eastern Canada, between eastern Ontario and western Québec. Except for pockets at high elevations, this is where the boreal biome reaches its most southerly limit in the world (Pouliot, 1998). In eastern Canada, this boreal biome is subdivided into two zones; to the south, between *ca* 48° to *ca* 49° N, lies the mixedwood, a forest dominated by balsam fir and white birch (*Betula papyrifera* Marsh.), with white spruce also abundant (Bérard, 1996). Some species reach their northern distribution limit in the mixedwood zone, such as sugar maple (*Acer saccharum* Marsh.), yellow birch (*Betula alleghaniensis* Britton), red pine (*Pinus resinosa* Ait.), white pine (*Pinus strobus* L.), and red maple (*Acer rubrum* L.) (Bergeron *et al.*, 1985; Bergeron & Gagnon, 1987; Engelmark *et al.*, 2000; Tremblay *et al.*, 2002). To the north lies the coniferous zone, where black spruce dominates.

Ecotones separating vegetation zones are highly sensitive to climatic conditions (Brubaker, 1986; Houle & Filion, 1993; Hogg & Schwarz, 1997; Loehle, 2000). Because these conditions vary in time and space, they can induce changes in the location of ecotones. It is generally supposed that the effects of the ongoing climate change may be more readily detected or predicted in boundary areas. While numerous studies have examined the transition between the boreal and tundra zones (Payette & Filion, 1985; Earle, 1993; Lavoie & Payette, 1994; Sirois, 1997; Luckman & Kavanagh, 2000; Pellatt *et al.*, 2000; Rupp *et al.*, 2000, 2001), few studies have focused on ecotones between two forested zones (Loehle, 2000).

Balsam fir and white spruce reach their northern distribution limit in the James Bay region, well above the 49th parallel, near the 54th and 56th parallel, respectively (Tremblay & Simon, 1989; Payette, 1993; Sirois *et al.*, 1999). According to Richard (1993), balsam fir stands are more scattered in western than in eastern Québec. This suggests that climate may not be the only factor determining the location of the boundary between the mixedwood and coniferous zones of the boreal biome (Bergeron *et al.*, 1985; Hofgaard *et al.*, 1991).

Several hypotheses could be put forward to explain the location of the boundary between the mixedwood and coniferous zones. For instance, a northwards reduction in the abundance of suitable sites for balsam fir could explain the transition (Bakusis & Hansen, 1965; Bergeron & Dubuc, 1989). If so, the location of the boundary may be a result of changes in edaphic conditions such as soil fertility or pH. Since organic matter decomposition is often reduced at low soil temperatures during the growing season, increased organic matter accumulation and possibly soil acidification could prevent the establishment of balsam fir in the coniferous zone as this species is intolerant of low pH levels (Fowells, 1965; Béland & Bergeron, 1993; Paré & Bergeron, 1996). A colder climate and the accumulation of organic matter may favour bryophytes, particularly *Sphagnum* species, and further limit balsam fir establishment in humid sites. Black spruce promotes conditions unsuitable to balsam fir by influencing soil microclimatic conditions i.e. decrease of soil temperature and, at the landscape scale, competitively hampers the expansion of balsam fir in otherwise suitable sites (McCune & Allen, 1985).

Major disturbances such as fires or phytophagous insect outbreaks may also be responsible for the increasing rarity of balsam fir stands towards the north. Indeed, in the coniferous zone, high severity disturbances are common and greatly influence vegetation structure and species abundance, and this varies with the severity, frequency and extent of the disturbance (Bergeron *et al.*, 1985; Bergeron & Gagnon, 1987). For example, large, severe fires can promote the abundance of species with aerial seed banks such as jack pine (*Pinus banksiana* Lamb.) and black spruce, which are adapted to this type of disturbance, but be detrimental to species such as balsam fir, white spruce and eastern white cedar (*Thuja occidentalis* L.). Moreover, mature and over-mature balsam fir stands are strongly affected by the spruce budworm (*Choristoneura fumiferana* Clemens); in some cases, this insect can cause nearly complete mortality (MacLean, 1980, 1984; Bergeron *et al.*, 1995). Higher balsam fir mortality in northern, almost pure stands, as compared to more southerly stands with a higher percentage of deciduous trees, may also partially explain the northwards disappearance of balsam fir in the black spruce-dominated coniferous zone (Bergeron *et al.*, 1995; Cappucino *et al.*, 1998)

The abundance of likely alternative but not mutually exclusive hypotheses illustrates the difficulty in identifying which ecological factors determine the location of the boundary between the mixedwood and coniferous zones. In this context, we ask the following questions: why does the mixedwood zone reach its northern limit around the 49th parallel and why is it replaced by the black spruce-dominated coniferous zone to the north? Our objective is to analyze the ecological factors that could explain the distribution of balsam fir-dominated stands at the stand and landscape scales and examine two hypotheses regarding the northern limit of the mixedwood zone. Our first hypothesis (H1) is that a lack of suitable sites in the coniferous zone is responsible for the northwards decrease in the abundance of balsam fir stands and their replacement by black spruce stands (Gu *et al.*, 2002). Our second hypothesis (H2) is that, at the landscape scale, balsam fir cannot spread easily to all suitable sites in the coniferous zone because post-disturbance re-colonization problems are increasingly frequent northwards and because of the increasing presence of the dominant black spruce, which is more competitive.

1.4. Methods

1.4.1. Study area

The study area is located in Quebec (Eastern Canada), between 48° and 51° N and between 70° 30' and 79° W (Fig. 1.1). The mixedwood zone is represented by the western balsam fir–white birch bioclimatic sub-domain, whereas the coniferous zone corresponds to the western black spruce-feathermoss bioclimatic sub-domain (Robitaille & Saucier, 1998; Table 1.1). In the ecological classification system of forested zones of Quebec, bioclimatic sub-domains are characterized by their late successional tree species, resulting from the equilibrium between climate and vegetation on mesic sites (Robitaille & Saucier, 1998). The mixedwood and coniferous zones differ in important climatic variables (Table 1.2).

We focused on several ecological regions on both sides of the boundary between the mixedwood (regions 5a-d) and coniferous (regions 6a, c, e) zones (Fig. 1.1). The western sector (5a and 6a) is generally flat and rich in clayey surficial deposits (Abitibi lowlands), has many lakes and bogs, and is interspersed with knolls, eskers and a few isolated hills. These hills are often rocky or covered with till. The ecological regions in the central sector (5b and 6c) have a more broken topography than in the western sector, as well as many large lakes and till-rich plateaus. To the east, regions 5c, 5d, and 6e have an even more accentuated topography, fewer lakes, rocky or till-covered hilltops, and organic deposits in depressions.

1.4.2. Sampling design

We used raw sampling plot data from the ecological inventory of the Québec Ministry of Natural Resources (MRNQ). Each sampling plot contained detailed information on topography, soils, surficial deposits, and canopy and understorey composition. These plots were distributed along 1-1.5 km transects that each contained five to six sampling plots. Plot density was one plot every 25 km^2 in the mixedwood zone, and one plot every 30-50 km^2 in the coniferous zone. A total of 5023 plots were used to characterize the study area. Plots were located in forests that had not been disturbed by large scale logging activities.

1.4.3. Ecological factors

We examined several ecological factors grouped according to whether they were permanent, i.e. they described abiotic or edaphic conditions at the stand or landscape scale, or dynamic, i.e. they described forest composition at the landscape scale. Because different ecological factors are relevant at different scales, we used a hierarchical approach and proceeded from the stand up to the landscape scale. This approach allowed us to control for local effects and for their interactions with other factors at the landscape scale. We characterized the landscape scale by using the relative abundance of stand types and surficial deposits of ecological districts, a finer unit of ecological classification than the ecological region, with a mean area of 259 km^2 (Robitaille & Saucier, 1998). Ecological regions 5a, 5b, 5c and 5d contained, respectively, 72, 71, 85 and 60 ecological districts. Regions 6a, 6c and 6e contained, respectively, 97, 57 and 54 districts. To control for topographic and elevation gradients that increased from the west (Abitibi lowlands) to the east (where the Canadian Shield emerges), we subdivided each bioclimatic zone into three sectors: West (regions 5a and 6a), Centre (regions 5b and 6c) and East (regions 5c, 5d and 6e) (Fig. 1.1).

1.4.4. Stand classification according to succession

In the MRNQ plots, tree species abundance is recorded as percentage cover in three vertical layers (canopy, shrub and regeneration). We used these percentages for balsam fir, white spruce and black spruce to estimate succession towards either a balsam fir- or black spruce-dominated stand. Percentage cover of white spruce, a species often associated with balsam fir, was added to that of balsam fir to characterize balsam fir stands. The cover classes were: ≥ 81% A; 61-80% B; 41-60% C; 26-40% D, 6-25% E, 1-5% F, sporadic species ≤ 1% + (Saucier *et al.*, 1994). We used the median values of these classes to calculate the respective proportions of balsam fir (balsam fir + white spruce) and black spruce in the coniferous component of the stands. A threshold of 60% black spruce was used to classify sites evolving towards black spruce dominance. This threshold was established according to the competitive ability and shade tolerance of the two species; balsam fir is generally more competitive and shade tolerant than black spruce under similar growing conditions (Bakusis & Hansen, 1965; Burns & Honkala, 1990). Therefore, when the proportion of balsam fir was greater than or equal to 40% of the coniferous component, the site was considered to be evolving towards balsam fir dominance. We excluded from the analyses any disturbed sites, sites with less than 20% balsam fir or spruce in canopy or regeneration layers, and jack pine sites.

1.4.5. Statistical analyses

Logistic regressions were carried out by first including the stand-scale variables, then the landscape-scale variables, allowing for the control of the influence of stand factors before including the landscape factors. Statistical analysis was done by using Wald chi-square tests in a hierarchical framework.

To address H1, "the lack of suitable sites in the coniferous zone is responsible for the replacement of balsam fir stands by black spruce stands", we used stepwise logistic regressions to identify the factors associated with the development of balsam fir (coded 1) versus black spruce (coded 0) stands. Stand-scale factors (Table 1.3) were included first. Each factor entered in the model took into account the intercorrelation among independent factors by working with the residuals of the previously entered factors. We retained the model residuals to later analyze their relationships with landscape factors. Qualitative variables at the stand scale, such as surficial deposit or slope, were coded into dummy variables.

The inclusion of surficial deposit (relative abundance at the landscape level) in the model was interpreted as indicative of the importance of the suitable sites availability for the probability of occurrence of balsam fir stands where suitable conditions are present (H2: "increasing post-disturbance re-colonization problems northwards"; Table 1.4). Moreover, the addition of factors describing the relative abundance of stand types within the forest mosaic was interpreted as a landscape effect contributing to lowered risk of recolonization failure because of the occurrence of seed trees near the disturbed sites (H2).

We produced a table with the analysis results to describe the suitable sites per bioclimatic zone, at the stand and landscape scales. This table allowed quantification of the abundance of suitable sites in the mixedwood versus coniferous zones. In this way, we were also able to quantify the abundance of suitable sites at the scale of the ecological region (Fig. 1.2). Using the model's predictive ability, we delineated the suitable sites for balsam fir stands by taking into account all of the explanatory parameters that were significant at the stand scale. By doing this, it was possible to classify suitable and unsuitable sites for balsam fir stands and determine the occupation rate of suitable sites at the scale of ecological regions. The relative availability of suitable sites was calculated for each zone, as well as the real occupation rate. The occupation rate provided information on the saturation of potential habitats by balsam fir stands according to ecological regions.

Ecological profiles were built to illustrate the relationship between the presence or absence of balsam fir stands and the variables identified by the logistic regression. Any deviations exceeding 20 % of the expected value were statistically significant at the $\alpha = 0.05$ level (Fig. 3; Legendre & Legendre, 1998).

1.5. Results

Many factors were significantly associated with the presence of balsam fir stands (Table 1.5). The χ^2 values indicate the relative importance of each variable in explaining balsam fir presence. At each step of the regression, the cumulative R^2 increased with each additional explanatory variable being entered. For all sectors, most of the variation is explained by stand-scale factors. However, the addition of landscape-scale factors was significant in all cases, with the saturated models explaining 34 % (West sector), 42 % (Centre sector) and 41 % (East sector) of the variation.

1.5.1. Stand scale

Irrespective of the sector, there was a significant relationship between the presence of balsam fir stands and the thickness of the organic horizon, the drainage and the slope (Table 1.5). Balsam fir stands were frequently encountered on sites with a thin layer of organic matter, moderate to strong slopes (11-20 %; >20 %), and moderate drainage (20-39; Fig. 1.3). This preference for mesic sites was more accentuated in the coniferous than in the mixedwood zone.

The presence of balsam fir stands showed a significant positive relationship with altitude in the West and Centre sectors, with moder humus in the West and East sectors, and with slope position in the East sector. Significant negative relationships were found with coarse mesic deposits in the West sector, and with organic deposits in the East sector.

1.5.2. Landscape scale

The occurrence of balsam fir stands showed a significantly negative relationship with the relative area covered by organic deposits (A_OH) in the West and Centre sectors, and with accentuated topography in the East sector (Table 1.5). Significant positive relationships were found between the occurrence of balsam fir stands and the number of lakes per 100 km^2 and the relative area of fine sub-hydric deposits (A_FSH) (West sector), the relative area of medium mesic deposits (A_MM) (Centre sector), and elevation (East sector).

Ecological districts with a high abundance of mixed stands dominated by white birch, a mixture of balsam fir and black spruce, or pure balsam fir stands showed significant positive relationships with the presence of balsam fir stands. Conversely, districts characterized by high abundance of jack pine stands and pure black spruce stands had significant negative relationships with balsam fir stands. Balsam fir depends on its residual seed trees to re-colonize the post-disturbed sites, therefore, it will have a greater chance of colonising a site in a landscape dominated by balsam fir stands than in a landscape dominated by black spruce and jack pine stands.

1.5.3. Regional variation in occupation of sites suitable for balsam fir stands

In general, sites potentially suitable for balsam fir stands proved rarer in the coniferous than in the mixedwood zone (Fig. 1.2). The 6c region had the lowest amount of potentially suitable sites (21.03%) of all the ecological regions studied. The difference between the two bioclimatic zones was lower in the East sector than in the other two sectors.

Balsam fir stands occupied less of the suitable sites in the coniferous than in the mixedwood zone (Fig. 1.2), irrespective of sector or spatial scale. At the landscape scale, there is an increasing gradient of saturation of suitable sites from west to east for both bioclimatic zones.

Our ability to predict the occupation of suitable sites increased from the local to landscape scale. This increase suggests an important role of landscape factors, particularly the contribution of forest cover, in explaining the occurrence of balsam fir stands.

In several cases, balsam fir stands occupied unsuitable sites (Fig. 1.4). In the mixedwood zone, this 'overflow' of balsam fir stands was more common in the East than in the West sector. Balsam fir stands were more common, and thus had a more random distribution, in the mixedwood zone. In the coniferous zone these stands appear more closely associated with the presence of lakes and rivers (Fig. 1.4a). This phenomenon was readily apparent in the West and Centre sectors, whereas balsam fir stands were more randomly distributed in the East sector.

Unoccupied but suitable sites were more abundant in the coniferous than in the mixedwood zone. These unoccupied suitable sites were more abundant in the West sector and were associated with lakes and rivers (Fig. 1.4b). This was also the case in region 6c, but suitable sites were less frequent in region 6e. Balsam fir stands on unsuitable sites were more abundant and randomly distributed in the mixedwood zone (Fig. 1.4c).

1.6. Discussion

1.6.1. Effects of stand scale factors

Overall, the factors that were significantly associated with stands evolving towards balsam fir dominance illustrate the ecological niche of balsam fir, the dominant species, and white spruce, its companion species. Balsam fir stands were usually restricted to mesic and mesotrophic sites, because balsam fir and white spruce typically are uncompetitive with species that are more tolerant of extreme conditions, such as black spruce, in sites that are too dry or too wet (Carleton & Maycock, 1978; Bergeron & Bouchard, 1984; Gauthier *et al.*, 2000).

On mesic sites, early successional stands dominated by trembling aspen and white birch generally evolve into balsam fir stands. On the other hand, dry or humid sites are generally recolonized by jack pine or black spruce after disturbance, evolving into black spruce stands. (Bergeron & Dubuc, 1989; Gauthier *et al.*, 2000; Lesieur *et al.*, 2002; Harper *et al.*, 2003). Balsam fir stands therefore tend to be replaced by black spruce stands at the extremes of the environmental gradient, on dry and coarse deposits as well as on humid organic deposits.

Whereas the clay deposits found in the southwestern part of the study area constitute mesic habitats that likely support balsam fir dominance (Bergeron & Bouchard, 1984), the same deposits are often covered with organic matter in the north (Brumelis & Carleton, 1988; Boudreault *et al.*, 2002), therefore favouring black spruce over balsam fir (Gauthier *et al.*, 2000; Harper *et al.*, 2003). In fact, Brumelis and Carleton (1988) showed that where forest harvesting disturbs the organic layer, black spruce stands can evolve towards trembling aspen and white birch stands that may in turn eventually develop into balsam fir stands.

The northwards decrease of available mesic sites in the West sector (Fig. 1.3) – due to weak slopes, low elevations, and imperfect drainage (Appendix 1.1) - partially explains the increasing lack of mixedwood forests, whose successional endpoint is the balsam fir stand (Bergeron *et al.*, 2004). However, our logistic regression models explain only part of the variation. Many local habitats suitable for balsam fir stands are occupied by black spruce stands, or the reverse. Both stand types can also be found growing on the same local site conditions.

Climate can partly explain the absence of mesic sites in the coniferous zone by its effect on the limiting factors mentioned above. We found a positive correlation between elevation and balsam fir stands; conditions will be more humid and colder in depressions than on hilltops. Such differences can segregate plant communities according to their tolerance to these habitat types. For example, in the ecotone between the boreal and deciduous forests, sugar maple stands tend to occur on hilltops whereas balsam fir stands are located in depressions (Bergeron *et al.*, 1985; Brumelis & Carleton, 1988; Cogbill & White, 1991; Barras & Kellman 1998; Bigras & Colombo, 2001; Goldblum & Rigg, 2002). Another example comes from the tree line in Alaska, where white spruce is invading upland sites following improving climatic conditions, but not bottomland sites (Hobbie & Chapin, 1998). Lowland soils in the same region are more susceptible to frost than the uplands, and permafrost is more extensive and permanent in the lowlands (Viereck *et al.*, 1993).

We therefore expect an inversion of vegetation levels, with balsam fir stands on hilltops and black spruce stands in depressions (Robitaille & Saucier, 1998). Low temperatures slow the decomposition of organic matter and promote its accumulation and acidification, thus limiting the establishment of balsam fir stands (Harper *et al.*, 2003). Our first hypothesis, that the lack of ecological sites suitable to balsam fir stands in the north is responsible for the transition between the mixedwood and coniferous zones, is verified, as is the inability of balsam fir stands to saturate these sites. However, this hypothesis cannot by itself explain the entirety of the observed pattern.

1.6.2. Effects of landscape factors

When considered at the landscape scale, the factors significantly associated with balsam fir stands are a reflection of the spatial dynamics of tree populations and their presence as seed sources. These factors can therefore promote the expansion (positive relationship) or regression (negative relationship) of balsam fir stands (Appendix 1.2). In other words, the ecological districts with a high abundance of a factor that promotes balsam fir stands have greater saturation of their suitable sites. This saturation depends on a sufficient quantity of balsam fir trees across the landscape, i.e. large source populations that are sufficiently well distributed to maximize the potential invasion of suitable sites (Fig. 1.4). Indeed, balsam fir is limited in its capacity to recolonize sites after forest fires for two main reasons: (i) recolonization occurs exclusively from seed trees that escaped fire (refuge populations) and (ii) its seeds are relatively heavy for a conifer and cannot disperse over long distances (Galipeau *et al.*, 1997; Bergeron *et al.*, 2004). It is only during mast years that seed dispersal is assured outside of balsam fir populations (Zarnovican & Laberge, 1997). This phenomenon seems more crucial in the coniferous zone where mast years occur more rarely than in the mixedwood zone (Messaoud *et al.*, 2007). It is therefore not surprising to observe clustering of balsam fir stands, especially where mesic sites are more abundant.

Rugged topography can play an important role in the extent and severity of forest fires. A more pronounced topography and the presence of lakes can limit fire expansion and thus provide a greater amount of areas protected from fire (Hély *et al.*, 2000; Kafka *et al.*, 2001; Bergeron *et al.*, 2004; Lefort *et al.*, 2004), from which balsam fir can reinvade disturbed sites. The distribution of balsam fir stands in the coniferous zone (Fig. 1.4) clearly illustrates their association with water courses that act as firebreaks. The abundance of deciduous species can also decrease fire severity (Hély *et al.*, 2000) and thus may contribute to the presence of balsam fir. Bergeron *et al.* (2004) showed that fires are larger and possibly more severe in the coniferous zone, where the topography is flatter, than in the mixedwood zone. Large fires and the absence of deciduous trees may contribute to the decrease in balsam fir stands to the north.

1.6.3. Historical factors

Our logistic regression models indicate that all the significant factors only explain 34-42 % of the variation in the distribution of balsam fir stands. The remaining variation is unexplained and may be related to historical factors (see McCune & Allen, 1985). Site history, whether at the local or landscape scale, can partially explain the spatial and temporal dynamics of balsam fir stands and their inability to saturate some mesic sites – an inability that is more frequent in the coniferous than in the mixedwood zone.

Two historical phenomena can potentially account for the lack of habitat saturation: (i) initial site colonization, and (ii) accidental elimination and replacement over the years. According to Richard (1980 and 1993), black spruce was the first tree species to invade after the retreat of glaciers and pro-glacial lake Barlow-Ojibway in Abitibi-Témiscamingue between 7200-8900 years ago. Balsam fir migrated afterwards, followed by other species adapted to warmer climate that benefited from a climatic improvement (higher temperature and precipitation) that caused longer fire cycles. According to palynological studies of past vegetation, black spruce has always been dominant in the coniferous zone whereas balsam fir always dominated the mixedwood zone (Richard, 1980, 1993; Liu, 1990; Carcaillet *et al.*, 2001).

Since black spruce arrived first and rapidly became dominant in the north, it may have had a competitive advantage over balsam fir.

If balsam fir had a higher saturation rate in the past, its regression, and thus habitat saturation decline, may have occurred in a gradual manner as fire eliminated populations. Indeed, conditions favourable to balsam fir started to deteriorate around 2600 years BP as climate became colder and drier, conditions leading to increased fire frequencies (Carcaillet *et al.*, 2001). This deterioration caused the southward retreat of several species, such as white pine, eastern white cedar and red pine, and their replacement by jack pine (Liu, 1990; Richard, 1980); it also constrained these species to specific ecological conditions, such as lake shores (Bergeron & Gagnon, 1987; Bergeron *et al.*, 1997).

At the landscape level, it seems this deterioration in environmental conditions produced a decline in species diversity (i.e. reduced deciduous trees in both bioclimatic zones), that may have been more important in the coniferous zone (Carcaillet *et al.*, in prep.). Balsam fir stands, lacking the protection against large fires provided by deciduous trees, became gradually rarer in the coniferous zone. Black spruce, better adapted to these new environmental conditions and freed from competition, was able to invade sites that could have been suitable for balsam fir.

It is therefore probable that balsam fir stands located in mesic sites, although rarer in the coniferous zone, were gradually replaced by black spruce at local and landscape scales (Larocque *et al.*, 2003; Carcaillet *et al.*, in prep.). Sites suitable for balsam fir stands, but where balsam fir is now absent, probably contained balsam fir stands during the interglacial maximum around 6000 BP. The balsam fir stands currently present in the coniferous zone may be the remnants of a formerly more abundant population (Fig. 4c; Liu, 1990). Therefore all these outcomes showed that these population refugia are unable to saturate suitable sites, which agrees with our second hypothesis.

1.7. Conclusion

This study aimed to explain the ecological factors responsible for the ecotone loaction between mixedwood and coniferous bioclimatic zones. At the local scale, suitable sites were less abundant in the coniferous zone which partly explained the rarity of balsam fir stands. At the landscape scale, the abundance of suitable sites and forest composition promoted the occupation level of balsam fir on suitable sites. These landscape conditions were also less abundant in the coniferous zone which therefore explained the failure of balsam fir stands to re-invade suitable sites.

In the coniferous zone, especially in the western sector, balsam fir stands tend to be more common both on suitable and unsuitable sites, in the vicinity of fire breaks such as rivers and lakes. This suggests that in the past, balsam fir stands were probably more abundant in the coniferous zone, but were gradually extracted and replaced by black spruce following the deterioration of climatic conditions and an increase in fire activity observed since the last 2500 years (Carcaillet *et al.*, in press).

Acknowledgements

The authors would like to acknowledge the Québec Ministry of Natural Resources for access to the sampling plots data as well as Pierre Grondin for his invaluable help. Special thanks to Patricia Wood, Adam A. Ali, Ronnie Drever, Hugo Asselin, Erol Yilmaz, Nicole Fenton and the reviewers for careful revision and English corrections that improved an early version of the manuscript. The research was funded by a NSERC discovery grant to Yes Bergeron.

1.8. References

Bakusis, E.V. & Hansen, H.S. (1965) *Balsam fir: a monographic review.* The University of Minnesota Press, Minneapolis.

Barras, N. & Kellman, M. (1998) The supply of regeneration micro-sites and segregation of tree species in a hardwood/coniferous transition zone. *Journal of Biogeography*, **25**, 871-881.

Béland, M. & Bergeron, Y. (1993) Ecological factors affecting abundance of commercial species advance growth in jack pine (*Pinus banksiana* Lamb.) stands of the boreal forest of northwestern Quebec. *Forestry Chronicle*, **69**, 561-568.

Bérard, J. A. (1996) *Manuel de foresterie.* Presses de l'Université Laval.

Bergeron, Y. & Bouchard, A. (1984) Use of ecological groups in analysis and classification of plant communities in a section of western Quebec. *Vegetatio*, **56**, 45-63.

Bergeron, Y. & Dubuc, M. (1989) Succession in the southern part of the Canadian boreal forest. *Vegetatio*, **79**, 51-63.

Bergeron, Y. & Gagnon, D. (1987) Age structure of red pine (*Pinus resinosa* Ait.) at its northern limit in Quebec. *Canadian Journal of Forest Research*, **17**, 129-137.

Bergeron, Y., Bouchard, A. & Massicotte, G. (1985) Gradient analysis in assessing differences in community pattern of three adjacent sectors within Abitibi, Quebec. *Vegetatio*, **64**, 55-65.

Bergeron, Y., Leduc, A., Morin, H. & Joyal, C. (1995) Balsam fir mortality following the last spruce budworm outbreak in northwestern Quebec. *Canadian Journal of Forest Research*, **25**, 1375-1384.

Bergeron, Y., Leduc, A. & Ting-Xian, L. (1997) Explaining the distribution of *Pinus* spp. in a Canadian boreal insular landscape. *Journal of Vegetation Science*, **8**, 37-44.

Bergeron, Y., Gauthier, S., Flannigan, M. & Kafka, V. (2004) Fire regimes at the transition between mixedwood and coniferous boreal forest in northerwestern Quebec. *Ecology*, **85**, 1916-1932.

Bigras, F.J. & Colombo, S.J. (2001) *Conifer cold hardiness*. Kluwer Academic, Dordrecht

Boudreault, C., Bergeron, Y., Gauthier, S. & Drapeau, P. (2002) Bryophyte and lichen communities in mature to old-growth stands in eastern boreal forests of Canada. *Canadian Journal of Forest Research*, **32**, 1080-1093.

Brubaker, L.B. (1986) Response of tree populations to climatic change. *Vegetatio*, **67**, 119-130.

Brumelis, G. & Carleton, T.J. (1988) The vegetation of postlogged black spruce lowlands in central Canada. I. Trees and tall shrubs. *Canadian Journal of Forest Research*, **18**, 1470-1478.

Burns, R.M. & Honkala, B.H. (1990) *Silvics of North America*. Department of Agriculture, Washington, D.C.

Cappuccino, N., Lavertu, D., Bergeron, Y. & Régnière, J. (1998) Spruce budworm impact, abundance and parasitism rate in a patchy landscape. *Oecologia*, **114**, 236-242.

Carcaillet, C., Bergeron, Y., Richard, P.J.H., Fréchette, B., Gauthier, S. & Prairie, Y.T. (2001) Changes of fires frequency in the eastern Canadian boreal forests during the Holocene: does vegetation composition or climate trigger the fire regime? *Journal of Ecology*, **89**, 930-946.

Carcaillet, C., Richard, P.J.H., Asnong, H., Capece, L. & Bergeron (in press). Fire and soil erosion history in East Canadian boreal and temperate forests. *Quaternary Science Reviews*

Carleton, T.J. & Maycock, P.F. (1978) Dynamics of the boreal forest south of James Bay. *Canadian Journal of Botany*, **56**, 1157-1173.

Cogbill, C.V. & White, P.S. (1991) The latitude-elevation relationship for spruce-fir forest and treeline along the Appalachian mountain chain. *Vegetatio*, **94**, 153-175.

Earle, C.J. (1993) Ribbon forest development in the forest-tundra of Wyoming: differing roles of trees establishing by layering or from seed. *Bulletin of the Ecological Society of America*, **74** (2 suppl.), 222

Engelmark, O., Bergeron, Y. & Flannigan, M.D. (2000) Age structure of eastern white pine, *Pinus strobus* L., at its northern distribution limit in Québec. *The Canadian Field Naturalist*, **114**, 601-604.

Fowells, H. A. (1965) *Silvics of forest trees of the United States*. Forest Service Handbook 271, United States Department of Agriculture.

Galipeau, C., Kneeshaw, D. & Bergeron, Y. (1997) White spruce and balsam fir colonization of a site in the southeastern boreal forest as observed 68 years after fire. *Canadian Journal of Forest Research*, **27**, 139-147.

Gauthier, S., De Grandpré, L. & Bergeron, Y. (2000) Differences in forest composition in two boreal forest ecoregions of Quebec. *Journal of Vegetation Science*, **11**, 781-790.

Goldblum, D. & Rigg, L.S. (2002) Age structure and regeneration dynamics of sugar maple at the deciduous/boreal forest ecotone, Ontario, Canada. *Physical Geography*, **23**, 115-129.

Gu, W., Heikkilä, R. & Hanski, I. (2002) Estimating the consequences of habitat fragmentation on extinction risk in dynamic landscapes. *Landscape Ecology*, **17**, 699-710.

Harper, K., Boudreault, C., De Grandpré, Drapeau, P., Gauthier, S. & Bergeron, Y. (2003) Structure, composition, and diversity of old-growth black spruce boreal forest of the Clay Belt region in Quebec and Ontario. *Environmental Reviews*, **11**, S79-98.

Hély, C., Bergeron, Y. & Flannigan, M.D. (2000) Effects of stand composition on fire hazard in mixed-wood Canadian boreal forest. *Journal of Vegetation Science*, **11**, 813-824.

Hobbie, S.E. & Chapin, F.S. (1998) An experimental test of limits to tree establishment in arctic tundra. *Journal of Ecology*, **86**, 449-461.

Hofgaard, A., Kullman, L. & Alexandersson, H. (1991) Response of old-growth montane *Picea abies* (L.) Karst. forest to climatic variability in northern Sweden. *New Phytologist*, **119**, 585-594.

Hogg, E.H. & Schwarz, A.G. (1997) Regeneration of planted conifers across climatic moisture gradients on the Canadian prairies: implications for distribution and climate change. *Journal of Biogeography*, **24**, 527-534.

Houle, G. & Filion, L. (1993) Interannual variations in the seed production of *Pinus banksiana* at the limit of the species distribution in northern Québec, Canada. *American Journal of Botany*, **80**, 1242-1250.

Kafka, V., Gauthier, S. & Bergeron, Y. (2001) Fire impacts and crowning in the boreal forest: study of a large wildfire in western Quebec. *International Journal of Wildland Fire*, **10**, 119-127.

Larocque, I., Bergeron, Y., Campbell, I.D. & Bradshaw, R.H.W. (2003) Fire-induced decrease in forest cover on a small rock outcrop in the Abitibi region of Québec, Canada. *Écoscience*, **10**, 515-524.

Lavoie, C. & Payette, S. (1994) Recent fluctuations of the lichen-spruce forest limit in subarctic Québec. *Journal of Ecology*, **82**, 725-734.

Lefort, P., Leduc. A., Gauthier, S. & Bergeron, Y. (2004) Recent fire regime (1945-1998) in boreal forest of western Québec. *Écoscience*, **11**, 433-445.

Legendre, P. & Legendre, L. (1998) *Numerical ecology*, 2nd English edition. Elsevier Science BV, Amsterdam.

Lesieur, D., Gauthier, S. & Bergeron, Y. (2002) Fire frequency and vegetation dynamics for the south-central boreal forest of Quebec, Canada. *Canadian Journal of Forest Research*, **32**, 1996-2009.

Liu, K.B. (1990) Holocene paleoecology of the boreal forest and Great Lakes-St. Lawrence forest in northern Ontario. *Ecological Monographs*, **60**, 179-212.

Loehle, C. (2000) Forest ecotone response to climate change: sensitivity to temperature response functional forms. *Canadian Journal of Forest Research*, **30**, 1632-1645.

Luckman, B. & Kavanagh, T. (2000) Impact of climate fluctuations on mountain environments in the Canadian Rockies. *Ambio*, **29**, 371-380.

McCune, B. & Allen, T.F.H. (1985) Will similar forests develop on similar sites? *Canadian Journal of Botany*, **63**, 367-376.

MacLean, D.A. (1980) Vulnerability of fir-spruce stands during uncontrolled spruce budworm outbreaks: a review and discussion. *Forestry Chronicle*, **56**, 213-221.

MacLean, D.A. (1984) Effects of spruce budworm outbreaks on the productivity and stability of balsam fir forests. *Forestry Chronicle*, **60**, 273-279.

Messaoud, Y., Bergeron, Y., Asselin, H. 2007. Reproductive potential of balsam fir (*Abies balsamea*), white spruce (*Picea glauca*), and black spruce (P. mariana) at the ecotone between mixedwood and coniferous forests in the boreal zone of western Quebec. *American Journal of Botany*, **94**, 746-754.

Paré, D. & Bergeron, Y. (1996) Influence of colonizing trees on soil properties following fire in the Canadian southern boreal forest. *Canadian Journal of Forest Research*, **26**, 1022-1031.

Payette, S. & Filion, L. (1985) White spruce expansion at the tree line and recent climatic change. *Canadian Journal of Forest Research*, **15**, 241-251.

Payette, S. (1993) The range limit of boreal tree species in Québec-Labrador: an ecological and palaeoecological interpretation. *Review of Palaeobotany and Palynology*, **79**, 7-30.

Pellatt, M.G., Smith, M.J., Mathewes, R.W., Walker, I.R. & Palmer, S.L. (2000) Holocene treeline and climate change in the subalpine zone near Stoyoma Mountain, Cascade Mountains southwestern British Columbia, Canada. *Arctic, Antarctic and Alpine Research*, **32**, 73-83.

Pouliot, Y. (1998) Le Québec dans le monde nordique. *Naturaliste Canadien*, **122**, 45-53.

Richard, P.J.H. (1980) Histoire postglaciaire de la végétation au sud du lac Abitibi, Ontario et Québec. *Géographie Physique et Quaternaire*, **34**, 77-94.

Richard, P.J.H. (1993) Origine et dynamique postglaciaire de la forêt mixte au Québec. *Review of Palaeobotany and Palynology*, **79**, 31-68.

Robitaille, A. & Saucier, J.-P. (1998) *Paysages régionaux du Québec méridional*. Les Publications du Québec.

Rupp, T.S., Starfield, A.M. & Chapin, F.S. (2000) A frame-based spatially explicit model of subarctic vegetation response to climatic change: comparison with a point model. *Landscape Ecology*, **15**, 383-400.

Rupp, T.S., Chapin, F.S. & Starfield, A.M. (2001) Modeling the influence of topographic barriers on treeline advance at the forest-tundra ecotone in northwestern Alaska. *Climatic Change*, **48**, 399-416.

Saucier, J.-P., Berger, J.-P., D'Avignon, H. & Racine, P. (1994) *Le point d'observation écologique*. Service des Inventaires Forestiers, Ministère des Ressources Naturelles, Québec.

Sirois, L. (1997) Distribution and dynamics of balsam fir (*Abies balsamea* (L.) Mill.) at its northern limit in the James Bay area. *Ecoscience*, **4**, 340-352.

Sirois, L., Bégin, Y. & Parent, J. (1999) Female gametophyte and embryo development of black spruce along a shore-hinterland climatic gradient of a recently created reservoir, northern Quebec. *Canadian Journal of Botany*, **77**, 61-69.

Tremblay, M. & Simon, J.-P. (1989) Genetic structure of marginal populations of white spruce (*Picea glauca*) at its northern limit of distribution in Nouveau-Québec. *Canadian Journal of Forest Research*, **19**, 1371-1379.

Tremblay, M.F., Bergeron, Y., Lalonde, D. & Mauffette, Y. (2002 The potential effects of sexual reproduction and seedling recruitment on the maintenance of red maple (*Acer rubrum* L.) populations at the northern limit of the species range. *Journal of Biogeography*, **29**, 365-373.

Viereck, L.A., Van Cleve, K., Adams, P.C. & R.E. Schlentner, R.E. (1993) Climate of the Tanana River floodplain near Fairbanks, Alaska. *Canadian Journal of Forest Research*, **23**, 899-913.

Zarnovican, R. & Laberge, C. (1997) Production de graines dans une sapinière de seconde venue dans la forêt modèle du Bas-Saint-Laurent. *Centre de Foresterie des Laurentides*, **1**, 1-2.

1.9. Biosketches

Yassine Messaoud is a PhD candidate in environmental sciences at Université du Québec en Abitibi-Témiscamingue (Canada).

Yves Bergeron is professor of forest ecology at Université du Québec en Abitibi-Témiscamingue (Canada). He is interested in forest dynamics at the stand and landscape scales.

Alain Leduc is an adjunct professor of forest ecology at Université du Québec à Montréal. His research interests are in forest dynamics and statistical analyses.

Table 1.1. Ecological classification of the studied territory (according to the Québec Ministry of Natural Resources).

Domains	**Zones**	**Ecological regions**	**Description**	**Area (km^2)**
Balsam fir-white birch	Western balsam fir-white birch	5a	Abitibi lowlands	≅ 27 000
		5b	Gouin reservoir hills	≅ 16 000
		5c	Saint-Maurice highlands hills	≅ 22 100
		5d	Lake Saint-Jean hills	≅ 20 100
Black spruce-moss	Western black spruce-moss	6a	Lake Matagami lowlands	≅ 49 100
		6c	Lake Opémisca lowlands	≅ 21 600
		6e	Nestaocano lake hills	≅ 22 400

Table 1.2. Selected climatic variables for the western bioclimatic zones.

	Balsam fir-white birch	**Black spruce-moss**
Average annual temperature (°C)	0-1	-2.5-0
Length of the growing season (days ≥ 5°)	150-160	120-155
Average annual precipitation (mm)	800-1200	700-1000
Percentage of precipitation falling as snow	40-45	25-50

Table 1.3. Stand scale factors considered in this study.

	Value
Aspect	North, Northeast, East, Southeast, South, Southwest, West, Northwest, null
Position on the slope	low, middle, high
Slope	In percentage
Altitude	In metres above sea level
Type of organic horizon*	Mull (MU), Moder (MD), Mor (MR), Organic Soil (OS), Peat (TO)
Organic horizon thickness	In cm
Texture of the B horizon	Fine (FB), medium (MB), coarse (GB)
Deposit type	Fine subhydric (FS), mesic middle (MM), mesic (GM), organic soil (OH), bedrock (R)
Gravel	In percentage
Drainage (classes)	00-19 (well); 20-39 (moderate); ≥ 40 (imperfect and poor)

* these types are accorded to the level of organic matter decomposition. Mull: well decomposed, Moder: moderate, MR: low. Organic soil: thickness of organic matter is ≥ 40 cm. Peat: presence of stagnant water permanently near the surface of soil.

Table 1.4. Landscape scale factors considered in this study.

		Value
Physical parameters	Relief	Dominance of Lowland (LL), hillside (HS), hills (H), high hills (HH) in each ecological district
	Elevation range	The length of the slope in metres
	A_FS	Area of fine subhydric deposit (%)
	A_MM	Area of middle mesic deposit (%)
	A_GM	Area of coarse mesic deposit (%)
	A_OH	Area of organic deposit (%)
	A_R	Area of bedrock (%)
	A_WATER	Area of water (%)
	Nb lakes/100km^2	Number of lakes per 100 km^2
Forest cover parameters (%)	WBF	White birch stands with fir
	WBR	White birch stands with conifers
	SF	Black spruce stands with fir
	F	Pure fir stands
	SS	Pure black spruce stands
	JP	Pure jack pine stands

Table 1.5: Results of logistic regressions between the presence/absence of balsam fir stands and the environmental variables at the stand and landscape scales, for each sector. The number of plots is 1986, 1142 and 1894 for the West, Center and East sectors, respectively, in both zones.

		Scale	Variable	Relationship	Chi-square	*p*	R^2
West		**Stand**	Organic horizon thickness	-	179.82	<0.001	0.2386
			Altitude	+	61.08	<0.001	
			Drainage	-/+*	45.79	<0.001	
			Slope	+	31.54	<0.001	
			MD	+	14.65	0.001	
			MB	+	10.10	0.002	
	Landscape	**Permanent**	A_OH	-	49.02	<0.001	0.2922
			Nb lakes/100 km^2	+	37.21	<0.001	
			A_FS	-	22.80	<0.001	
		Dynamic	WBR	+	64.43	<0.001	0.3352
			SF	+	18.42	<0.001	
Center		**Stand**	Altitude	+	167.80	<0.001	0.3574
			Drainage	-/+	56.19	<0.001	
			Slope	+	52.92	<0.001	
			Organic horizon thickness	-	31.89	<0.001	
			GM	-	10.91	0.01	
	Landscape	**Permanent**	A_OH	-	38.32	<0.001	0.4025
			A_MM	+	11.49	0.001	
		Dynamic	WBF	+	33.97	<0.001	0.4210
East		**Stand**	Slope	+	146.05	<0.001	0.2817
			OH	-	53.69	<0.001	
			Low	-	40.64	<0.001	
			Organic horizon thickness	-	37.68	<0.001	
			Drainage	-/+	25.57	0.001	
			MD	+	12.69	0.004	
			GM	-	12.33	0.004	
	Landscape	**Permanent**	Elevation range	+	84. 99	<0.001	0.3544
			HH	-	38. 17	<0.001	
			Al_min	-	19.11	<0.001	
		Dynamic	JP	-	51.30	<0.001	0.4065
			SS	-	50.83	<0.001	
			F	+	14.41	0.001	
			WBR	+	10.30	0.001	

* The relationship was positive with moderate and negative with good and imperfect drainage.

1.10. Figure legends

Figure 1.1. Distribution of the Québec Ministry of Natural Resources temporary sampling plots in the study area (the bold red line indicates the limit between the mixedwood and coniferous subdomains). The different colours indicates the sectors.

Figure 1.2. Percentage of the sampling plots suitable for balsam fir stands in each ecological region.

Figure 1.3. Ecological profiles of balsam fir stands in the mixedwood (black bars) and coniferous (grey bars) zones. The y-axis of these profiles represents the ratio of the difference between the observed (Obs) and expected (Exp) values divided by the observed values (Obs-Exp)/Obs; Legendre and Legendre, 1998). Positive and negative ratios indicate that balsam fir stands are found more or less often than expected in sites presenting a particular value of a variable (N.S.: not significant for the sector). The units of measurement are given in Table 1.3.

Figure 1.4. Distribution of suitable sites with (a) presence and (b) absence of balsam fir stands. (c) Overflow of balsam fir stands. Numbers indicate the saturation rate of balsam fir stands (in % of total suitable sites) at the (a) stand and (b) landscape scales, and in cases of overflow in unsuitable sites at (c) the landscape scale for each ecological region. The lakes and rivers are in blue.

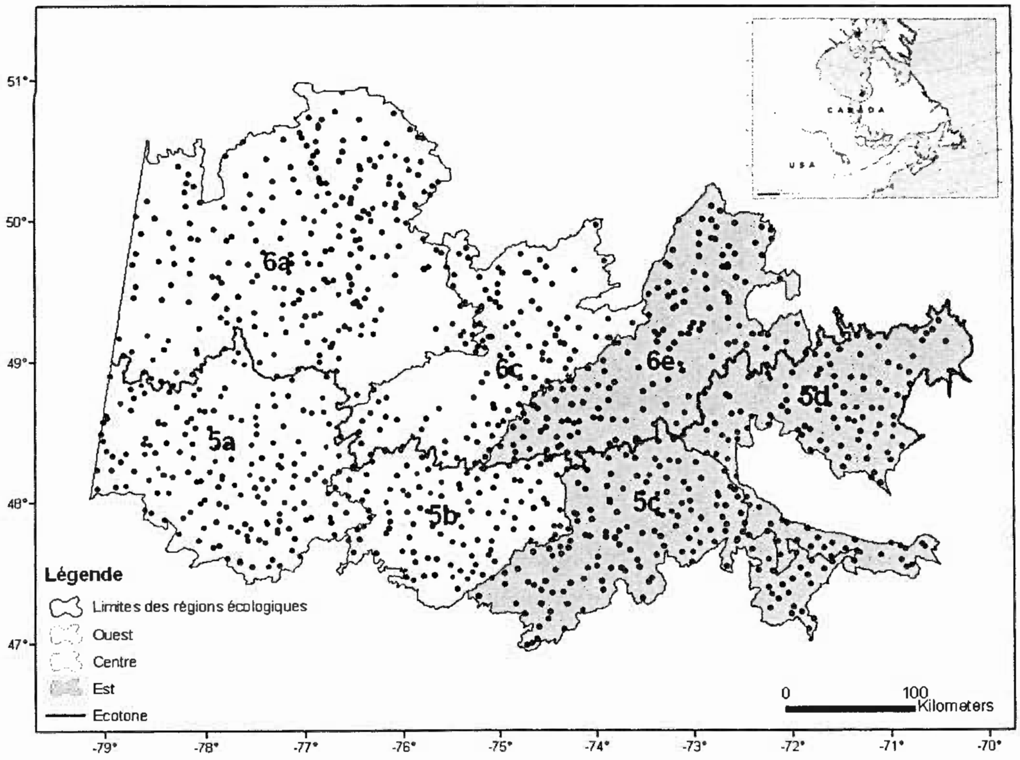

51°
50°
49°
48°
47°
-79°
-78°
-77°
-76°
-75°
-74°
-73°
-72°
-71°
-70°
6a
6c
6e
5a
5b
5c
5d
CANADA
USA
Légende
Limites des régions écologiques
Ouest
Centre
Est
Ecotone
0
100
Kilometers

Fig. 1.1

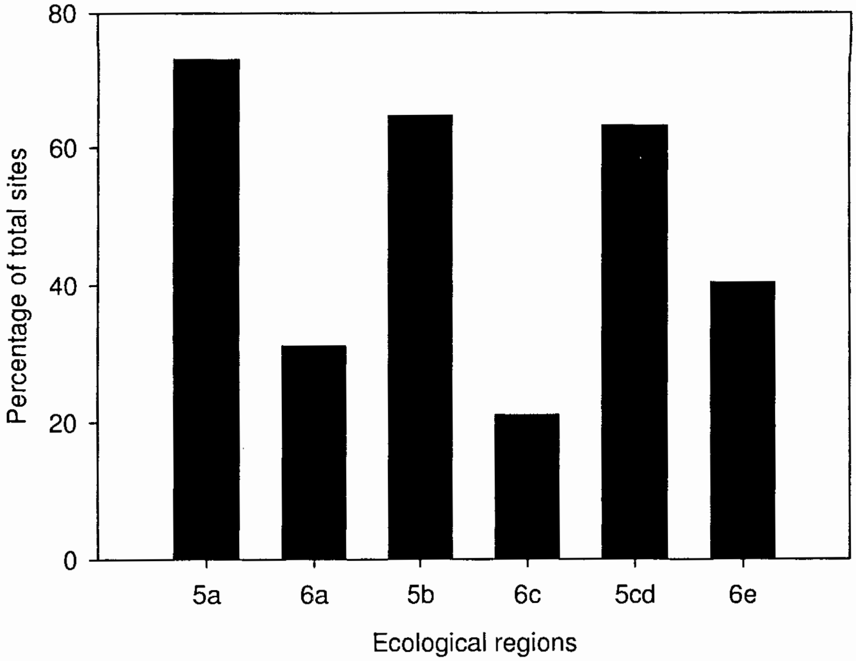

80
60
40
20
0
Percentage of total sites
5a
6a
5b
6c
5cd
6e
Ecological regions

Fig. 1.2.

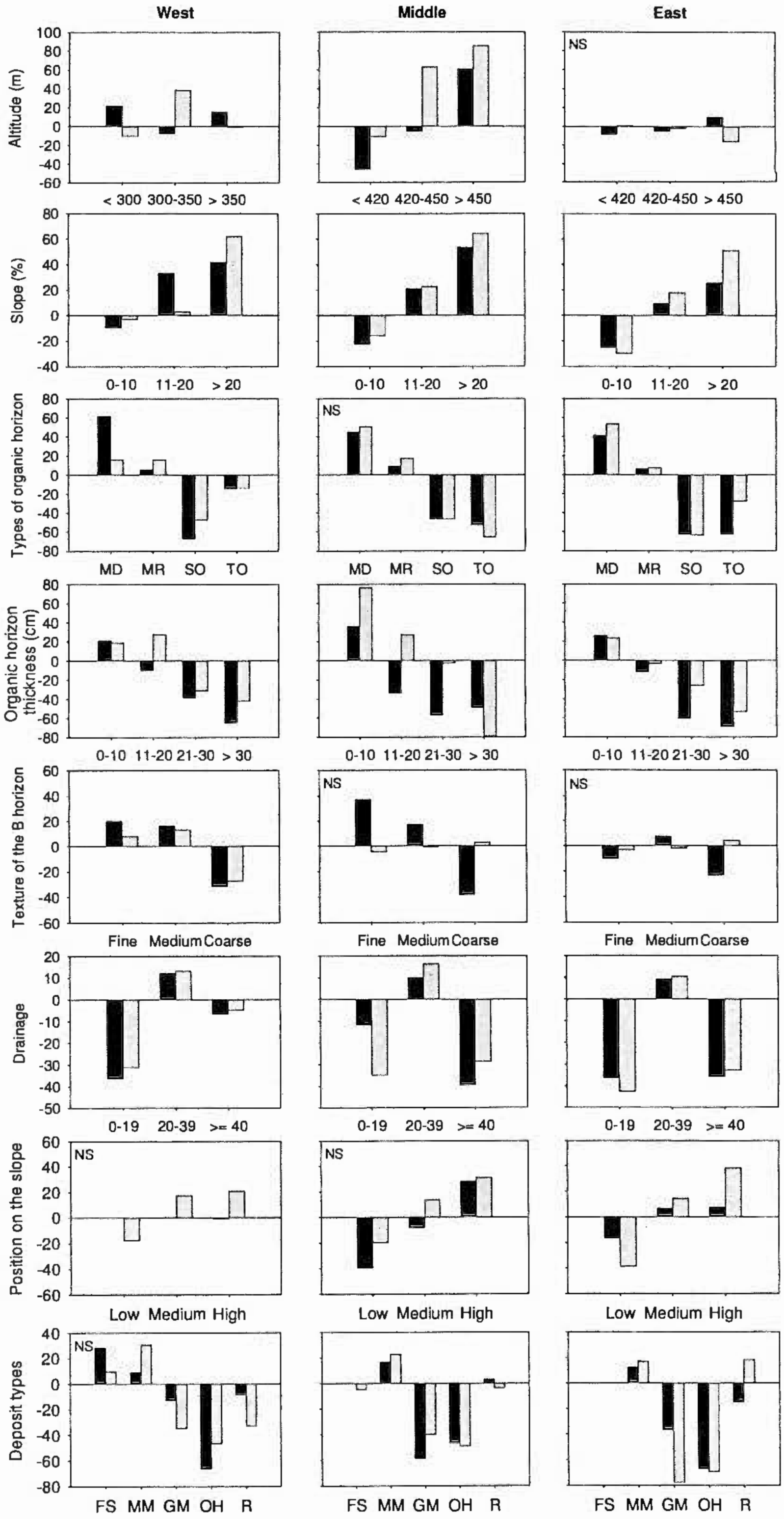

West
Middle
East
Altitude (m)
100
80
60
40
20
0
-20
-40
-60
NS
< 300 300-350 > 350
< 420 420-450 > 450
< 420 420-450 > 450
Slope (%)
0-10 11-20 > 20
Types of organic horizon
NS
MD MR SO TO
Organic horizon thickness (cm)
0-10 11-20 21-30 > 30
Texture of the B horizon
NS
NS
Fine Medium Coarse
Drainage
0-19 20-39 >= 40
Position on the slope
NS
NS
Low Medium High
Deposit types
NS
FS MM GM OH R

Fig. 1.3.

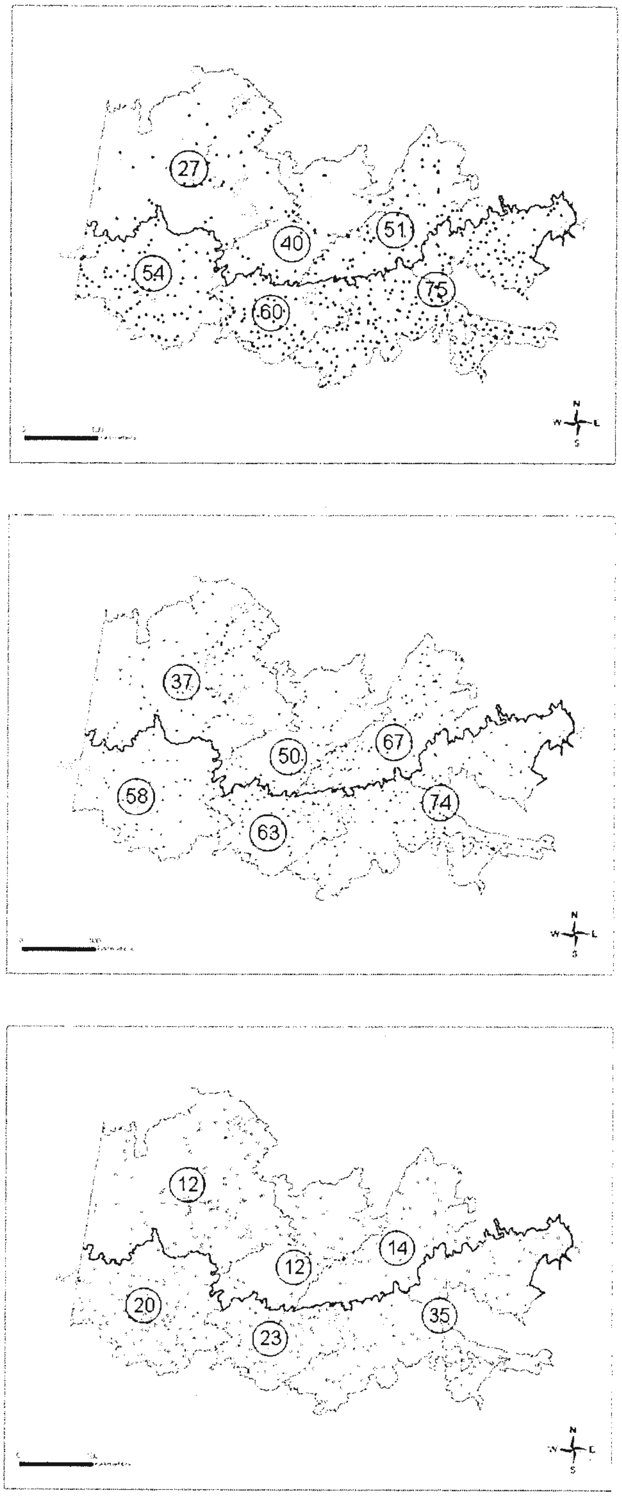
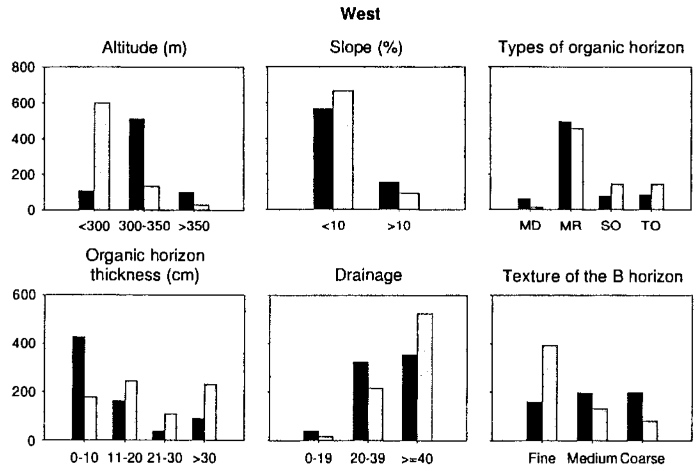
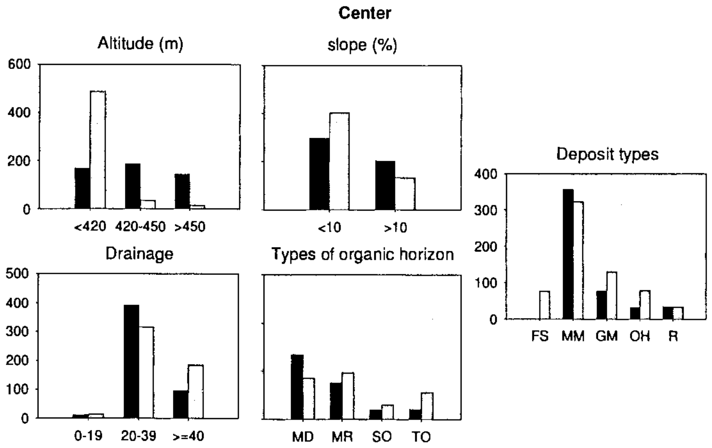
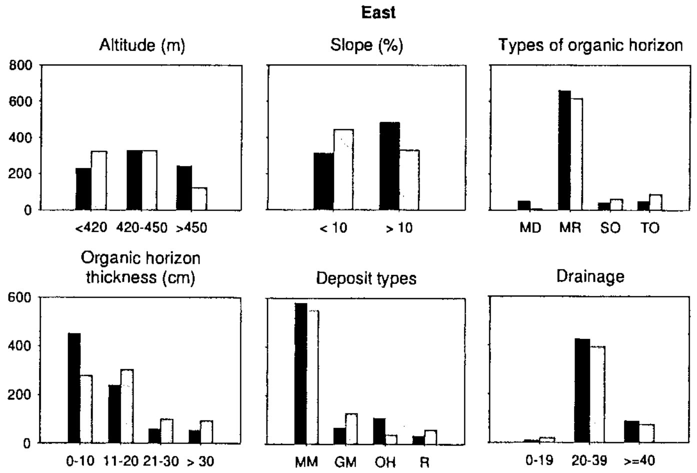


Fig. 1.4.

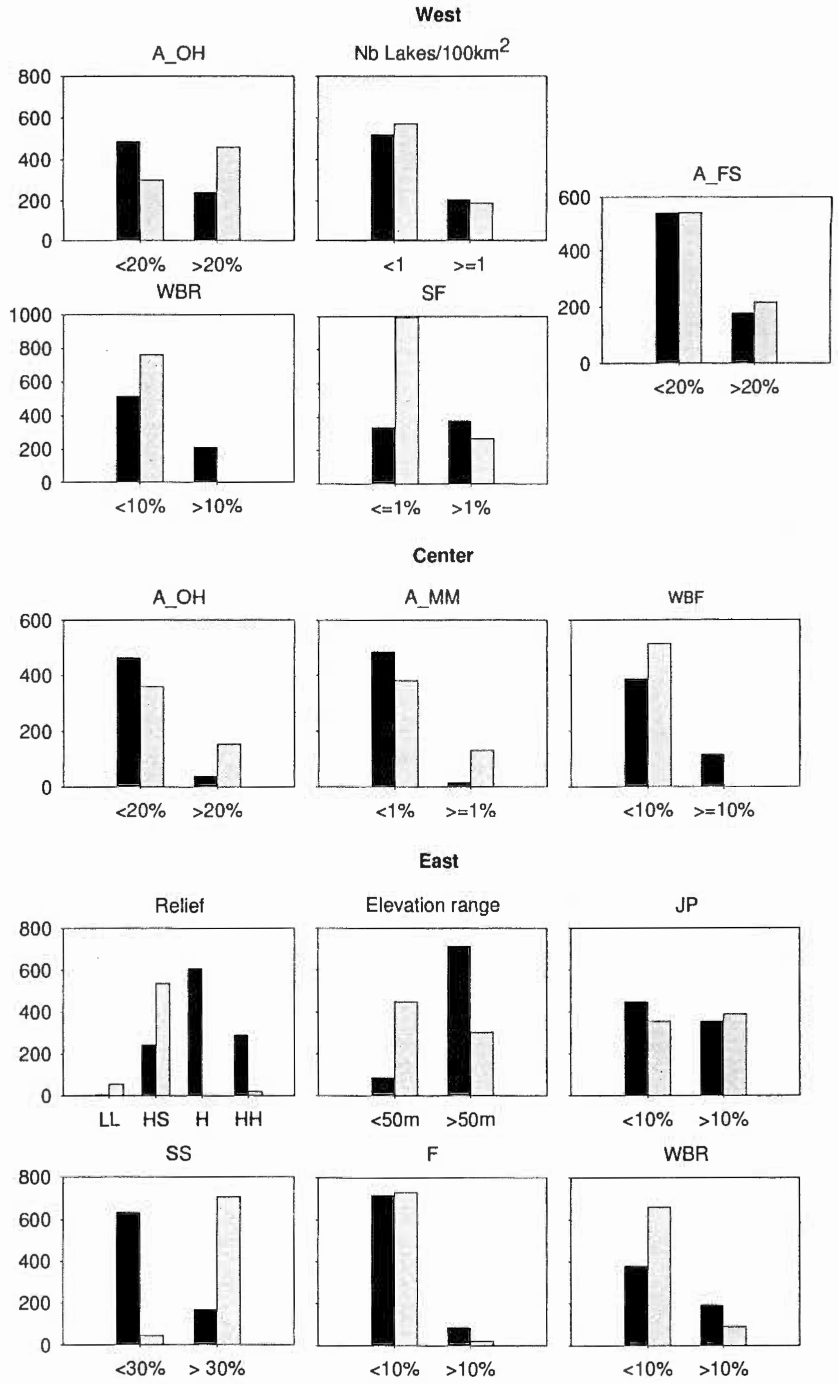
Appendix 1.1. Stand-scale factors significantly associated with the presence of balsam fir stands in the mixedwood (black) and coniferous (grey) zones. The *y*-axis represents the number of sampling plots in which balsam fir stands occur.


West
Altitude (m)
800
600
400
200
0
<300 300-350 >350
Slope (%)
<10 >10
Types of organic horizon
MD MR SO TO
Organic horizon thickness (cm)
600
400
200
0
0-10 11-20 21-30 >30
Drainage
0-19 20-39 >=40
Texture of the B horizon
Fine Medium Coarse


Center
Altitude (m)
600
400
200
0
<420 420-450 >450
slope (%)
<10 >10
Drainage
500
400
300
200
100
0
0-19 20-39 >=40
Types of organic horizon
MD MR SO TO
Deposit types
400
300
200
100
0
FS MM GM OH R


East
Altitude (m)
800
600
400
200
0
<420 420-450 >450
Slope (%)
< 10 > 10
Types of organic horizon
MD MR SO TO
Organic horizon thickness (cm)
600
400
200
0
0-10 11-20 21-30 > 30
Deposit types
MM GM OH R
Drainage
0-19 20-39 >=40

Appendix 1.2. Landscape-scale factors significantly associated with the presence of balsam fir stands in the mixedwood (black) and coniferous (grey) zones. The *y*-axis represents the number of sampling plots in which balsam fir stands occur.


West
A_OH
800
600
400
200
0
<20%
>20%
Nb Lakes/100km2
<1
>=1
A_FS
600
400
200
0
<20%
>20%
WBR
1000
800
600
400
200
0
<10%
>10%
SF
<=1%
>1%
Center
A_OH
600
400
200
0
<20%
>20%
A_MM
<1%
>=1%
WBF
<10%
>=10%
East
Relief
800
600
400
200
0
LL
HS
H
HH
Elevation range
<50m
>50m
JP
<10%
>10%
SS
800
600
400
200
0
<30%
> 30%
F
<10%
>10%
WBR
<10%
>10%

Appendix 1.2

CHAPITRE II

Reproductive potential of balsam fir (*Abies balsamea*), white spruce (*Picea glauca*), and black spruce (*Picea mariana*) at the ecotone between mixedwood and coniferous forests in the boreal zone of western Québec

Yassine Messaoud[2], Yves Bergeron and Hugo Asselin

NSERC-UQAT-UQAM Industrial Chair in Sustainable Forest Management, Université du Québec en Abitibi-Témiscamingue, 445 boul. de l'Université, Rouyn-Noranda, Québec, J9X 5^{E}4, Canada.

[2] Author for correspondence: yassine.messaoud@uqat.ca

Article publié en 2007 dans American journal of Botany, volume 94, pp. 746-754

2.1. Abstract

The reproductive potentials of balsam fir and white spruce (co-dominants in mixedwood forests) and black spruce (dominant in coniferous forests) were studied to explain the location of the ecotone between the two forest types in the boreal zone of Québec. Four sites were selected along a latitudinal gradient crossing the ecotone. Cone crop, number of seeds per cone, percent filled seeds, and percent germination were measured for each species. Balsam fir and white spruce cone crops were significantly lower in the coniferous than in the mixedwood forest, while black spruce showed greater crop constancy and regularity between both forest types. Mast years were more frequent for black spruce than for balsam fir in both forest types. The number of seeds per cone was more related to cone size than to forest type for all species. Black spruce produced mainly more filled seeds in the coniferous forest than balsam fir or white spruce. The sum of growing degree-days and the maximum temperature of the warmest month (both for the year prior to cone production) significantly affected balsam fir cone production. The climate-related northward decrease in reproductive potential of balsam fir and white spruce could partly explain the position of the northern limit of the mixedwood forest.

Key words: Boreal zone; mixedwood forest; coniferous forest; cone and seed production; *Abies balsamea*; *Picea glauca*; *Picea mariana*; ecotone.

2.2. Résumé

Le potentiel reproducteur du sapin baumier et de l'épinette blanche (Co-dominants dans la forêt mixte) et de l'épinette noire (dominants dans la forêt coniférienne) a été étudié pour expliquer la localisation de l'écotone entre deux types de forêt à l'intérieur de la zone boréale du Québec. Quatre sites ont été choisis le long d'un gradient latitudinal traversant l'écotone. Le nombre de cônes et de graines par cône ainsi que le pourcentage des graines pleines et du taux de germination ont été mesurés pour chaque espèce. Le nombre de cônes du sapin baumier et de l'épinette blanche était sensiblement inférieur dans la forêt coniférienne par rapport à la forêt mixte, alors que l'épinette noire montrait une plus grande constance et une régularité de production entre les deux types de forêt. Les années de paisson pleine étaient plus fréquentes pour l'épinette noire que pour le sapin baumier dans les deux types de forêt. Le nombre de graines par cône était davantage lié à la taille des cônes qu'au type de forêt et ce quelque soit l'espèce. L'épinette noire produit principalement plus de graines pleines dans la forêt coniférienne que le sapin baumier et l'épinette blanche. Le nombre de degré jours ainsi que la température maximale du mois le plus chaud (tous les deux pendant l'année avant la production de cône) affecte de manière significative la production de cônes de sapin baumier. La diminution au nord de ces conditions climatiques favorables au potentiel reproducteur du sapin baumier et de l'épinette blanche pourrait en partie expliquer la position de la limite nordique de la forêt mixte.

Mots clés: Zone boréale; forêt mixte; forêt coniférienne; production de cônes et de graines; *Abies balsamea*; *Picea glauca*; *Picea mariana*; écotone.

2.3. Introduction

The northern limit of a species' distribution is often related to reduced reproductive capacity, i.e. low seed quantity and viability due to cooler and shorter growing seasons (Krebs, 1972; Larsen, 1980; Lavoie and Payette, 1994; Zasada, 1995). Cold temperatures are known to kill flowers (Matthews 1955; Owens and Blake, 1985), favour cone abortion and damage (Zasada, 1971; Owens et al., 1991), and stop seed maturation (Sirois et al., 1999; Garcia et al., 2000; Parantainen and Pulkkinen, 2002). Henttonen et al. (1986) mentioned that a species growing close to its alpine or arctic distribution limit often fails to produce mature and viable seeds due to insufficient flower production and unfavourable temperatures during seed maturation.

Several studies have documented the strong effect of climate on cone initiation, flowering, pollination, fertilization, seed development, embryo maturation, and germination success (Pigott and Huntley, 1981; Owens and Blake, 1985; Pigott, 1992; Sirois, 2000). Despland and Houle (1997) emphasized the importance of slope aspect in cone production, with more cones being produced on southern aspects because of higher light and temperature. Most of the aforementioned studies were conducted at the altitudinal or latitudinal limit of a given species' distribution, characterized by extreme ecological conditions such as shallow soils and strong wind (Loehle, 2000). Few studies, however, were conducted at the ecotone between two forest types. This study aims to better understand the limitations in the reproductive potential of three coniferous species (balsam fir (*Abies balsamea*), white spruce (*Picea glauca*) and black spruce (*Picea mariana*)) that could explain the location of the ecotone between the mixedwood and coniferous forests of the boreal zone of Québec. The mixedwood forest is dominated by balsam fir, white spruce and paper birch (*Betula papyrifera*), while the coniferous forest is dominated by black spruce. Disjunct populations of mixedwood species are found above the ecotone between the mixedwood and coniferous forests, but fail to occupy all of the few potentially suitable sites (Messaoud et al., 2007a). Reduced balsam fir and white spruce reproductive capacity was suggested as a possible explanation for the weaker performance of mixedwood species in the coniferous forest (Messaoud et al., 2007b).

With thin bark and absence of an aerial seed bank, balsam fir and white spruce are not adapted to fire (Bakusis and Hansen, 1965; Albani et al., 2005). Black spruce bears semi-serotinous cones remaining on the trees for a long time until their opening is triggered by fire, favouring seed dispersal on burned sites (Gauthier et al., 2000). Fire could thus contribute to limit mixedwood species distribution by killing dominant mature balsam fir and white spruce (seed sources) and contribute to their local extinction (Bergeron et al., 2004; Albani et al., 2005). A combination of factors such as climate, fire and availability of suitable sites have similarly been reported to explain the northern limit of red pine (*Pinus resinosa*) in Manitoba (Sutton et al., 2002) and Québec (Flannigan and Bergeron, 1998).

Owens and Blake (1985) mentioned that the reproductive capacity of balsam fir, white spruce and black spruce depends on the climatic conditions of the previous year, as their reproductive cycle lasts two years. Vegetative buds change to reproductive buds (males and females strobili) in the first year and develop in the spring of the second year. Pollination and seed maturation occur during the summer, followed by seed dispersal in the fall. Also important is the capacity to store energy, as large amounts are needed for reproduction and for seeds to accumulate the reserves essential to seedling survival following germination. The existence of a trade-off between cone production and growth has been documented by several authors (Eis et al., 1965; El-Kassaby and Barclay, 1992; Woodward et al. 1994; Lechowicz, 1995).

The objective of this study was to determine if the location of the ecotone between mixedwood and coniferous forests is due to reproductive limitation of the mixedwood dominant species (balsam fir and white spruce) in the coniferous zone (dominated by black spruce).Therefore, we documented the reproductive performance of balsam fir, white spruce and black spruce along a latitudinal gradient crossing the ecotone between the mixedwood and coniferous forests of the boreal zone of Québec. We tested the hypotheses that (1) as none of the studied species reaches its northern limit in the ecotone, they will show a gradual northward decrease of reproductive output rather than a lack of reproduction as is often observed at the northern limit of a species' distribution, and (2) mast years will occur less frequently toward the north of the gradient, where favourable climatic conditions are less frequent. Although the three species will be affected by the latitudinal gradient, we expect black spruce to be less affected than balsam fir and white spruce, thus benefiting from a competitive advantage in the coniferous forests.

2.4. Material and methods

2.4.1. Study area

The study area is located in northwestern Québec, near the Ontario border, and is part of the Québec and Ontario Clay Belt formed by the lacustrine deposits of proglacial lake Barlow-Ojibway (Veillette, 1994; Fig. 2.1). The area is composed of two bioclimatic sub-domains characterized by different late-successional species on mesic sites: the southern balsam fir – paper birch bioclimatic sub-domain (herein called mixedwood forest) and the northern black spruce – moss bioclimatic sub-domain (herein called coniferous forest). The limit between these two sub-domains is located at ca. 49° N. Trembling aspen (*Populus tremuloides*), paper birch, and jack pine (*Pinus banksiana*) are abundant immediately after fire in both forest types. The altitude generally varies between 300 and 400 m a.s.l. and low hills are scattered in an otherwise flat landscape. Topography is more accentuated in the mixedwood than in the coniferous forest (Asselin, 1995; Gauthier et al., 2000).

The climate of the study area is continental, with cold winters and warm summers. Mean annual temperature in the mixedwood forest is 1.2 °C (Amos meteorological station – 48° 34' N; 78° 07' W; 310 m elevation). Mean temperature of the coldest (January) and warmest (July) months are -17.3 °C and 17.2 °C, respectively. Mean annual precipitation is 918 mm, from which 248 falls as snow. There are 1400 growing degree-days above 5 °C (from May to October). In the coniferous forest, the mean annual temperature is -0.7 °C (Matagami meteorological station – 49° 46' N; 77° 49' W; 281 m elevation). Mean temperature of the coldest (January) and warmest (July) months are -20.0 °C and 16.1 °C, respectively. Mean annual precipitation is 906 mm, from which 314 falls as snow. There are 1169 growing degree-days above 5 °C (Environment Canada, 2002).

Four sites were selected along a latitudinal gradient crossing the ecotone between the mixedwood and coniferous forests (Fig. 2.1): Lake Montalais (48° 01' N, 79° 24' W; 302 m elevation), Lake Duparquet (48° 30' N, 79° 12' W; 291 m elevation), Cochrane (49° 13' N, 80° 39' W; 281 m elevation), and Maskouchis (50°13' N, 78° 44' W; 376 m elevation). Lakes Montalais and Duparquet are in the mixedwood forest, while Maskouchis is in the coniferous forest. The site Cochrane is situated in the Ontario province (Fig. 2.1). Although there is no equivalent of classification of bioclimatic domains in this province, Cochrane would be according to its latitude included in the coniferous forest.

All four sites have a moderate moisture regime (Brais and Camiré, 1998), but surface deposits vary: clay (Lake Duparquet), till (Lake Montalais), and sand (Cochrane and Maskouchis).

2.4.2. Sampling

Three mature trees of balsam fir, white spruce and black spruce, distributed in 4 different diameter classes (10-15, 15-20, 20-25, and 25-30 cm), were selected and cut at each site during the summers of 2001, 2002 and 2004 for a total of 12 trees per species per year. We measured diameter at breast height of mature trees (DBH > 10 cm) surrounding each selected individual inside a 5 m radius to evaluate the competition between these individuals and the selected trees. Cones were harvested and put in paper bags.

Cone production was documented retrospectively for a 10 year period (1991-2000) for balsam fir and black spruce. Black spruce cones can stay on the branches for a long time after ripening, and the central axes of balsam fir cones also stay on the branches for a long time after cones have shed their scales. Because white spruce cones fall one year after seed dispersal, a retrospective study was not possible for that species.

For each individual tree, one branch was sampled from each of the ten topmost whorls in the canopy. Each of the ten whorls on the main trunk representing the past 10 years (period 1991-2000). The branch was composed to branchlets separated by each other by whorls. The top of each branch or trunk corresponded to the year of harvesting (2001). After the branchlets were dated, cone age could easily be determined as cones are formed one year after branchlets (Silvertown and Dodd, 1999). Spruce and fir have the same reproductive cycle and cone production occurs one year after vegetative bud differentiation. The mean number of branches per whorl was counted to estimate cone production per whorl and total cone production. Data were used to estimate cone production per diameter class and total cone production per site using cut down trees.

2.4.3. Seed extraction and viability test

We measured the length and width of 10 cones per tree for 2001 and 2002 and 20 cones per tree for 2004. Seeds were extracted manually for balsam fir and white spruce. Black spruce semi-serotinous cones had to be heated at 55 °C to induce opening before seed extraction could be performed. The proportion of empty seeds was estimated using a separator from the Centre de semences forestières de Berthierville. This machine is composed of a ventilation shaft where air is introduced in controlled conditions. Seeds are introduced in the shaft, the lighter empty seeds are attracted to a pipe and accumulated in a container, while the heavier filled seeds fall in another container. Results were verified on a subsample of seeds classified as empty or filled using X-ray. Seeds from all the cones of a tree were put together. A seed counter or a weighting method was used to count seeds when large quantities were involved (especially for balsam fir). The weighting method consisted of weighting 10 sub-samples of 100 seeds for each site. When the coefficient of variation between subsamples was small (< 4 %), we estimated the quantity of seeds using the weight as a reference. Otherwise we used manual count.

Germination tests were performed on 201 seeds per tree. Seeds were stratified during 4 weeks at 4 °C before being sowed in garden peat. The experimentation was carried out for slightly more than two months in a greenhouse with temperatures varying between 15-25 °C.

2.4.4. Climatic data

In order to assess the relationship between cone production (1991-2004) and climate variables, climatic data were obtained for each site from NATGRID (National Geo-Referenced Information for Decision-makers). These data were estimated by extrapolations from the meteorological stations located closest to our four study sites for the period 1990-2003 (Fig. 2.1; Appendix) The climate variables were sum of growing degree-days ≥ 5 °C (GDD; starting when the mean daily temperature was ≥ 5 °C for five consecutive days after March 1st and ending when the minimum temperature reached less than -2 °C after August 1st; Mackey et al., 1996), maximum temperature of the warmest month, minimum temperature of the coldest month and precipitation of the wettest month. The relationship between cone production and climate variables was assessed using variables from the year of cone production and the year before.

2.4.5. Statistical analyses

The effect of forest type (mixedwood vs. coniferous) on cone production, number of seeds per cone, percent filled seeds, and percent germination was assessed using analyses of covariance (ANCOVA). The explaining factors were DBH, competition and seed size (length and width). This analysis was chosen to control the effect of one of these explaining factors. Therefore analyses were carried out in two steps. The first step consisted of a multiple regression to determine which of these factors significantly influenced cone and seed production. ANCOVAs were then performed using only the most significant covariate(s) obtained from the first step. The competition index (C_i) was calculated as follows:

$$C_i = \frac{BA_1}{BA_2}$$

where BA_1 is the basal area of the sampled tree, and BA_2 is the combined basal area of the surrounding trees with diameters ≥ than that of the sampled tree.

Analysis of variance (ANOVA) was used in the absence of significant covariates. Multiple comparisons between sites were performed using the Tukey test. Correlation tests were used for the relationship between cone production and climate variables. All analyses were computed using the SAS software (Cody and Smith, 1991).

2.5. Results

2.4.1. Long-term cone production (1991-2000)

Long-term cone production was significantly related to DBH and forest type for balsam fir, but not for black spruce (Table 2.1). Mean balsam fir cone production was significantly lower in the coniferous forest than in the mixedwood forest (Fig. 2.2). In addition, the difference of cone production between the two forest types increased with increasing DBH. Black spruce cone production did not differ between forest types and none of the measured variables was found significant for that species.

2.5.2. Recent cone production (2001-2004)

Recent cone production was significantly related to forest type for the three species in 2002 and for balsam fir and black spruce in 2004 (Table 2.1), with more cones being produced in the mixedwood forest than in the coniferous forest (Fig. 2.3). Recent cone production was also significantly related to DBH for balsam fir in 2002, and for black spruce in 2002 and 2004 (Table 2.1; Fig. 2.3). The absence of a DBH effect in white spruce cone production could be a sampling artefact, as only the larger trees (20-30 cm) were sampled. Competition from surrounding trees did not significantly affect cone production whatever the species or year.

2.5.3. Periodicity of cone production

For the entire study period (1991-2004), balsam fir produced cones every two years, with total crop failures between two production years (Fig. 2.4). Mast years were determined following Tranquillini (1979) as years with cone production ≥ 50 % of the mean cone production. Between 1991 and 2004, balsam fir had five mast years in the mixedwood forest, and two in the coniferous forest. Contrary to balsam fir, black spruce produced cones every year (Fig. 2.4). Mast years occurred six times in the mixedwood forest and two times in the coniferous forest. However, cone production was probably underestimated for the period before 1995 as the fragile cones fell during sampling. When looking only at the period 1995-2004, mast years were more frequent for black spruce than for balsam fir in both forest types (6 vs. 4 in the mixedwood forest and 2 vs. 1 in the coniferous forest).

2.5.4. Seed production

The number of seeds per cone was significantly influenced by cone size in all species, but not by DBH or competition index (Table 2.2). There was no difference in seed number per cone between forest types after controlling for the effect of cone size, except for black spruce in 2002 and 2004 and for balsam fir in 2004 (fewer seeds per cone in the coniferous forest) (Table 2.3). Cone size was significantly smaller in the coniferous than in the mixedwood forest for all species (data not shown).

2.5.5. Percent filled seeds and percent seed germination

Neither DBH nor competition index significantly affected the percentage of filled seeds or the percentage of germination, whatever the species or year. The percentage of filled seeds was not significantly different between forest types for the three species, except in 2004 when it was lower in the coniferous forest for balsam fir and black spruce (Table 2.3). The percentage of seed germination was significantly lower in the coniferous forest only for balsam fir in 2004 and for black spruce in 2002 and 2004 (Table 2.3). Notably, the difference was larger for balsam fir than for black spruce in 2004.

2.5.6. Effect of climate on cone production

Correlations between cone production and climate variables between 1991 and 2004 showed no variable was significant for black spruce (Table 2.4). For balsam fir, only the number of growing degree-days ≥ 5 °C and the maximum temperature of the warmest month (both for the year prior to cone production) were significant.

2.6. Discussion

Long-term cone production differed with respect to species and forest type. Total balsam fir cone production was lower in the coniferous than in the mixedwood forest for the period 1991-2000. Furthermore, balsam fir only produced cones every second year, with total crop failures between two production years (Fig. 2.4). The trends found for balsam fir are supported by the limited data (2001-2004) available for the companion species white spruce, which only produced cones in 2002, and in lesser amounts in the coniferous forest. Moreover, only dominant and co-dominant trees produced cones, as white spruce is less shade-tolerant than balsam fir with regards to cone production (Greene et al., 2002). In contrast, black spruce cone crops were quite similar in both forest types and showed greater regularity. These results are concordant with those of Sirois (2000) who did not find any evidence of a decreasing black spruce cone production along a latitudinal gradient extending from the continuous coniferous forest to the tundra. It thus appears that the lower reproductive potential of balsam fir and white spruce compared to black spruce in the coniferous forest may partly explain the shift in species dominance occurring at the ecotone between the mixedwood and coniferous forests.

Owens and Blake (1985) pointed out that cone phenology of fir and spruce extends over two years and requires good climate conditions during both years: a warm and dry summer in the first year will stimulate cone development, and a warm and moist summer during the second year will favour cone elongation (Owens and Molder, 1977; van der Meer et al., 2002). The probability of having two good summers in a row seems to be lower in the coniferous forest and this could explain the positive relationship between balsam fir cone production and the maximum temperature of the warmest month and sum of growing degree-days ≥ 5 °C of the previous year (Table 2.4). Lower balsam fir and white spruce cone production in the coniferous forest thus seems to be more readily explained by climatic limitations than endogenous factors. Indeed, genetic diversity does not seem to be limiting as the species are not close to their distribution limit (Shea and Furnier, 2002). Furthermore, Tremblay and Simon (1989) did not find evidence of low white spruce genetic diversity at its northern distribution limit well north of our study area. The fact that populations are fragmented probably did not affect seed quality as found by Wang (2003) for isolated European beech populations. Soil fertility was not limiting either as the best potential sites for balsam fir (coarse xeric surface deposits) were those located in the coniferous forest (Birot, 1965). Competition from the surrounding mature trees was not shown here to be a significant factor, contrary to what other authors found for *Abies pinsapo* (Arista and Talavera, 1996) and *Pinus resinosa* (Sutton et al., 2002). Insect outbreaks such as those of the spruce budworm (*Choristoneura fumiferana*) do not seem to play an important role in the northern part of the latitudinal gradient (Sirois, 2000).

Our results showing a significant positive relationship between climate (growing degree-days and maximum temperature of the warmest month of the year preceding cone production) and cone production for balsam fir corroborate those of other authors that studied different species along latitudinal or altitudinal gradients (white spruce (Zasada et al., 1978; Zasada, 1988); *Betula pubescens* (Kullman, 1993); *Pinus banksiana* (Houle and Filion, 1993; Asselin et al., 2003); *Picea abies* (Mencuccini et al., 1995); black spruce (Sirois, 2000); and *Acer rubrum* (Tremblay et al. 2002)). In these and other areas, lower temperatures, shorter growing seasons, and late spring frosts are responsible for compromising reproduction (Henttonen et al., 1986; Zasada, 1988; Houle and Filion, 1993; Sirois et al., 1999; Garcia et al., 2000).

2.6.1. Implications at the landscape scale

In western Québec, balsam fir reaches its northern distribution limit near lake Duncan in the James Bay area (ca. 54° N; Sirois, 1997). White spruce reaches its northern limit at ca. 56° N (Tremblay and Simon, 1989) and black spruce is present from the coniferous forest to the shrub-tundra where it reaches its northern distribution limit (ca. 59° N; Payette, 1993). Therefore, the location of the ecotone between the mixedwood and coniferous forests (49 °N) does not correspond to the northern limit of either balsam fir or white spruce. Nevertheless, the reproductive capacity of balsam fir and white spruce was significantly lower in the coniferous forest, contrary to black spruce which reproduced equally well in both forest types. This implies a competitive advantage of black spruce over balsam fir and white spruce. Black spruce produces smaller and fewer cones (Young and Young, 1992) and therefore has lower reproductive costs (Tranquillini, 1979; Woodward et al., 1994; Fleming and Mossa, 1995; Hobbie and Chapin, 1998). At the landscape scale, Messaoud et al. (2007) found that balsam fir stands are less abundant and confined to lake and river borders in the coniferous forest. Furthermore, lower reproductive capacity and larger seed size may make it more difficult for trees to invade new suitable habitats which are rare and far away from seed sources (Davis et al., 1986; Galipeau et al., 1997; Asselin et al., 2001; Clark et al., 2001). While climate fluctuations are regarded as the main factor responsible for decreased reproductive capacity for balsam fir and white spruce in the coniferous forest, the absence of aerial seed banks could also play a role. The serotinous cones of black spruce remain on the branches for long periods and thus constitute an aerial seed bank. Seed dispersal is delayed until disturbance by fire, when seeds from many production years (good and poor) are released. Balsam fir and white spruce do not have aerial seed banks and post-fire seed dispersal depends on the presence of nearby mature trees (Albani et al., 2005) with enough viable seeds. Zarnovican and Laberge (1997) mentioned that it is only during mast years that seed dispersal is assured outside balsam fir populations. Tremblay et al. (2002) found that low seed production and larger periodicity between two good years for *Acer rubrum* (red maple) limit the potential of northern populations to invade and colonize sites cleared by disturbances. This is supported by our results showing that there were three times fewer balsam fir mast years in the coniferous than in the mixedwood forest (Fig. 2.4).

Since climate limits the metapopulation dynamics of balsam fir and white spruce in the coniferous forest through its effects on their reproductive capacity, climate change (increased temperatures and precipitations) could substantially increase the reproductive capacity of northern populations of balsam fir and white spruce. The effect of climate change on black spruce might be less important as this species appears less sensitive to climate fluctuations (Table 2.5). Increased viable seed production would allow balsam fir and white spruce to colonize more sites following disturbance and increase their proportions at the landscape scale. However, a time lag of species response may occur because of the specific species migration rates which are related to seed size, availability of suitable habitats, and competition with the dominant species (Sykes and Prentice, 1996; Davis et *al.*, 1998).

2.7. Conclusion

This study aimed to explain the reproductive output responsible for the position of the ecotone between mixedwood and coniferous forests. Even if this ecotone did not represent the northern limit of the distribution of balsam fir and white spruce, their reproductive traits were mainly lower in coniferous than in mixedwood forest. Furthermore, balsam fir had lower mast years frequency in coniferous forest. Our outcome confirmed the importance of these mast years for the mixedwood tree species especially in coniferous forest where even if cone production was lower the difference in seed traits between the two forest types was weaker or nil. Since our outcome confirmed the influence of the GDD on long-term cone production of balsam fir, the temperature of the warmest summer appear to play a stronger role. As we expected, black spruce was not influenced by these climate data.

The effects of climate on reproductive output of the dominant tree species contribute to explain together with habitat availability (Messaoud et al 2007) and disturbance regimes (Bergeron et al. 2004) the position of the ecotone between mixedwood and coniferous forests.

Aknowledgment: The authors thank Benoît St-Vincent for help in the field and Natacha Roudeix for help in the lab. The Centre des semences forestières de Berthierville kindly provided the seed separator. We also thank Alain Leduc for statistical analyses. This project was financed by an NSERC discovery grant to Yves Bergeron.

2.8. Litterature cited

Albani, M., D. W. Andison & J.P. Kimmins. 2005. Boreal mixedwood species composition in relationship to topography and white spruce seed dispersal constraint. *Forest Ecology and Management* 209: 167-180.

Arista, M. & S. Talavera. 1996. Density effect on the fruit-set, seed crop viability and seedling vigour of *Abies pinsapo*. *Annals of Botany* 77: 187-192.

Asselin, H., M.-J. Fortin & Y. Bergeron. 2001. Spatial distribution of late-successional coniferous species regeneration following disturbance in southwestern Québec boreal forest. *Forest Ecology and Management* 140: 29-37.

Asselin, H., S. Payette, M.-J. Fortin & S. Vallée. 2003. The northern limit of *Pinus banksiana* Lamb. In Canada: explaining the difference between the eastern and western distributions. *Journal of Biogeography* 30 : 1709-1718.

Asselin, M. 1995. L'Abitibi-Témiscamingue : trois sous-régions, une région. *In* O. Vincent [ed.], Histoire de l'Abitibi-Témiscamingue. Collection Les régions du Québec, no. 7, Institut québécois de recherche sur la culture, Québec, Canada, 21-65.

Bakusis, E. V. & H. S. Hansen. 1965. Balsam fir: a monographic review. The University of Minnesota Press, Minneapolis.

Bérard, J.A. Manuel de foresterie. Presses de l'Université Laval, Quebec.

Bergeron, Y., S. Gauthier, M. Flannigan & V. Kafka. 2004. Fire regimes at the transition between mixedwood and coniferous boreal forest in northerwestern Quebec. *Ecology* 85 : 1916-1932.

Birot, P. 1965. Les formations végétales du globe. Société d'édition d'enseignement supérieur, Paris, France.

Brais, S. & C. Camiré. 1998. Soil compaction induced by careful logging in the claybelt region of northwestern Quebec (Canada). *Canadian Journal of Soil Science* 78: 197-206.

Clark, J. S., M. Lewis & L. Horvath. 2001. Invasion by extremes: population spread with variation in dispersal and reproduction. *American Naturalist* 157: 537-554.

Cody, R. P. & J. K. Smith. 1991. Applied statistics and the programming language. Fourth edition. Prentice Hall, Upper Saddle River, New Jersey, USA.

Davis, M. B., K. D. Wood, S. L. Webb & R. P. Futyma. 1986. Dispersal versus climate: expansion of *Fagus* and *Tsuga* into the upper Great Lakes. *Vegetatio* 67: 93-103.

Davis, A. J., Jenkinson, L. S., Lawton, B. S. & S. Wood. 1998. Making mistakes when predicting shifts in species range in response to global warming. *Nature* 391: 783-786.

Despland, E. & G. Houle. 1997. Aspect influences cone abundance within the crown of *Pinus banksiana* Lamb. Trees at the limit of the species distribution in northern Québec (Canada). *Ecoscience* 4: 521-525.

Eis, S., E. H. Garman & L. F. Ebell. 1965. Relation between cone production and diameter increment of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), grand fir (*Abies grandis* (Dougl.) Lindl.) and western white pine (*Pinus monticola* Dougl.). *Canadian Journal of Botany* 43: 1553-1559.

El-Kassaby, Y.A. & H. J. Barclay. 1992. Cost of reproduction in Douglas-fir. *Canadian Journal of Botany* 70: 1429-1432.

Environment Canada. 2002. Canadian climate normals 1971-2000. Atmospheric Environment Service, Environment Canada, Ottawa, Ontario, Canada.

Flannigan, M. D. & Y. Bergeron. 1998. Possible role of disburbance in shaping the northern distribution of *Pinus resinosa*. *Journal of Vegetation Science* 9: 477-482.

Fleming, R. L. & D. S. Mossa. 1995. Direct seeding of black spruce in northwestern Ontario: temporal changes in seedbed coverage and receptivity. *Forestry Chronicle* 71: 219-227.

Galipeau, C., D. Kneeshaw & Y. Bergeron. 1997. White spruce and balsam fir colonization of a site in the southeastern boreal forest as observed 68 years after fire. *Canadian Journal of Forest Research* 27: 139-147.

Garcia, D., R. Zamora, J. M. Gomez, P. Jordano & J. A. Hodar. 2000. Geographical variation in seed production, predation and abortion in *Juniperus communis* throughout its range in Europe. *Journal of Ecology* 88: 436-446.

Gauthier, S., L. DeGrandpré & Y. Bergeron. 2000. Differences in forest composition in two boreal forest ecoregions of Quebec. *Journal of Vegetation Science* 11: 781-790.

Greene, D. F., C. Messier, H. Asselin & M.-J. Fortin. 2002. The effect of light availability and basal area on cone production in *Abies balsamea* and *Picea glauca*. *Canadian Journal of Botany* 80: 370-377.

Henttonen, H., M. Kanninen, M. Nygren & R. Ojansuu. 1986. The maturation of *Pinus sylvestris* seeds in relation to temperature climate in northern Finland. *Scandinavian Journal of Forest Research* 1: 243-249.

Hobbie, S. E. & F. S. Chapin. 1998. An experimental test of limits to tree establishment in arctic tundra. *Journal of Ecology* 86: 449-461.

Houle, G. & L. Filion. 1993. Interannual variations in the seed production of *Pinus banksiana* at the limit of the species distribution in northern Québec, Canada. *American Journal of Botany* 80: 1242-1250.

Krebs, C. J. 1972. Ecology. Harper and Row, New York, USA.

Kullman, L. 1993. Tree limit dynamics of *Betula pubescens* ssp. *Tortuosa* in relation to climate variability: evidence from central Sweden. *Journal of Vegetation Science* 4: 765-772.

Larsen A. J. 1980. The boreal ecosystem. Academic Press, Toronto, Canada.

Lavoie, C. & S. Payette. 1994. Recent fluctuations of the lichen-spruce forest limit in subarctic Québec. *Journal of Ecology* 82: 725-734.

Lechowicz, M. J. 1995. Seasonality of flowering and fruiting in temperate forest trees. *Canadian Journal of Botany* 73: 175-182.

Loehle, C. 2000. Forest ecotone response to climate change: sensitivity to temperature response functional forms. *Canadian Journal of Forest Research* 30 : 1632-1645.

Mackey, B. G., D. W. McKenney, Y.-Q. Yang, J. P. MacMahon & M. F. Hutchinson. 1996. Site regions revisited: a climatic analysis of Hills' site regions for the province of Ontario using a parametric method. *Canadian Journal of Forest Research* 26: 333-354.

Mencuccini, M., P. Piussi & A. Z. Sulli. 1995. Thirty years of seed production in a subalpine Norway spruce forest: patterns of temporal and spatial variation. *Forest Ecology and Management* 76: 109-125.

Messaoud, Y., Bergeron, Y. & A. Leduc. 2007. Ecological factors explaining the location of the boundary between the mixedwood and coniferous bioclimatic zones in the boreal biome of eastern North America. *Global Ecology and Biogeography* 16: 90-102.

Owens, J. N. & M. D. Blake. 1985. Forest tree seed production. A review of the literature and recommendations for future research. Canadian Forest Service, Petawawa National Forestry Institute, Information Report PI-X-53.

Owens, J. N. & M. Molder. 1977. Bud development in *Picea glauca*. II. Cone differentiation and early development. *Canadian Journal of Botany* 55: 2746-2760.

Owens, J. N., A. M. Colangeli & S. J. Morris. 1991. Factors affecting seed set in Douglas-fir (*Pseudotsuga menziesii*). *Canadian Journal of Botany* 69: 229-238.

Parantainen, A. & P. Pulkkinen. 2002. Pollen viability of scots pine (*Pinus sylvestris*) in different temperature conditions: high levels of variation among and within latitudes. *Forest Ecology and Management* 167: 149-160.

Payette, S. 1993. The range limit of boreal tree species in Québec-Labrador: an ecological and palaeoecological interpretation. *Review of Palaeobotany and Palynology* 79: 7-30.

Pigott, C. D. 1992. Are species distributions determined by failure to set seed? *In* C. Marshall and J. Grace, Fruit and seed production. Aspects of environmental physiology and ecology. Cambridge University Press, Cambridge, UK, 203-216.

Pigott, C. D. & J. P. Huntley. 1981. Factors controlling the distribution of *Tilia cordata* at the northern limits of its geographical range. *New Phytologist* 87: 817-839.

Shea, K. L. & G. R. Furnier. 2002. Genetic variation and population structure in central and isolated populations of balsam fir, *Abies balsamea* (Pinaceae). *American Journal of Botany* 89: 783-791.

Silvertown, J. & M. Dodd. 1999. The demographic cost of reproduction and its consequences in balsam fir (*Abies balsamea*). *American Naturalist* 29: 321-332.

Sirois, L. 1997. Distribution and dynamics of balsam fir (*Abies balsamea* (L.) Mill.) at its northern limit in the James Bay area. *Ecoscience* 4: 340-352.

Sirois, L. 2000. Spatiotemporal variation in black spruce cone and seed crops along a boreal forest-tree line transect. *Canadian Journal of Forest Research* 30: 900-909.

Sirois, L., Y. Bégin & J. Parent. 1999. Female gametophyte and embryo development of black spruce along a shore-hinterland climatic gradient of a recently created reservoir, northern Quebec. *Canadian Journal of Botany* 77: 61-69.

Sutton, A., R. J. Staniforth & J. Tardif. 2002. Reproductive ecology and allometry of red pine (*Pinus resinosa*) at the northwestern limit of its distribution range in Manitoba, Canada. *Canadian Journal of Botany* 80: 482-493.

Sykes, M. T. & I. C. Prentice. 1996. Climate change, tree species distributions and forest dynamics: a case study in the mixed conifer/northern hardwoods zone of northern Europe. *Climatic Change* 34: 161-177.

Tranquillini, W. 1979. Physiological ecology of the Alpine timberline. Springer, New York, USA.

Tremblay, M. & J.-P. Simon. 1989. Genetic structure of marginal populations of white spruce (*Picea glauca*) at its northern limit of distribution in Nouveau-Québec. *Canadian Journal of Forest Research* 19: 1371-1379.

Tremblay, M. F., Y. Bergeron, D. Lalonde & Y. Mauffette. 2002. The potential effects of sexual reproduction and seedling recruitment on the maintenance of red maple (*Acer rubrum* L.) populations at the northern limit of the species range. *Journal of Biogeography* 29: 365-373.

Van der Meer, P. J., I. T. M. Jorritsma & K. Kramer. 2002. Assessing climate change effects on long-term forest development: adjusting growth, phenology, and seed production in a gap model. *Forest Ecology and Management* 162: 39-52.

Veillette, J. J. 1994. Evolution and paleohydrology of glacial lakes arlow and Ojibway. *Quaternary Science Reviews* 13: 945-971.

Wang, K. S. 2003. Relationship between empty seed and genetic factors in European beech (*Fagus sylvatica* L.). *Silva Fennica* 37: 419-428.

Woodward, A., G. Silsbee, E. G. Schreiner & J. Means. 1994. Influence of climate on radial growth and cone production in subalpine fir (*Abies lasiocarpa*) and mountain hemlock (*Tsuga mertensiana*). *Canadian Journal of Forest Research* 24: 1133-1143.

Young, J. A. & C. G. Young. 1992. Seeds of woody plants in North America. Timber Press, Portland, Oregon, USA.

Zarnovican, R. & C. Laberge. 1997. Production de graines dans une sapinière de seconde venue dans la forêt modèle du Bas-Saint-Laurent. Natural Resources Canada, Centre de Foresterie des Laurentides, Notes de Recherche 1 : 1-2.

Zasada, J. C. 1971. Frost damage to white spruce cones in interior Alaska. United States Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station, Portland, Oregon, Research Note PNW-149.

Zasada, J. C. 1988. Embryo growth in Alaskan white spruce seeds. *Canadian Journal of Forest Research* 18: 64-67.

Zasada, J. C. 1995. Natural regeneration of white spruce – information needs and experience from the Alaskan boreal forest. *In* C. R. Ramsey [ed.], Innovative silviculture systems in boreal forests. Proceedings of a symposium held in Edmonton, Alberta, Canada, October 2-8 1994.

Zasada, J. C., M. J. Foote, F. J. Deneke & R. H. Parkerson. 1978. Case history of an excellent white spruce cone and seed crop in interior Alaska: cone and seed production, germination, and seedling survival. United States Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station, Portland, Oregon, Research Note PNW-65.

2.9. Tables caption

Table 2.1. Results of the ANCOVA between long-term (1991-2000) and recent cone production (for balsam fir, white spruce, and black spruce) and diameter at breast height (DBH), competition index (C_i), and forest type. Significant relationships in bold. Grey columns indicate years without cone production.

Table 2.2. Results of the ANCOVA between the quantity of seeds per cone (for balsam fir, white spruce, and black spruce) and cone size (length and width), tree diameter at breast height (DBH), competition index (C_i), and forest type. Significant relationships in bold. Grey columns indicate years without cone production.

Table 2.3. Results of Tukey's multiple comparisons between percent filled seeds and percent germination for the three species and for both forest type. Grey columns indicate years without cone production. The letters right of each number indicate similarities (same letter) or differences (different letters) between forest types (lower case letters) and between species (capital letters) at $\alpha = 0.05$.

Table 2.4. Results of correlation tests between cone production by balsam fir and black spruce and the different climate variables measured along the latitudinal gradient. Significant relationships ($p < 0.05$) in bold. Variables with _1 are for the year previous to cone production. GDD (growing degree-days), Tmaxwar (maximum temperature of the warmest month), Tmincol (minimum temperature of the coldest month), Ppwet (precipitation of the wettest month).

2.10. Figures legends

Figure 2.1. Study area and location of sampling sites along the latitudinal gradient. A) Lake Montalais; B) Lake Duparquet; C) Cochrane; D) Maskouchis. The dotted red line indicates the limit between the mixedwood and coniferous forests of the boreal zone of Québec.

Figure 2.2. A) Regression between cone production and diameter at breast height (DBH) for balsam fir for the period 1991-2000. Black and white triangles indicate cone production in mixedwood and coniferous forests, respectively. B) Average cone production (with standard deviation) for black spruce for the period 1991-2000. The letters beside each regression line or on top of each bar in the histogram indicate that cone production is similar (same letter) or different (different letter) between the two forest types (Tukey test) at $\alpha = 0.05$.

Figure 2.3. Regression between recent (2001-2004) cone production and diameter at breast height (DBH) for the three species and for each forest type. Black triangles and circles indicate cone production in the mixedwood forest and white triangles and circles indicate cone production in the coniferous forest. In cases where DBH was not a significant variable, average cone production (with standard deviation) is shown. The letters beside each regression line or on top of each bar in the histograms indicate that cone production is similar (same letter) or different (different letter) between the two forest types (Tukey test) at $\alpha = 0.05$. No data available for 2003.

Figure 2.4. Periodicity of cone production for balsam fir (black) and black spruce (grey). The values are expressed as deviation from the mean cone production for both forest types. Mast years are indicated by asterisks. Total crop failures are indicated by a 0. No data available for 2003 (X).

2.12. Appendices

Appendix. Meteorological stations used for the climate data in Canada and United States for the year 1990 (Mc Kenney et al., 2006).

Table 2.1. Results of the ANCOVA between long-term (1991-2000) and recent cone production (for balsam fir, white spruce, and black spruce) and diameter at breast height (DBH), competition index (Ci), and forest type. Significant relationships in bold. Grey columns indicate years without cone production.

Balsam fir	1991-2000	2001	2002	2004
N	45		44	48
R^2	0.6160		0.4183	0.1335
DBH	**< 0.0001**		**< 0.0001**	N.S.
C_i	N.S.		N.S.	N.S.
Forest type	**0.0205**		**0.0007**	**0.0107**
White spruce				
N			24	
R^2			0.5674	
DBH			N.S.	
C_i			N.S.	
Forest type			**< 0.0001**	
Black spruce				
N	44	41	36	49
R^2	0.0142	0.0836	0.4811	0.4586
DBH	N.S.	N.S.	**0.0249**	**0.0015**
C_i	N.S.	N.S.	N.S.	N.S.
Forest type	N.S.	N.S.	**< 0.0001**	**< 0.0001**

N.S.: non significant.

Table 2.2. Results of the ANCOVA between the quantity of seeds per cone (for balsam fir, white spruce, and black spruce) and cone size (length and width), tree diameter at breast height (DBH), competition index (Ci), and forest type. Significant relationships in bold. Grey columns indicate years without cone production.

Balsam fir	2001	2002	2004
N		34	21
R^2		0.3847	0.7331
Length		N.S.	**0.0022**
Width		**0.0007**	N.S.
DBH		N.S.	N.S.
C_i		N.S.	N.S.
Forest type		N.S.	N.S.
White spruce			
N		19	
R^2		0.4813	
Length		N.S.	
Width		**0.0022**	
DBH		N.S.	
C_i		N.S.	
Forest type		N.S.	
Black spruce			
N	15	25	28
R^2	0.5332	0.2877	0.8353
Length	N.S.	N.S.	**< 0.0001**
Width	**0.0057**	**0.0092**	N.S.
DBH	N.S.	N.S.	N.S.
C_i	N.S.	N.S.	N.S.
Forest type	N.S.	N.S.	**< 0.0001**

N.S.: non significant.

Table 2.3. Results of Tukey's multiple comparisons between percent filled seeds and percent germination for the three species and for both forest type. Grey columns indicate years without cone production. The letters right of each number indicate similarities (same letter) or differences (different letters) between forest types (lower case letters) and between species (capital letters) at □ = 0.05.

		2001		**2002**		**2004**	
		Mixedwood	**Coniferous**	**Mixedwood**	**Coniferous**	**Mixedwood**	**Coniferous**
Seeds per cone	Balsam fir			$193.58^{A} \pm 59.07$	$180.58^{A} \pm 34.47$	$250.86^{A} \pm 29.80$	$193.38^{B} \pm 45.42$
	White spruce			$74.31^{A} \pm 7.41$	$86.71^{A} \pm 40.01$		
	Black spruce			$30.59^{A} \pm 21.67$	$20.39^{B} \pm 17.93$	$49.08^{A} \pm 18.99$	$15.37^{B} \pm 7.26$
Filled seeds (%)	Balsam fir			$47.72^{Aa} \pm 12.61$	$49.11^{Aa} \pm 18.75$	$85.39^{Aa} \pm 6.85$	$29.66^{Ba} \pm 19.17$
	White spruce			$52.54^{Aa} \pm 18.16$	$57.64^{Aa} \pm 16.64$		
	Black spruce	$89.00^{A} \pm 8.44$	$93.39^{A} \pm 3.57$	$88.22^{Ab} \pm 6.90$	$91.61^{Ab} \pm 7.66$	$66.90^{Ab} \pm 12.15$	$49.59^{Bb} \pm 13.18$
Germination (%)	Balsam fir			$61.44^{Aa} \pm 24.95$	$55.70^{Aa} \pm 25.99$	$75.85^{Aa} \pm 10.95$	$8.59^{Ba} \pm 10.06$
	White spruce			$32.44^{Ab} \pm 12.46$	$33.69^{Ab} \pm 17.82$		
	Black spruce	$42.75^{A} \pm 17.5$	$48.8^{A} \pm 24.85$	$54.95^{Aa} \pm 26.61$	$28.67^{Bb} \pm 21.60$	$71.81^{Aa} \pm 7.83$	$38.78^{Bb} \pm 23.20$

Table 2.4. Results of correlation tests between cone production by balsam fir and black spruce and the different climate variables measured along the latitudinal gradient. Significant relationships ($p < 0.05$) in bold. Variables with _1 are for the year previous to cone production. GDD (growing degree-days), Tmaxwar (maximum temperature of the warmest month), Tmincol (minimum temperature of the coldest month), Ppwet (precipitation of the wettest month).

	GDD_1	GDD	Tmaxwar_1	Tmaxwar	Tmincol_1	Tmincol	Ppwet_1	Ppwet
Balsam fir	**0.3731**	-0.0548	**0.4723**	-0.2401	0.0919	0.1220	0.0980	-0.2500
Black spruce	0.2079	-0.0167	0.0938	0.0385	-0.0810	-0.0198	0.0922	-0.2635

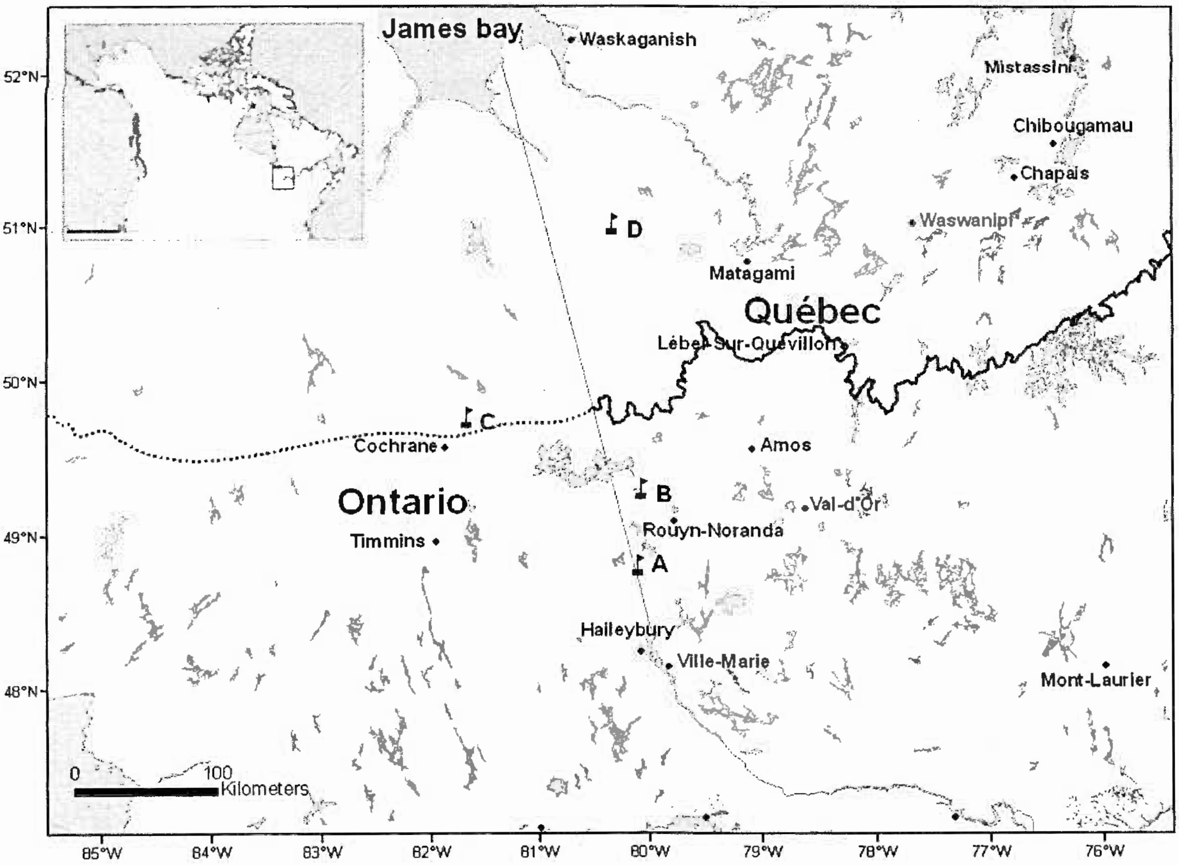

James bay
Waskaganish
Mistassini
Chibougamau
Chapais
Waswanipi
D
Matagami
Québec
Lebel-Sur-Quévillon
C
Cochrane
Amos
Ontario
B
Val-d'Or
Rouyn-Noranda
Timmins
A
Haileybury
Ville-Marie
Mont-Laurier
0
100
Kilometers
52°N
51°N
50°N
49°N
48°N
85°W
84°W
83°W
82°W
81°W
80°W
79°W
78°W
77°W
76°W

Fig. 2.1.

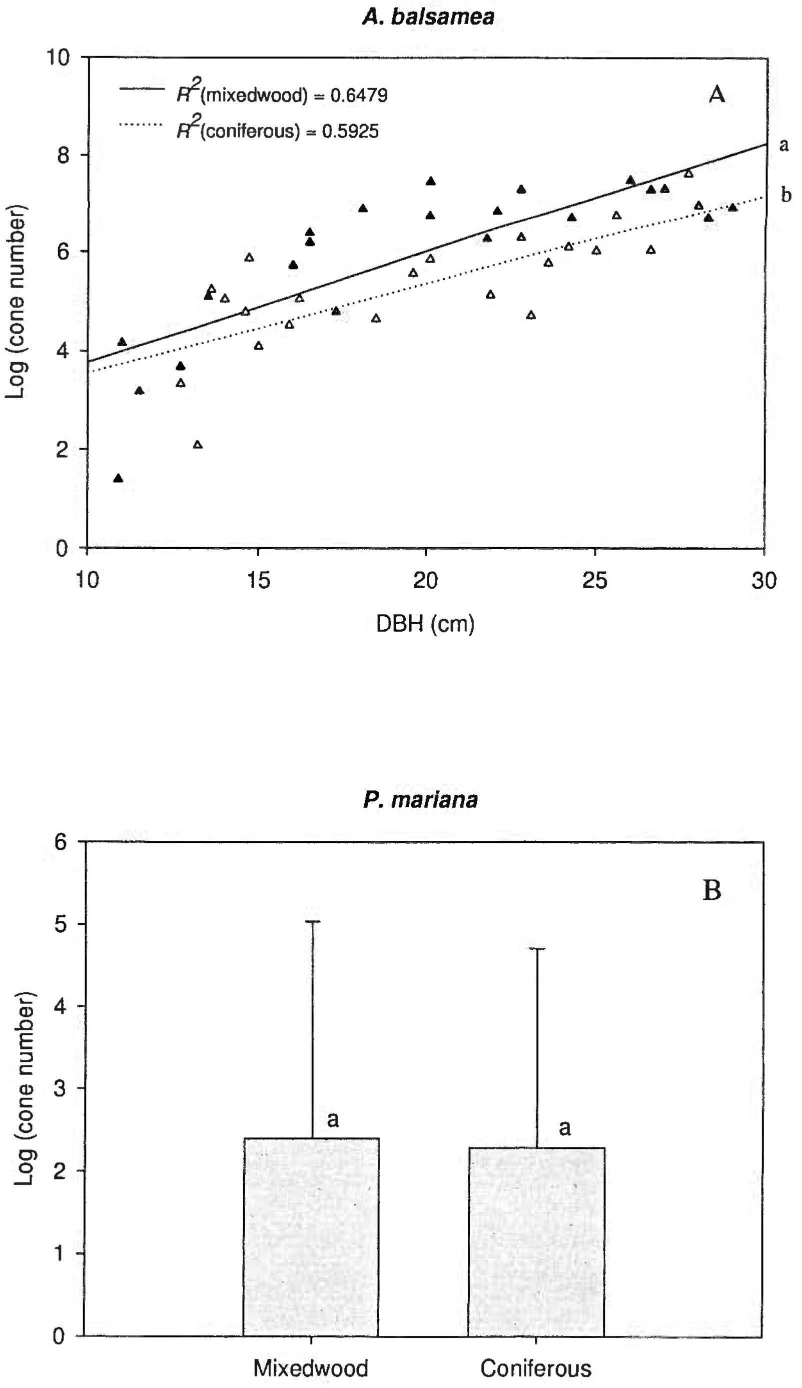

A. balsamea
10
8
6
4
2
0
Log (cone number)
R^2(mixedwood) = 0.6479
R^2(coniferous) = 0.5925
A
a
b
10
15
20
25
30
DBH (cm)
P. mariana
6
5
4
3
2
1
0
Log (cone number)
B
a
a
Mixedwood
Coniferous

Fig. 2.2.

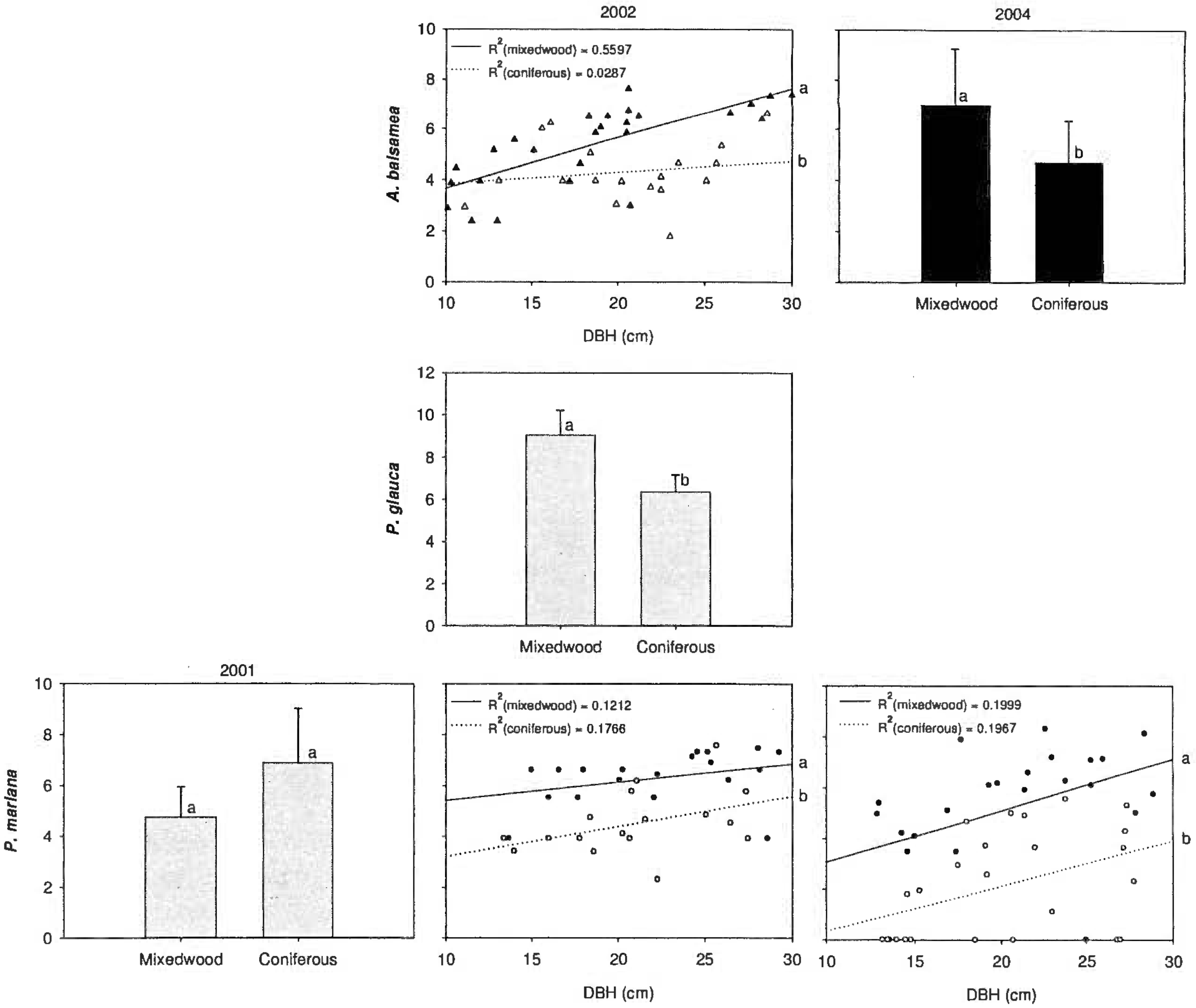

2002
R^2(mixedwood) = 0.5597
R^2(coniferous) = 0.0287
A. balsamea
10
8
6
4
2
0
a
b
10
15
20
25
30
DBH (cm)
2004
a
b
Mixedwood
Coniferous
P. glauca
12
10
8
6
4
2
0
a
b
Mixedwood
Coniferous
2001
P. mariana
10
8
6
4
2
0
a
a
Mixedwood
Coniferous
R^2(mixedwood) = 0.1212
R^2(coniferous) = 0.1766
a
b
10
15
20
25
30
DBH (cm)
R^2(mixedwood) = 0.1999
R^2(coniferous) = 0.1967
a
b
10
15
20
25
30
DBH (cm)

Fig. 2.3.

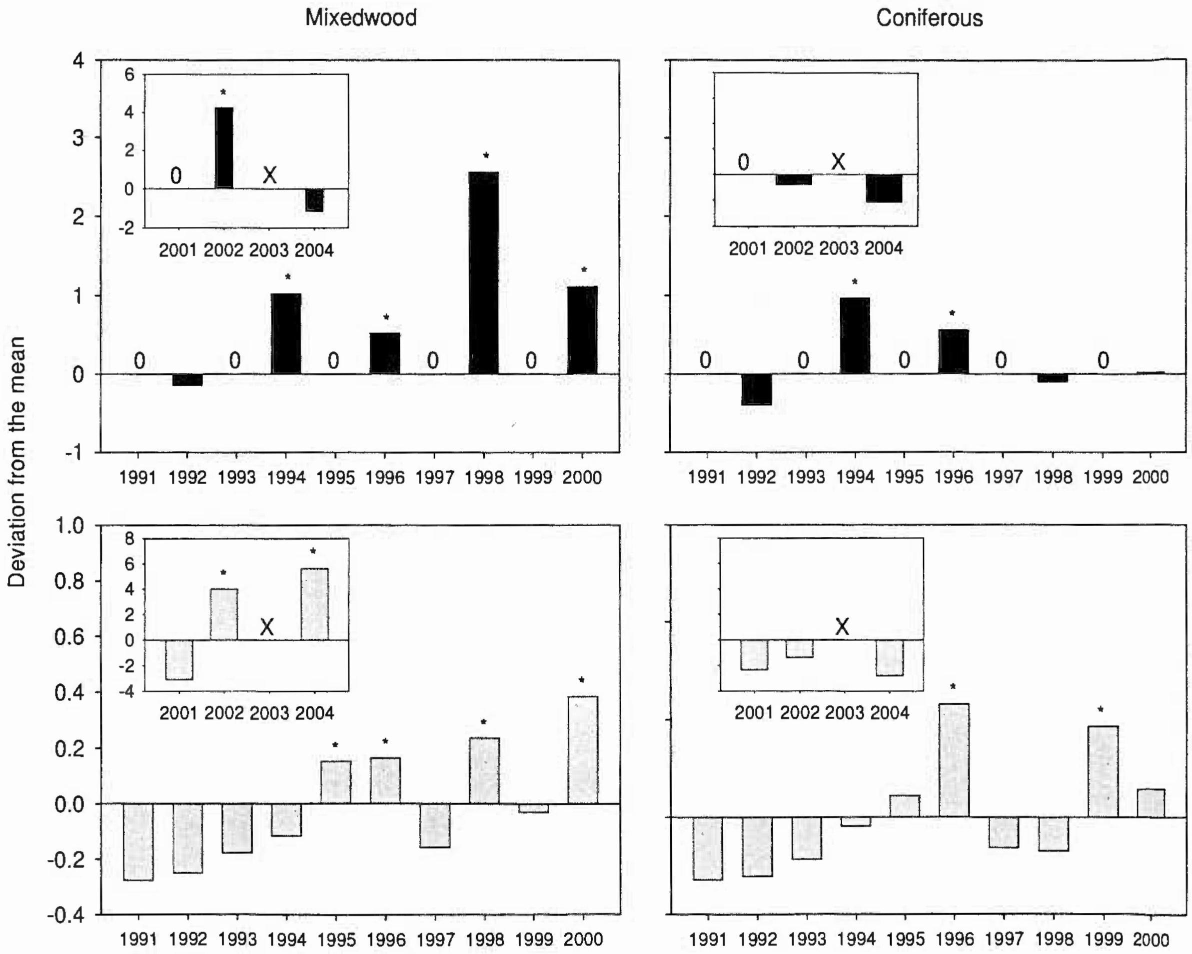
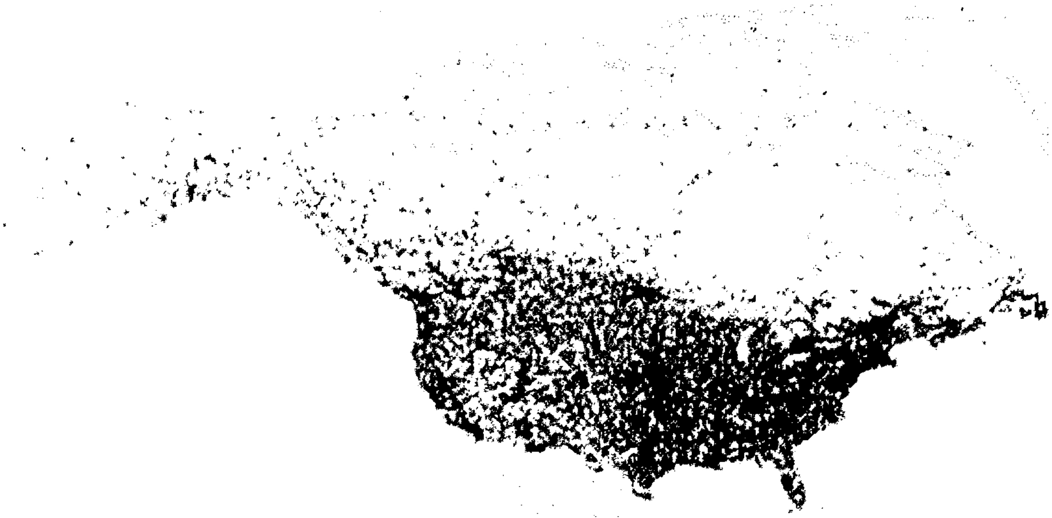

Mixedwood
Coniferous
Deviation from the mean
4
3
2
1
0
-1
6
4
2
0
-2
0
X
2001 2002 2003 2004
1991 1992 1993 1994 1995 1996 1997 1998 1999 2000
1.0
0.8
0.6
0.4
0.2
0.0
-0.2
-0.4
8
6
4
2
0
-2
-4

Fig. 2.4.



Appendix 2.1.

CHAPITRE III

Comparison of balsam fir (Abies balsamea L.) recruitment dynamics in the mixedwood and coniferous forests of the boreal zone of eastern North America

Messaoud, Y.[1,*]; Asselin, H. [1,2] & Bergeron, Y. [1,3]
[1]NSERC/UQAT/UQAM Industrial Chair in Sustainable Forest Management, Université du Québec en Abitibi-Témiscamingue, 445 boul. de l'Université, Rouyn-Noranda, QC, J9X 5E4;
[2]E-mail hugo.asselin@uqat.ca;
[3]E-mail yves.bergeron@uqat.ca;
*Corresponding author; E-mail yassine.messaoud@uqat.ca

Article soumis en 2007 dans Journal of Biogeography

3.1. Abstract

Aim The boreal zone of eastern North America is subdivided into two continuous forest types: the Abies balsamea (balsam fir)-dominated mixedwood forest and the Picea mariana (black spruce)-dominated coniferous forest. The goal of this study was to determine if the location of the ecotone between the two forest types (located ca 49° N) could be explained by a northward decrease in recruitment and increase in mortality rate of balsam fir, thus explaining the shift to black spruce dominance.

Location Northwestern Quebec and northeastern Ontario, Canada.

Methods Balsam fir regeneration and mature trees were sampled in four study sites located across the ecotone between the mixedwood and coniferous forests (between 48□ 01' and 50□ 13' N). Regeneration abundance and height, as well as abundance and basal area of mature trees, were sampled in 10 plots per site. In addition, data from 561 permanent samplings plots from the dendrometry inventory of the Quebec Ministry of Natural Resources distributed throughout the two forest types were used. ANOVAs and ANCOVAs were used to compare recruitment between the two forest types. Regressions of stem abundance against height were used to estimate initial recruitment and mortality rate.

Results Regeneration was less abundant (and therefore initial recruitment was lower) in coniferous compared to mixedwood forests. Furthermore, mortality rate was higher in coniferous compared to mixedwood forests. In addition, higher abundances of balsam fir saplings in coniferous forests were found on till deposits, compared to clay and sand.

Main conclusions The location of the boundary between mixedwood and coniferous forests can be attributed to lower initial recruitment and higher mortality rate of balsam fir in coniferous compared to mixedwood forests, most likely due to cooler temperatures and shorter growing seasons, with growth substrate probably playing only a marginal role.

Key words: *Abies balsamea*; boreal zone; coniferous forest; ecotone; initial recruitment; mixedwood forest; mortality rate.

3.3. Introduction

Species at their northern limit show higher sensitivity to climate conditions (Greenwood et al., 2002; Holtmeier et al., 2003) and the northern limit of a species' distribution is sensitive to minor changes in climate, which can induce a reduction of regeneration potential (Hobbie & Chapin, 1998; Kullman, 2002; Bigras et al., 2004; Norman & Taylor, 2005). Frost is known to kill or cause heavy damages to seedlings (Langvall & Örlander, 2001; Langvall et al., 2001), thus reducing establishment and survival.

Other climate-driven factors may hamper regeneration. Caspersen and Saprunoff (2005) mentioned that tree recruitment is limited both by seed supply and availability of suitable germination sites. At their northern distribution limit, species produce less viable seeds due to reduced occurrence of suitable climatic conditions (Pigott, 1992; Kullman, 1993; Garcia et al., 2000; Sirois, 2000; Tremblay et al., 2002). Furthermore, Schupp (1995) pointed out that ecological conditions favourable for seed germination might not necessarily be good for seedling survival. Indeed, soil fertility is lower in colder climates because low soil temperatures inhibit organic matter decomposition and decrease soil evaporation, therefore decreasing nutrient availability. Suitable germination and establishment sites are thus increasingly less frequent towards the northern limit of a species' distribution, hence limiting or delaying recruitment despite increased seed production due to climate warming (Suarez et al., 1999; Lloyd, 2005).

Numerous studies of species regeneration were conducted at the latitudinal and altitudinal tree lines (e.g. Payette et al., 1982; Morin & Payette, 1984; Kullman, 2001) in extreme environments characterized by harsh ecological conditions such as shallow soils and strong winds (Loehle, 2000). Such conditions are different from those encountered at ecotones located in less extreme areas such as between two forest types. Although some studies were conducted in forested areas where species reach their northern limit (Tremblay et al., 2002; Flannigan & Bergeron, 1998; Engelmark et al., 2000), few have concentrated on the dynamics of the ecotone between two forest types (Goldblum & Rigg, 2002), where a given species does not reach its distribution limit, but nevertheless decreases in abundance towards higher latitudes or altitudes.

This study aims to determine if a northward decrease of recruitment and increase of mortality rate of balsam fir (Abies balsamea L.) might explain the transition from the southern mixedwood forests (dominated by balsam fir) and the northern coniferous forests (dominated by black spruce (Picea mariana (Mill.) B.S.P.)) in the boreal zone of western Quebec and eastern Ontario. Although balsam fir populations are found in the coniferous forest, they are less abundant than in the mixedwood forest and fail to occupy all potentially suitable mesic sites (Messaoud et al., 2007a). Reduced balsam fir seed production towards the north was shown to be partly responsible for the location of the transition between mixedwood and coniferous forests (Messaoud et al., 2007b). The objective of the present study was to look at later life stages and determine if reduced recruitment and increased mortality rates of balsam fir in the coniferous forest compared to the mixedwood forest could also play a role in the location of the boundary between the two forest types. Balsam fir is less cold tolerant than black spruce (Bakusis & Hansen, 1965), thus the latter species benefits from a competitive advantage in coniferous forests. Hence, we expected lower initial recruitment and higher mortality rate for balsam fir in the coniferous forest, where climatic conditions favourable to seedling establishment and survival occur less often than in mixedwood forests.

3.4. Material and methods

3.4.1. Study area

The study area is located in northwestern Quebec and northeastern Ontario and is part of the Quebec and Ontario Clay Belt formed by lacustrine deposits left by proglacial lake Barlow-Ojibway (Veillette, 1994; Fig. 1A). In Quebec, the area is composed of two bioclimatic sub-domains characterized by different late-successional species on mesic sites: the southern Abies balsamea – Betula papyrifera bioclimatic sub-domain (herein called mixedwood forest) and the northern Picea mariana – mosses bioclimatic sub-domain (herein called coniferous forest) (Saucier et al., 1998). Although the classification system is different, it was possible to prolong the limit between the two vegetation zones in Ontario using the work of Mackey et al. (1996) and OMNR (2003). Trembling aspen (Populus tremuloides Michx.), paper birch (Betula papyrifera Marsh.) and jack pine (Pinus banksiana Lamb.) are abundant immediately after fire in both forest types. Altitude generally varies between 300 and 400 m a.s.l. and low hills are scattered in an otherwise flat landscape. Topography is more accentuated in the mixedwood than in the coniferous forest (Asselin, 1995; Gauthier et al., 2000).

Climate in the study area is continental, with cold winters and warm summers. Mean annual temperature in the mixedwood forest is 1.2 °C (Amos meteorological station – 48° 34' N; 78° 07' W; 310 m elevation). Mean temperature of the coldest (January) and warmest (July) months are 17.3 °C and 17.2 °C, respectively. Total annual precipitation is 918 mm, from which 248 falls as snow. In the coniferous forest, mean annual temperature is 0.7 °C (Matagami meteorological station – 49° 46' N; 77° 49' W; 281 m elevation). Mean temperature of the coldest (January) and warmest (July) months are 20.0 °C and 16.1 °C, respectively. Total annual precipitation is 906 mm, from which 314 falls as snow. There are 1400 and 1169 growing degree-days above 5 °C in the mixedwood and coniferous forests, respectively (Environment Canada, 2002).

Four sites were selected along a latitudinal gradient crossing the ecotone between the mixedwood and coniferous forests (Fig. 1A): Lake Montalais (48° 01' N, 79° 24' W; 302 m elevation), Lake Duparquet (48° 30' N, 79° 12' W; 291 m elevation), Cochrane (49° 13' N, 80° 39' W; 281 m elevation), and Maskouchis (50°13' N, 78° 44' W; 376 m elevation). Lakes Montalais and Duparquet are in the mixedwood forest, while Cochrane and Maskouchis are in the coniferous forest. All four sites have a moderate moisture regime (Brais & Camiré, 1998), but surface deposits vary: clay (fine subhydric; Lake Duparquet), till (medium mesic; Lake Montalais), and sand (coarse xeric; Cochrane and Maskouchis).

3.4.2. Sampling

3.4.2.1. Field data

Within each site, a 50 m x 5 m transect was set up and subdivided into ten adjacent 25 m2 quadrats. Small seedlings (< 15 cm high) were counted in four 1 m2 plots located at the corners of each quadrat. Tall seedlings (> 15 cm high and < 2 cm of diameter at breast height (DBH)) were counted and their height was measured in half of each quadrat. Saplings (2-10 cm DBH) were counted and their height was measured in each of the 10 quadrats. Finally, DBH and number of mature trees (> 10 cm DBH) were noted in all the quadrats. Abundance values were transformed in ln(stems/ha).

3.4.2.2. Archival data

In addition to field data, 561 permanent plots from the Quebec Ministry of Natural Resources (QMNR) were used (Fig. 1B). Saplings and mature balsam fir trees were counted and their DBH measured in each 400 m2 circular plot. Only plots located on clay, till, and sand were used, to ease comparisons with the four field sites. Furthermore, data from 5852 sampling plots from the QMNR ecological inventory were used to compare the distribution of surface deposits (clay, till and sand) in mixedwood and coniferous forests.

3.4.3. Statistical analyses

Comparisons of the number of stems for each regeneration class (small seedlings, tall seedlings, saplings) between the two forest types (mixedwood vs. coniferous) were made using analyses of variance (ANOVAs). Multiple comparisons between the two forest types were performed using Tukey's test. Analyses were performed using the SAS software (Cody & Smith, 1991).

Mortality rate and initial recruitment were assessed for each forest type using regressions of stem number against height. Height was used rather than age because: (1) it better represents the recruitment of new trees in the canopy and (2) age determination is complicated by the presence of missing rings (Parent et al., 2002). Such regressions usually follow either one of two models: a negative exponential function describing constant mortality, or a power function describing a higher mortality rate in earlier years (Hett & Loucks, 1976; Tardif et al., 1994):

$$\ln(\text{stem number}) = \ln(B) - b * \text{height} \text{ [negative exponential]}$$

$$\ln(\text{stem number}) = \ln(B) - b * \ln(\text{height}) \text{ [power function]}$$

where b is mortality rate and B is initial recruitment.

Analyses of covariance (ANCOVAs) were also conducted on the QMNR data set to evaluate the relationship between the abundance of balsam fir saplings and forest type, while accounting for surface deposit (covariable). A Chi-squared test was used to compare the distributions of surface deposits between the two forest types.

3.5. Results

3.5.1. Field data

Balsam fir regeneration was less abundant in coniferous than in mixedwood forests for all height classes, although the difference was not significant for tall seedlings (Table 1). The abundance of mature balsam fir trees and the proportion of larger trees did not significantly differ between forest types (Table 2).

Regressions of stem number against height were best fitted by the negative exponential model in the mixedwood forest (Fig. 2). In the coniferous forest, the power function model best fitted the data for individuals < 2 m high, while the negative exponential model showed a better fit for individuals > 2 m high (Fig. 2).

Initial recruitment (intercept of the linear regressions presented in Fig. 2) was higher in mixedwood than in coniferous forests ($p < 0.0001$) and mortality rate (slope of the regressions) was higher in coniferous than in mixedwood forests ($p < 0.0001$), whatever the chosen regression model.

3.5.2. Archival data

Forest type and surface deposit both had a significant effect on the abundance of balsam fir saplings, while the effect of the abundance of mature trees was not significant (Table 3). As with field data, balsam fir saplings were less abundant in the coniferous forest (ln(abundance) = 5.81 ± 2.01) than in the mixedwood forest (6.41 ± 0.91). Controlling for surface deposit, sapling abundance was significantly lower in coniferous forests only on fine subhydric (FS) and coarse xeric (CX) substrates (Table 4). Controlling for forest type, saplings were less abundant on coarse xeric than on fine subhydric or medium mesic substrates in the coniferous forest (Table 4). As was found in the field, the abundance of mature balsam fir trees and the proportion of larger trees did not significantly differ between forest types (Table 2).

3.6. Discussion

Balsam fir recruitment dynamics differed with respect to forest type. Lower initial recruitment and higher mortality rate were observed in coniferous forests compared to mixedwood forests.

3.6.1. Initial recruitment

The presence of nearby seed trees has frequently been mentioned as an important factor explaining regeneration abundance (Galipeau et al., 1997; Asselin et al., 2001; Albani et al., 2005). Our results show that basal area of mature trees did not significantly affect regeneration abundance. Balsam fir basal area was not significantly different in the mixedwood and coniferous forests (Table 2), and thus could not explain differences in regeneration abundance (Tables 1, 3 & 4). However, Messaoud et al. (2007b) showed that balsam fir trees of comparable basal area produced less seeds in coniferous than in mixedwood forests. Lower initial balsam fir recruitment in coniferous compared to mixedwood forests can thus be explained by reduced seed supply.

Another explanation for lower initial recruitment in coniferous forests could be the lack of suitable sites for germination and establishment at the local scale (Schupp, 1995; Weisberg & Baker, 1995; Chhin & Wang, 2002; Holtmeier et al., 2003; Houle & Filion, 2003). Balsam fir is more frequently found on mesic sites, which are more frequent in mixedwood forests (Fig. 3; Chi-squared; $p < 0.0001$). Nevertheless, the species can regenerate on many different substrates, as its large seeds provide enough nutrients and allow seedlings to rapidly grow tall (Simard et al., 1998). Consequently, the availability of suitable sites is not likely the most limiting factor for balsam fir recruitment in coniferous forests, as found by Messaoud et al. (2007a) who showed that balsam fir failed to occupy all potentially suitable (mesic) sites in the coniferous forest. Similar results were also obtained for other tree species in more limiting areas such as altitudinal or latitudinal tree lines (Sjögersten & Wookey, 2004, 2005).

3.6.2. Mortality rate

Balsam fir regeneration dynamics was best fitted by a negative exponential model in the mixedwood forest, suggesting constant mortality through time (Fig. 2). In the coniferous forest, a combination of power function model (for individuals < 2 m high) and negative exponential model (for individuals > 2 m high) suggested a higher mortality rate in earlier years, corroborating the findings of Hett and Loucks (1976).

Higher seedling mortality in the coniferous forest could be due to the sensitivity of balsam fir to temperature variations, as shown for other coniferous (Picea glauca in Dang and Cheng (2004)) or deciduous (Betula pubescens in Karlsson & Weih (2001)) tree species. While precipitation amounts are comparable in our study area for mixedwood and coniferous forests, mean annual temperature and number of growing degree-days above 5□ C are appreciably lower in the coniferous than in the mixedwood forest. According to Bakusis and Hansen (1965), balsam fir is less cold tolerant than black spruce, and this might partly explain the transition between mixedwood and coniferous forests.

Drought was shown to be responsible for high mortality rates in Picea glauca, Abies magnifica and Thuja occidentalis (Chappell & Agee, 1996; Hogg & Schwarz, 1997; Matthes & Larson, 2006). However, the probability of drought occurrence was lower in coniferous than in mixedwood forests because lower temperatures prevent high soil evaporation (Harte et al., 1995; Sjögersten & Wookey, 2004). Furthermore, small seedlings in both forest types were found under forest cover offering protection from dryness (Harmon, 1987; Breshears et al., 1998; Oleskog & Sahlen, 2000). Nevertheless, drought stress can affect balsam fir recruitment in extreme conditions, such as on coarse xeric substrates (Table 4), more frequent in the coniferous forest (Fig. 3).

3.6.3. Climate change and the transition between mixedwood and coniferous forests

The northern limit of balsam fir dominance (ca 49° N), and thus the transition between mixedwood and coniferous forests, can be linked to lower initial recruitment and higher mortality rate in the coniferous compared to the mixedwood forest. These two factors are most likely linked to cooler temperatures and shorter growing seasons in northern compared to southern sites and could explain why balsam fir fails to occupy all potentially suitable sites in the coniferous forest (Messaoud et al., 2007a). Nevertheless, the few balsam fir populations found in the coniferous forest appear to be able to persist for a long time in the absence of major disturbance (Sirois, 1997). Global warming is expected to favour seed supply (van der Meer et al., 2002), which could lead to increased balsam fir establishment in the vicinity of balsam fir stands in the coniferous forest. Indeed, Lloyd et al. (2003) and Gamache and Payette (2005) found that white and black spruce recently colonized well drained forest tundra sites in response to warmer climate conditions. Kullman (2001) also showed a rise of the tree limit in the Scandinavian mountains in response to recent climate warming. Such fast responses to a warmer climate were fostered by the species producing small seeds and the tundra sites being free of trees and readily colonisable. However, the invasion of new sites by balsam fir in the coniferous forest could be slower because its larger seeds travel less far (Young & Young, 1992; Asselin et al., 2001). Furthermore, in closed forests (compared to tundra), establishment could be slower due to competition with black spruce.

Acknowledgements: This project was financed by an NSERC discovery grant to Yves Bergeron. Alain Leduc, Natacha Roudeix, and Benoît St-Vincent provided help in the field and in the lab.

3.7. References

Albani, M., Andison, D. W. & Kimmins, J. P. (2005) Boreal mixedwood species composition in relationship to topography and white spruce seed dispersal constraint. Forest Ecology and Management, 209, 167-180.

Asselin, H., Fortin, M.-J. & Bergeron, Y. (2001) Spatial distribution of late-successional coniferous species regeneration following disturbance in southwestern Québec boreal forest. Forest Ecology and Management, 140, 29-37.

Asselin, M. (1995) L'Abitibi-Témiscamingue : trois sous-régions, une région. Histoire de l'Abitibi-Témiscamingue (ed. by O. Vincent), pp. 21-65. Collection Les régions du Québec, no. 7, Institut québécois de recherche sur la culture, Québec, Canada.

Bakusis, E. V. & Hansen, H. S. (1965) Balsam fir: a monographic review. The University of Minnesota Press, Minneapolis, USA.

Bigras, F. J., Coursolle, C. & Margolis, H. A. (2004) Survival and growth of Picea glauca seedlings as a function of freezing temperatures and exposure times during budbreak and shoot elongation. Scandinavian Journal of Forest Research, 19, 206-216.

Brais, S. & Camiré, C. (1998) Soil compaction induced by careful logging in the claybelt region of northwestern Quebec (Canada). Canadian Journal of Soil Science, 78, 197-206.

Breshears, D. D., Nyhan, J. W., Heil, C. E. & Wilcox, B. P. (1998) Effects of woody plants on microclimate in a semiarid woodland: soil temperature and evaporation in canopy and intercanopy patches. International Journal of Plant Sciences, 159, 1010–1017.

Burns, R. M. & Honkala, B. H. (1990) Silvics of North America: Vols. 1 and 2. USDA Forest Service, Agricultural Handbook 654.

Caspersen, J. P. & Saprunoff, M. (2005) Seedling recruitment in a northern temperate forest: the relative importance of supply and establishment limitation. Canadian Journal of Forest Research, 35, 978-989.

Chappell, C. B. & Agee, J. K. (1996) Fire severity and tree seedling establishment in Abies magnifica forests, southern Cascades, Oregon. Ecological Applications, 6, 628-640.

Chhin, S. & Wang, G. G. (2002) Spatial and temporal pattern of white spruce regeneration within mixed-grass prairies in the Spruce Woods Provincial Park of Manitoba. Journal of Biogeography, 29, 903-912.

Cody, R. P. & Smith, J. K. (1991) Applied statistics and the programming language. 4th ed. Prentice Hall, Upper Saddle River, New Jersey, USA.

Dang, Q.-L. & Cheng, S. (2004) Effects of soil temperature on ecophysiological traits in seedlings of four boreal tree species. Forest Ecology and Management, 194, 379-387.

Engelmark, O., Bergeron, Y. & Flannigan, M. D. (2000) Age structure of eastern white pine, Pinus strobus L., at its northern distribution limit in Québec. Canadian Field-Naturalist, 114, 601-604.

Environment Canada. (2002) Canadian climate normals 1971-2000. Atmospheric Environment Service, Environment Canada, Ottawa, Ontario, Canada.

Flannigan, M. D. & Bergeron, Y. (1998) Possible role of disturbance in shaping the northern distribution of Pinus resinosa. Journal of Vegetation Science, 9, 477-482.

Galipeau, C., Kneeshaw, D. & Bergeron, Y. (1997) White spruce and balsam fir colonization of a site in the southeastern boreal forest as observed 68 years after fire. Canadian Journal of Forest Research, 27, 139-147.

Gamache, I. & Payette, S. (2005) Latitudinal response of subarctic tree lines to recent climate change in eastern Canada. Journal of Biogeography, 32, 849-862.

Garcia, D., Zamora, R., Gomez, J. M., Jordano, P. & Hodar, J. A. (2000) Geographical variation in seed production, predation and abortion in Juniperus communis throughout its range in Europe. Journal of Ecology, 88, 436-446.

Gauthier, S., DeGrandpré, L. & Bergeron, Y. (2000) Differences in forest composition in two boreal forest ecoregions of Quebec. Journal of Vegetation Science, 11, 781-790.

Goldblum, D. & Rigg, L. S. (2002) Age structure and regeneration dynamics of sugar maple at the deciduous/boreal forest ecotone, Ontario, Canada. Physical Geography, 23, 115-129.

Greene, D. F. & Johnson, E. A. (1994) Estimating the mean annual seed production of trees. Ecology, 75, 642-647.

Greenwood, M. S., Livingston, W. H., Day, M. E., Kenaley, S. C., White, A. S. & Brissette, J. C. (2002) Contrasting modes of survival by jack and pitch pine at a common range limit. Canadian Journal of Forest Research, 32, 1662-1674.

Harmon, M. E. (1987) The influence of litter and humus accumulations and canopy openness on Picea sitchensis (Bong.) Carr. and Tsuga heterophylla (Raf.) Sarg. seedlings growing on logs. Canadian Journal of Forest Research, 17, 1475-1479.

Harte, J., Torn, M.S., Chang, F.-R., Feifarek, B., Kinzig, A.P., Shaw, R. & Shen K. (1995) Global warming and soil microclimate: results from a meadow-warming experiment. Ecological Applications, 5, 132-150.

Hett, J. M. & Loucks, O. L. (1976) Age structure models of balsam fir and eastern hemlock. Journal of Ecology, 64, 1029-1044.

Hobbie, S. E. & Chapin, F. S. (1998) An experimental test of limits to tree establishment in arctic tundra. Journal of Ecology, 86, 449-461.

Hogg, E. H. & Schwarz, A. G. (1997) Regeneration of planted conifers across climatic moisture gradients on the Canadian prairies: implications for distribution and climate change. Journal of Biogeography, 24, 527-534.

Holtmeier, F. K., Anschlag, K., Broll., G. & Müterthies, A. (2003) Regeneration of trees in the treeline ecotone: northern Finnish Lapland. Fennia, 181, 103-128.

Houle, G. & Filion, L. (2003) The effects of lichens on white spruce seedling establishment and juvenile growth in a spruce-lichen woodland of subarctic Québec. Écoscience, 10, 80-84.

Karlsson, P. S. & Weih, M. (2001) Soil temperatures near the distribution limit of the mountain birch (Betula pubescens ssp. czerepanovii): implications for seedling nitrogen economy and survival. Arctic, Antarctic, and Alpine Research, 33, 88-92.

Kullman, L. (1993) Tree limit dynamics of Betula pubescens ssp. tortuosa in relation to climate variability: evidence from central Sweden. Journal of Vegetation Science, 4, 765-772.

Kullman, L. (2001) 20th century climate warming and tree-limit rise in the southern scandes of Sweden. Ambio, 30, 72-80.

Kullman, L. (2002) Rapid recent range-margin rise of tree and shrub species in the Swedish Scandes. Journal of Ecology, 90, 68-77.

Langvall, O. & Örlander, G. (2001) Effects of pine shelterwoods on microclimate and frost damage to Norway spruce seedlings. Canadian Journal of Forest Research, 31, 155-164.

Langvall, O., Nilsson, U. & Örlander, G. (2001) Frost damage to planted Norway spruce seedlings-influence of site preparation and seedling type. Forest Ecology and Management, 141, 223-235.

Lloyd, A. H. (2005) Ecological histories from Alaskan tree lines provide insight into future change. Ecology, 86, 1687-1695.

Lloyd, A. H., Rupp, T. S., Fastie, C. L. & Starfield, A. M. (2003) Patterns and dynamics of treeline advance on the Seward Peninsula Alaska. Journal of Geophysical Research, 108, doi:10.1029/2001JD000852, 15 p.

Loehle, C. (2000) Forest ecotone response to climate change: sensitivity to temperature response functional forms. Canadian Journal of Forest Research, 30, 1632-1645.

Mackey, B. G., McKenney, D. W., Yang, Y.-Q., McMahon, J.P. & Hutchinson, M. F. (1996) Site regions revisited: a climatic analysis of Hills' site regions for the province of Ontario using a parametric method. Canadian Journal of Forest Research, 26, 333-354.

Marie-Victorin, frère. (1995) Flore laurentienne, 3e édition mise à jour et annotée. Presses de l'Université de Montréal, Montréal, Québec, Canada.

Matthes, U. & Larson, D.W. (2006) Microsite and climatic controls of tree population dynamics: an 18-year study on cliffs. Journal of Ecology, 94, 402-414.

Messaoud, Y., Bergeron, Y. & Leduc, A. (2007a) Ecological factors explaining the location of the boundary between the mixedwood and coniferous bioclimatic zones in the boreal biome of eastern North America. Global Ecology and Biogeography, 16, 90-102.

Messaoud, Y., Bergeron, Y. & Asselin, H. (2007b) Reproductive potential of balsam fir (Abies balsamea), white spruce (Picea glauca), and black spruce (P. mariana) at the ecotone between mixedwood and coniferous forests in the boreal zone of western Quebec. American Journal of Botany, 94, 746-754.

Morin, A. & Payette, S. (1984) Expansion récente du mélèze à la limite des forêts (Québec nordique). Canadian Journal of Botany, 62, 1404-1408.

Norman, S. P. & Taylor, A. H. (2005) Pine forest expansion along a forest-meadow ecotone in northeastern California, USA. Forest Ecology and Management, 215, 51-68.

Oleskog, G. & Sahlen, K. (2000) Effects of seedbed substrate on moisture conditions and germination of Pinus sylvestris seeds in a clearcut. Scandinavian Journal of Forest Research, 15, 225-236.

OMNR. (2003) Silviculture guide to managing spruce, fir, birch, and aspen mixedwoods in Ontario's boreal forest. Version 1.0. Ontario Ministry of Natural Resources, Queen's Printer for Ontario.

Parent, S., Morin, H. & Messier, C. (2002) Missing growth rings at the trunk base in suppressed balsam fir saplings. Canadian Journal of Forest Research, 32, 1776-1783.

Payette, S., Deshaye, J. & Gilbert, H. (1982) Tree seed populations at the treeline in Rivière aux Feuilles area, northern Quebec, Canada. Arctic and Alpine Research, 14, 215-221.

Pigott, C. D. (1992) Are the distributions of species determined by failure to set seed? Fruit and seed production: aspects of development, enviromental physiology and ecology (ed. by C. Marshall & J. Grace), pp. 203–216. Cambridge University Press, Cambridge, UK.

Saucier, J.-P., Grondin, P., Robitaille, A. & Bergeron, J.-F. (1998) Les zones de végétation et les domaines bioclimatiques du Québec. Comité sur la carte des régions écologiques (3e version). Gouvernement du Québec, Québec, Canada.

Schupp E. W. (1995) Seed-seedling conflicts, habitat choice, and patterns of plant recruitment. American Journal of Botany, 82, 399-409.

Simard, M.-J., Bergeron, Y. & Sirois, L. (1998) Conifer seedling recruitment in a southeastern Canadian boreal forest: the importance of substrate. Journal of Vegetation Science, 9, 575-582.

Sirois, L. (1997) Distribution and dynamics of balsam fir (Abies balsamea (L.) Mill.) at its northern limit in the James Bay area. Écoscience, 4, 340-352.

Sirois, L. (2000) Spatiotemporal variation in black spruce cone and seed crops along a boreal forest – tree line transect. Canadian Journal of Forest Research, 30, 900-909.

Sjögersten, S. & Wookey, P. A. (2004) Decomposition of mountain birch leaf litter at the forest-tundra ecotone in the Fennoscandian mountains in relation to climate and soil conditions. Plant and Soil, 262, 215-227.

Sjögersten, S. & Wookey, P. A. (2005) The role of soil organic matter quality and physical environment for nitrogen mineralization at the forest-tundra ecotone in Fennoscandia. Arctic, Antarctic, and Alpine Research, 37, 118-126.

Suarez, F., Binkley, D. & Kaye, M. W. (1999) Expansion of forest stands into tundra in the Noatak National preserve, northwest Alaska. Écoscience, 6, 465-470.

Tardif, J., Dery, S. & Bergeron, Y. (1994) Sexual regeneration of black ash (Fraxinus nigra Marsh.) in a boreal floodplain. American Midland Naturalist, 132, 124-135.

Tremblay, M. F., Bergeron, Y., Lalonde, D. & Mauffette, Y. (2002) The potential effects of sexual reproduction and seedling recruitment on the maintenance of red maple (Acer rubrum L.) populations at the northern limit of the species range. Journal of Biogeography, 29, 365-373.

Van der Meer, P. J., Jorritsma, I. & Kramer, K. (2002) Assessing climate change effects on long-term forest development: adjusting growth, phenology, and seed production in a gap model. Forest Ecology and Management, 162, 39-52.

Veillette, J. J. (1994) Evolution and paleohydrology of glacial lakes Barlow and Ojibway. Quaternary Science Reviews, 13, 945-971.

Weisberg, P. J. & Baker, W. L. (1995) Spatial variation in tree seedling and krummholz growth in the forest-tundra ecotone of Rocky Mountain National Park, Colorado, USA. Arctic and Alpine Research, 27, 116-129.

Young, J. A. & Young, C. G. (1992) Seeds of woody plants in North America. Timber Press, Portland, Oregon, USA.

3.8. Table captions

Table 3.1. Number of balsam fir individuals per hectare (ln-transformed) for each regeneration stage and for each forest type with standard deviation from the mean. The letters at right of each number indicate similar (same letter) or different (different letters) values for the two forest types (Tukey test, $\alpha = 0.05$).

Table 3.2. Comparison of mixedwood and coniferous forests for basal area of mature balsam fir trees (with standard deviation from the mean), percentage of total basal area attributable to balsam fir, number of mature balsam fir trees per hectare, and percentage of mature balsam fir trees with DBH > 20 cm. The letters at right of each number indicate similar (same letter) or different (different letters) values for the two forest types (Tukey test, $\alpha = 0.05$).

Table 3.3. Results of the ANCOVAs for the relationship between sapling abundance (stems/ha), basal area of mature trees (m2/ha), and surface deposit (covariable) using archival data.

Table 3.4. Comparison of sapling abundance between the two forests types on each surface deposit. FS = fine subhydric (clay), MM = medium mesic (till) and CX = coarse xeric (sand). The letters at right of each number indicate similar (same letter) or different (different letters) values for the two forest types (Tukey test, $\alpha = 0.05$). Capital letters indicate comparisons between forest types and lower case letters indicate comparisons between surface deposits for each forest type.

3.9. Biosketches

Yassine Messaoud is a PhD student in environmental sciences at Université du Québec en Abitibi-Témiscamingue (UQAT), Canada.

Hugo Asselin is a postdoctoral fellow at UQAT. His research interests are in forest ecology, palaeoecology, and aboriginal forestry.

Yves Bergeron is professor of forest ecology and management at UQAT. He is interested in forest dynamics at the stand and landscape scales.

3.10. Figure captions

Figure 3.1. (A) Map of the study area showing the four sites sampled in the field (black triangles: A: lake Montalais, B: lake Duparquet, C: Cochrane, D: Maskouchis). Also shown are the limits between mixedwood and coniferous forests in western Québec (red line, after Saucier et al. (1998)) and in northeastern Ontario (approximate, after Mackey et al. (1996) and OMNR (2003)). (B) Quebec side of the study area showing the location of the 561 permanent plots from the Quebec Ministry of Natural Resources used as archival data in this study.

Figure 3.2. Regressions of stem number against height for the mixedwood and coniferous forests according to the exponential negative function (upper panels) and power function (lower panels).

Figure 3.3. Percentage of the different surface deposits in each forest type. FS = fine subhydric (clay), MM = middle mesic (till) and CX = coarse xeric (sand).

Table 3.1. Number of balsam fir individuals per hectare (ln-transformed) for each regeneration stage and for each forest type with standard deviation from the mean. The letters at right of each number indicate similar (same letter) or different (different letters) values for the two forest types (Tukey test, $\alpha = 0.05$).

	Mixedwood forest	Coniferous forest
Small seedlings	$8.00^{a} \pm 1.094$	$6.76^{b} \pm 0.93$
Tall seedlings	$7.51^{a} \pm 2.63$	$7.28^{a} \pm 3.34$
Saplings	$7.54^{a} \pm 0.71$	$2.76^{b} \pm 3.49$

Table 3.2. Comparison of mixedwood and coniferous forests for basal area of mature balsam fir trees (with standard deviation from the mean), percentage of total basal area attributable to balsam fir, number of mature balsam fir trees per hectare, and percentage of mature balsam fir trees with DBH > 20 cm. The letters at right of each number indicate similar (same letter) or different (different letters) values for the two forest types (Tukey test, $\alpha = 0.05$).

		Forest type	
		Mixedwood	Coniferous
Field data	Basal area of mature balsam fir trees (m^2/ha)	0.66^{a} (1.61)	4.15^{a} (8.26)
	Percentage of the total basal area attributable to balsam fir	39.76	41.67
	Number of mature balsam fir trees/ha	760^{a}	1280^{a}
	Percentage of mature balsam fir trees/ha with DBH > 20 cm	5	37
Archival data	Basal area of mature balsam fir trees (m^2/ha)	5.56^{a} (13.32)	4.33^{a} (10.84)
	Percentage of the total basal area attributable to balsam fir	26.02	21.57
	Average number of mature balsam fir trees/ha	191^{a}	173^{a}
	Percentage of mature balsam fir trees/ha with DBH > 20 cm	36	1.73

Table 3.3. Results of the ANCOVAs for the relationship between sapling abundance (stems/ha), basal area of mature trees (m2/ha), and surface deposit (covariable) using archival data.

Statistic	
N (field + archive data)	601
Basal area of mature balsam fir trees	N.S.
Surface deposit	**< 0.0001**
Forest type	**< 0.0001**
Surface deposit*Forest type	**< 0.0001**

Table 3.4. Comparison of sapling abundance between the two forests types on each surface deposit. FS = fine subhydric (clay), MM = medium mesic (till) and CX = coarse xeric (sand). The letters at right of each number indicate similar (same letter) or different (different letters) values for the two forest types (Tukey test, $\alpha = 0.05$). Capital letters indicate comparisons between forest types and lower case letters indicate comparisons between surface deposits for each forest type.

Surface deposits	FS		MM		CX	
Forest types	Mixedwood	Coniferous	Mixedwood	Coniferous	Mixedwood	Coniferous
Saplings (ln(stems/ha))	$6.62^{Aa} \pm 0.93$	$6.08^{Ba} \pm 0.93$	$6.40^{Aa} \pm 1.01$	$6.41^{Aa} \pm 0.90$	$6.32^{Aa} \pm 0.93$	$3.63^{Bb} \pm 3.35$

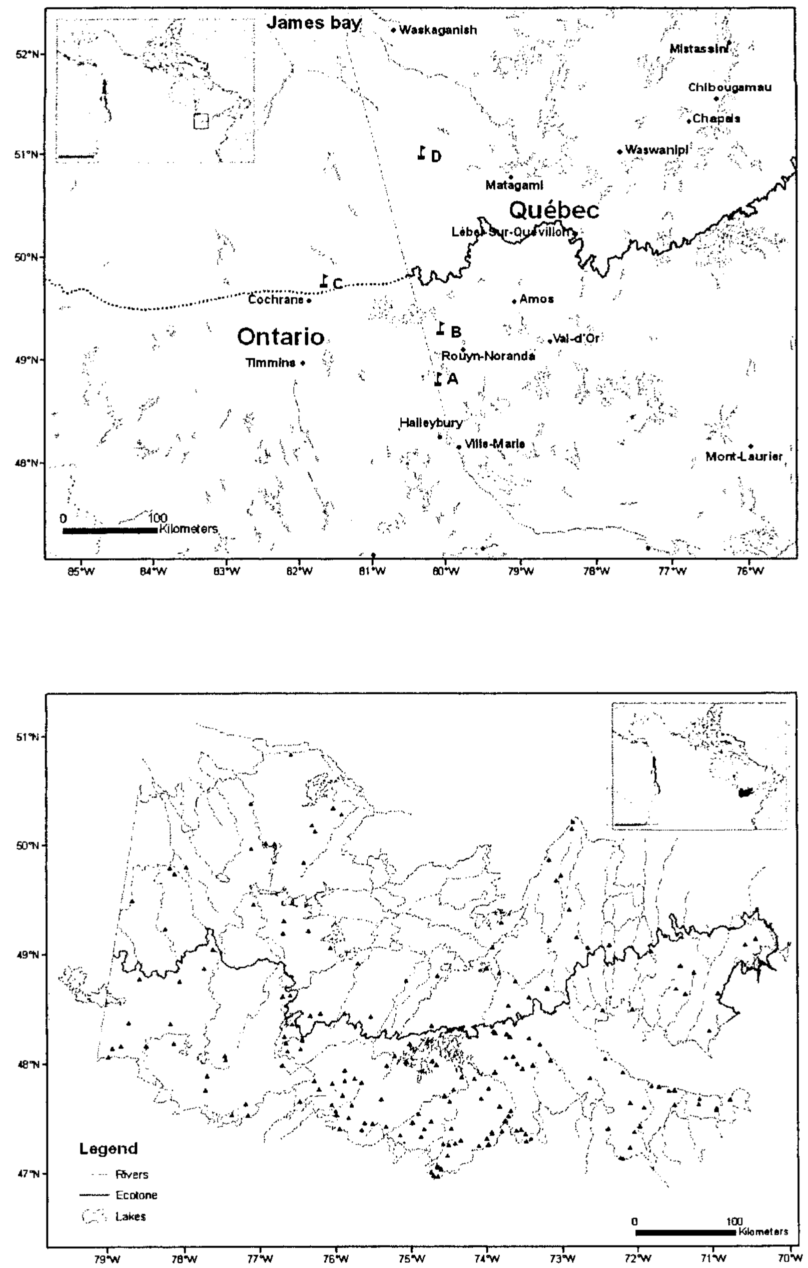

James bay
Waskaganish
Mistassini
Chibougamau
Chapais
Waswanipi
D
Matagami
Québec
Lebel-sur-Quévillon
C
Cochrane
Amos
Ontario
B
Val-d'Or
Rouyn-Noranda
Timmins
A
Haileybury
Ville-Marie
Mont-Laurier
0
100
Kilometers
52°N
51°N
50°N
49°N
48°N
85°W
84°W
83°W
82°W
81°W
80°W
79°W
78°W
77°W
76°W
Legend
Rivers
Ecotone
Lakes
0
100
Kilometers
51°N
50°N
49°N
48°N
47°N
79°W
78°W
77°W
76°W
75°W
74°W
73°W
72°W
71°W
70°W

Fig. 3.1.

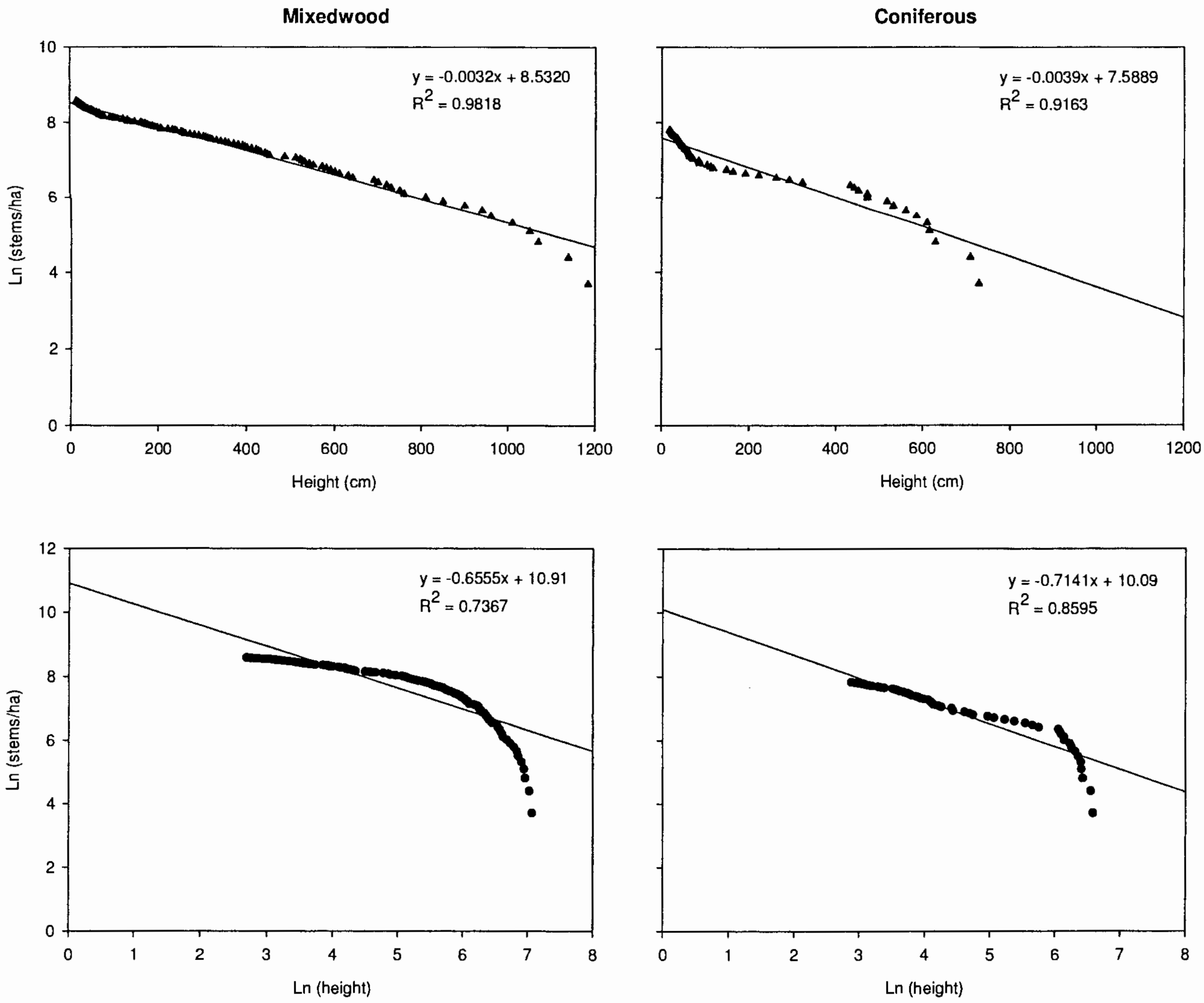

Mixedwood
Coniferous
y = -0.0032x + 8.5320
R2 = 0.9818
y = -0.0039x + 7.5889
R2 = 0.9163
Ln (stems/ha)
Height (cm)
0
200
400
600
800
1000
1200
0
2
4
6
8
10
y = -0.6555x + 10.91
R2 = 0.7367
y = -0.7141x + 10.09
R2 = 0.8595
Ln (height)
0
1
2
3
4
5
6
7
8
12

Fig. 3.2.

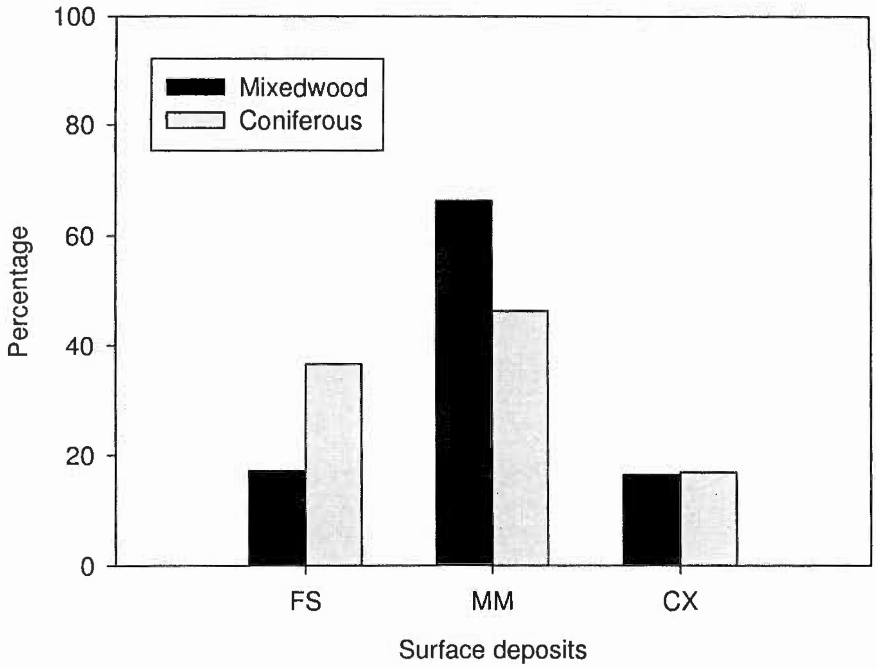

100
80
60
40
20
0
Percentage
Mixedwood
Coniferous
FS
MM
CX
Surface deposits

Fig. 3.3.

CHAPITRE IV

Comparison of balsam fir (Abies balsamea), white spruce (Picea glauca) and black spruce (P. mariana) site index values in mixedwood and coniferous forests of the boreal zone of western Québec

Yassine Messaoud1*, Hugo Asselin[1], Yves Bergeron[1] and Pierre Grondin[2]

[1]NSERC/UQAT/UQAM Industrial Chair in sustainable forest management, Université du Québec en Abitibi-Témiscamingue, 445 boul. de l'Université, Rouyn-Noranda, QC, J9X 5E4.

[2]Direction de la recherche forestière, Ministère des Ressources naturelles et de la Faune, 2700 rue Einstein, Sainte-Foy, QC, G1P 3W8.

* Corresponding author; E-mail yassine.messaoud@uqat.ca

Article soumis en 2007 dans Canadian Journal of Forest Research

4.1. Abstract

Site index of balsam fir and white spruce (co-dominants in mixedwood forests) and black spruce (dominant in coniferous forests) were studied in an attempt to explain the location of the boundary between these two bioclimatic domains of the boreal zone of Québec. A northward decrease of site index values was expected to occur for all species, but to be more evident for mixedwood species, thus conferring a competitive advantage to black spruce in the coniferous forest. Site index values were lower in coniferous than in mixedwood forests for all species, but the difference was only significant for black spruce. Furthermore inter-species comparisons showed that black spruce had the lowest site index values in both bioclimatic domains and on all site types. Therefore, black spruce does not benefit from a competitive height growth advantage over mixedwood species in the coniferous forest and the explanation for the location of the boundary between mixedwood and coniferous forests should be sought elsewhere.

Keywords: Boreal zone; mixedwood forest; coniferous forest; site index; height growth; Abies balsamea; Picea glauca; Picea mariana.

4.2. Résumé

L'indice de qualité de station (IQS) du sapin baumier et de l'épinette blanche (co-dominants dans la forêt mixte) et de l'épinette noire (dominante dans la forêt coniférienne) a été étudié dans le but d'expliquer la localisation de la frontière entre ces deux domaines bioclimatiques de la zone boréale du Québec. L'hypothèse à l'étude était qu'une diminution vers le nord de l'IQS serait observée chez toutes les espèces, mais de façon plus marquée pour les espèces de la forêt mixte, conférant ainsi un avantage compétitif à l'épinette noire dans la forêt coniférienne. L'IQS était plus faible dans la forêt coniférienne que dans la forêt mixte pour toutes les espèces, mais la différence était significative seulement pour l'épinette noire. De plus, des comparaisons interspécifiques ont montré que l'épinette noire avait les plus faibles valeurs d'IQS dans les deux domaines bioclimatiques et sur tous les types de sols. Ainsi, l'épinette noire ne bénéficie pas d'un avantage compétitif relié à une meilleure croissance en hauteur dans la forêt coniférienne et l'explication de la localisation de la frontière entre les forêts mixte et coniférienne devrait être cherchée ailleurs.

Mots clés: Zone boréale; Forêt mixte; Forêt coniférienne; Indice de qualité de station (IQS); croissance en hauteur; Abies balsamea; Picea glauca; Picea mariana.

4.3. Introduction

Black spruce (*Picea mariana*), balsam fir (*Abies balsamea*) and white spruce (*Picea glauca*) are the most widespread late-successional dominant coniferous tree species in the boreal zone of eastern North America (Burns and Honkala, 1990). Two bioclimatic domains occur in the boreal zone, differentiated by their dominant late-successional species (Saucier et al., 1998). Balsam fir and white spruce dominate in the southern part of the zone, hereafter called the mixedwood forest because paper birch (Betula papyrifera) is the main companion species. Black spruce dominates in the northern part of the boreal zone, hereafter called the coniferous forest. North of the limit between mixedwood and coniferous forests, balsam fir and white spruce are less abundant and their populations are more scattered (Messaoud et al., 2007a). This suggests that these species might be less competitive than black spruce in the coniferous forest, and this could contribute to the explanation of the location of the boundary between the two bioclimatic domains (Larsen, 1980; Arris and Eagleton, 1989).

Most research on long-term tree growth trends involves radial growth, and height growth has been given less attention (Goelz and Burk, 1998). Climate is responsible for slow shoot growth of stunted trees at the arctic and alpine tree lines, where extreme conditions prevail (Kullman, 1990; Payette et al., 1994; Payette and Delwaide, 1994). Niveo-aeolian erosion and desiccation of supranival shoots slow tree growth at the tree line (Hadley and Smith, 1983, 1989). The 20th century climate change (increase of growing degree-days in summer and higher snow cover in winter) results in increased shoot elongation (Hofgaard et al., 1991; Gamache et Payette, 2004). In the boreal forest, where height growth is not hampered by erosion and where species have an arboreal growth form, the site index has been widely used to evaluate forest productivity. The site index is a measure of the height of dominant and codominant trees at a reference age, usually 50 years (Klinka et al., 1996; Nigh et al., 2004; Wang, 2004). Site index and height growth are strongly influenced by climate conditions and site quality (nutrients and moisture availability) (Béland and Bergeron, 1996; Klinka et al., 1996; Chen et al., 2002; Nigh et al., 2004; Wang et al., 2004). Therefore, a higher site index indicates better growth conditions (Wang and Huang, 2000). Site index values of many species decrease with increasing latitude or altitude (Klinka et al., 1996; Wang et al., 2004) and species reaching their distribution limit usually perform less than the dominant species in the area (Klinka et al., 1996).

In this study we compared site index values of the dominant and codominant species of the mixedwood (balsam fir and white spruce) and coniferous (black spruce) forests of the boreal zone in an attempt to explain the position of the boundary between the two bioclimatic domains. We expected a northward decrease of site index values, more evident for balsam fir and white spruce than for black spruce, thus conferring a competitive advantage to black spruce over balsam fir and white spruce in the coniferous compared to the mixedwood forest.

4.4. Material and methods

4.4.1. Study area

The study area is located in northwestern Québec and northeastern Ontario (Fig. 1), and is part of the Québec and Ontario Clay Belt formed by deposits left by proglacial lake Barlow-Ojibway (Veillette, 1994). Trembling aspen (Populus tremuloides), paper birch, and jack pine (Pinus banksiana) are abundant immediately after fire in mixedwood and coniferous forests. Low hills are scattered in an otherwise flat landscape and topography is more accentuated in the mixedwood than in the coniferous forest (Asselin, 1995).

The climate of the study area is continental, with cold winters and warm summers. Mean annual temperature in the mixedwood forest is 1.2 °C (Amos meteorological station – 48° 34' N; 78° 07' W; 310 m elevation). Mean temperature of the coldest (January) and warmest (July) months are -17.3 °C and 17.2 °C, respectively. Mean annual precipitation is 918 mm, from which 248 falls as snow. There are 1400 growing degree-days above 5 °C. In the coniferous forest, the mean annual temperature is -0.7 °C (Matagami meteorological station – 49° 46' N; 77° 49' W; 281 m elevation). Mean temperature of the coldest (January) and warmest (July) months are -20.0 °C and 16.1 °C, respectively. Mean annual precipitation is 906 mm, from which 314 falls as snow. There are 1169 growing degree-days above 5 °C (Environment Canada, 2002).

4.4.2. Sampling

Four sites were selected along a latitudinal gradient crossing the ecotone between mixedwood and coniferous forests (Fig. 1): Lake Montalais (48° 01' N, 79° 24' W; 302 m elevation), Lake Duparquet (48° 30' N, 79° 12' W; 291 m elevation), Cochrane (49° 13' N, 80° 39' W; 281 m elevation), and Muskuchii (50°13' N, 78° 44' W; 376 m elevation). Lakes Montalais and Duparquet are in the mixedwood forest, while Cochrane and Muskuchii are in the coniferous forest. All four sites have a moderate moisture regime (Brais and Camiré, 1998), but surface deposits vary: clay (Lake Duparquet), till (Lake Montalais), and sand (Cochrane and Muskuchii).

Nine dominant and codominant trees of each species (balsam fir, white spruce, black spruce) without major defects were measured (total height) and cut at each site. Each tree was subsampled for stem analysis (Zarnovican 1985) by taking discs of the main stem at 0.0 (base), 0.4, 1.0, 1.3, 2.0 m, and at each meter until stem diameter was ≤ 2 cm. All discs were sanded before growth rings were counted under a dissecting microscope.

Site index (SI), corresponding to the height of a tree at a given age of free height growth (Chen et al., 1998), was determined by stem analysis. The tree with the shortest period of free height growth (25 years) – a balsam fir sampled at the Muskuchii site (Appendix) – was taken as a reference to estimate SI, which therefore represents tree height 25 years after the suppression period.

Furthermore, potential site index data from 221 sites sampled by the Ministère des Ressources naturelles et de la Faune du Québec (Grondin et al., 2000) were used to compare species performance between the two bioclimatic domains (Fig. 1). The potential site index corresponds to the site index that would be obtained for a three at a particular site if periods of "abnormally" slow growth were replaced by periods of "normal" growth. For shade-tolerant species such as those considered in this study, periods of slow growth generally correspond to suppression during the seedling and sapling years, when the individual grows below a canopy of older trees, or to episodes of defoliation due to insect outbreaks. The potential site index at 50 years (PSI) was calculated using the Chapman-Richards model function, which allows to remove suppression periods due to subcanopy growth when individuals are shorter than 1.3 m and defoliation by pest insects or other local disturbances later on (Richards, 1959; Chen et al., 1998, Grondin et al., 2000). The plots were distributed among three site types characterized by texture and drainage regime: fine subhydric (FS), medium mesic (MM) and coarse xeric (CX).

4.4.3. Statistical analyses

Analyses of variance (ANOVA) and Tukey's comparison tests were conducted using the SAS software (Cody and Smith, 1991) to compare age, DBH, height and site index values between bioclimatic domains, between species and between site types.

4.5. Results

4.5.1. Comparisons between bioclimatic domains

Mean age and DBH of the sampled trees were generally not significantly different between bioclimatic domains, although white spruce trees from the sites sampled in this study were slightly older in coniferous than in mixedwood forests (Table 1). Mean height and site index (SI) or potential site index (PSI) values were generally lower in the coniferous than in the mixedwood forests for the three species considered, although the differences were only significant for black spruce (Table 1). Whereas PSI values for black spruce did not significantly differ between bioclimatic domains when considering site type, balsam fir and white spruce showed lower PSI values in coniferous forests on fine subhydric (FS) deposits (Table 2).

4.5.2. Comparisons between species

Black spruce trees were older and white spruce trees had higher DBH than the other species, both in mixedwoods and coniferous forests (Table 1). Depending which dataset was considered, mean height either did not vary between species or showed a gradation from shorter balsam fir trees to taller white spruce trees, with black spruce showing intermediate values. SI and PSI values were lower for black spruce than for balsam fir and white spruce in both bioclimatic domains (Table 1), and whatever the site type considered (Table 2).

4.6. Discussion

Site index values were lower in coniferous than in mixedwood forests for all species, but the difference was only significant for black spruce. Furthermore inter-species comparisons showed that black spruce had the lowest SI and PSI values in both forest types and on all site types. Indeed, although balsam fir and white spruce PSI values on FS sites were significantly lower in coniferous compared to mixedwood forests (Table 2), the difference did not suffice to confer a competitive advantage to black spruce. Although site type has been shown to affect tree growth (Béland and Bergeron, 1996; Martin and Gower, 2006), our results thus suggest that responses are similar among boreal tree species. Interspecies differences in growth response to site type are probably more important when early development stages are considered (Messaoud et al. submitted).

A northward decrease of site index values was already observed for several boreal tree species, and mostly related to climatic factors (Ung et al., 2001; Hamel et al., 2004). Again, however, the same trend is common to most species and interspecific competition was shown not to affect height growth (Longpré et al., 1994). Because most widely-distributed boreal tree species show erected growth forms up to their northern distribution limit (Payette, 1993; Sirois, 1997; Flannigan and Bergeron, 1998; Engelmark et al., 2000; Asselin et al., 2003), factors affecting seed production and seedling recruitment probably play a more important role in explaining distribution limits or boundaries between bioclimatic domains (Henttonen et al., 1986; Pigott, 1992; Houle and Filion, 1993; Barras and Kellman, 1998; Hobbie and Chapin, 1998; Sirois, 2000; Tremblay et al. 2002; Messaoud et al., 2007b).

4.7. Conclusion

The location of the ecotone between mixedwood and coniferous forests does not appear to be linked to a faster northward decrease of balsam fir and white spruce site index values compared to black spruce. Since mixedwood species fail to occupy all potentially favourable sites in the coniferous forest (Messaoud et al., 2007a), the explanation for the location of the ecotone between mixedwood and coniferous forests must lie elsewhere, most likely in the effects on seed production and seedling establishment of disturbances (Bergeron et al., 2004) and climate variables (Messaoud et al., 2007b), sometimes linked with physical attributes of the sites (Grondin et al., 2007).

4.8. References

Arris, L.L., and Eagleson, P.S. 1989. Evidence of a physiological basis for the boreal-deciduous forest ecotone in North America. Vegetatio 82: 55-58.

Asselin, H., Payette, S., Fortin, M.-J., and Vallée, S. 2003. The northern limit of Pinus banksiana Lamb. in Canada: explaining the difference between the eastern and western distributions. J. Biogeogr. 30: 1709-1718.

Asselin, M. 1995. L'Abitibi-Témiscamingue : trois sous-régions, une région. In Histoire de l'Abitibi-Témiscamingue. Edited by O. Vincent. Collection Les régions du Québec, no. 7, Institut québécois de recherche sur la culture, Québec, Canada, 21-65.

Barras, N., and Kellman, M. 1998. The supply of regeneration micro-sites and segregation of tree species in a hardwood/coniferous transition zone. J. Biogeogr. 25: 871-881.

Béland, M., and Bergeron, Y. 1996. Height growth of jack pine (Pinus banksiana) in relation to site types in boreal forests of Abitibi, Québec. Can. J. For. Res. 26: 2170-2179.

Bergeron, Y., Gauthier, S., Flannigan, M., and Kafka, V. 2004. Fire regimes at the transition between mixedwood and coniferous boreal forest in northwestern Quebec. Ecology 85: 1916-1932.

Brais, S., and Camiré, C. 1998. Soil compaction induced by careful logging in the claybelt region of northwestern Quebec (Canada). Can. J. Soil Sci. 78: 197-206.

Burns, R.M., and Honkala, B.H. 1990. Silvics of North America. Department of Agriculture, Washington, D.C. USDA. Forest Service Agriculture Handbook 654.

Chen, H.Y.H., Klinka, K., and Kabzems, R.D. 1998. Height growth and site index models for trembling aspen (Populus tremuloides Michx.) in northern British Columbia. For. Ecol. Manage. 102: 157-165.

Chen, H.Y.H., Krestov, P.V., and Klinka, K. 2002. Trembling aspen site index in relation to environmental measures of site quality at two spatial scales. Can. J. For. Res. 32: 112-119.

Cody, R.P., and Smith, J.K. 1991. Applied statistics and the programming language, 4th ed. Prentice Hall, Upper Saddle River, New Jersey, USA.

Engelmark, O., Bergeron, Y., and Flannigan, M.D. 2000. Age structure of eastern white pine, Pinus strobus L., at its northern distribution limit in Quebec. Can. Field-Nat. 114: 601-604.

Environment Canada. 2002. Canadian climate normals 1971-2000. Atmospheric Environment Service, Environment Canada, Ottawa, Ontario, Canada.

Flannigan, M.D., and Bergeron, Y. 1998. Possible role of disturbance in shaping the northern distribution of Pinus resinosa. J. Veg. Sci. 9: 477-482.

Gamache, I., and Payette, S. 2004. Height growth response of tree line black spruce to recent climate warming across the forest-tundra of eastern Canada. J. Ecol. 92: 835-845.

Goelz, J.C.G., and Burk, T.E. 1998. Long-term trends in height growth of jack pine in north central Ontario. For. Sci. 44: 158-164.

Grondin, P., Noël, J., Hotte, D., Tardif, P., and Lapointe, C. 2000. Croissance potentielle en hauteur et dynamique des espèces forestières sur les principaux types écologiques des régions écologiques 5a et 6a (Abitibi). Gouvernement du Québec, Ministère des Ressources naturelles, Direction de la recherche forestière, Rapport interne n° 461, 125 p.

Grondin, P., Noël, J., and Hotte, D. 2007. L'intégration de la végétation et de ses variables explicatives à des fins de classification et de cartographie d'unités homogènes du Québec méridional. Gouvernement du Québec, Ministère des Ressources naturelles et de la Faune, Direction de la recherche forestière, Mémoire de recherche forestière n° 150, 80 p.

Hadley, J.L., and Smith, W.K. 1983. Influence of wind exposure on needle desiccation and mortality for timberline conifers in Wyoming, U.S.A. Arctic Alpine Res. 15: 127-135.

Hadley, J.L., and Smith, W.K. 1989. Wind erosion of leaf surface wax in alpine timberline conifers. Arctic Alpine Res. 21: 392-398.

Hamel, B., Bélanger, N., and Paré, D. 2004. Productivity of black spruce and jack pine stands in Quebec as related to climate, site biological features and soil properties. For. Ecol. Manage. 191: 239-251.

Henttonen, H., Kanninen, M., Nygren, M., and Ojansuu, R. 1986. The maturation of Pinus sylvestris seeds in relation to temperature climate in northern Finland. Scand. J. For. Res. 1: 243-249.

Hobbie, S.E., and Chapin, F.S. 1998. An experimental test of limits to tree establishment in arctic tundra. J. Ecol. 86: 449-461.

Hofgaard, A., Kullman, L., and Alexandersson, H. 1991. Response of old-growth montane Picea abies (L.) Karst. forest to climatic variability in northern Sweden. New Phytol. 119: 585-594.

Houle, G., and Filion, L. 1993. Interannual variations in the seed production of Pinus banksiana at the limit of the species distribution in northern Québec, Canada. Am. J. Bot. 80: 1242-1250.

Klinka, K., Wang, Q., Carter, R.E., and Chen, H.Y.H. 1996. Height growth-elevation relationships in subalpine forests of interior British Columbia. For. Chron. 72: 193-198.

Kullman, L. 1990. Dynamics of altitudinal tree-limits in Sweden: a review. Norsk Geogr. Tidsskrift 44: 103-116.

Larsen A.J. 1980. The boreal ecosystem. Academic Press, Toronto, Canada.

Longpré, M.-H., Bergeron, Y., Paré, D., and Béland, M. 1994. Effect of companion species on the growth of jack pine (Pinus banksiana). Can. J. For. Res. 24: 1846-1853.

Mackey, B.G., McKenney, D.W., Yang, Y.-Q., McMahon, J.P., and Hutchinson, M.F. 1996. Site regions revisited: a climatic analysis of Hills' site regions for the province of Ontario using a parametric method. Can. J. For. Res. 26: 333-354.

Martin, J.L., and Gower, S.T. 2006. Boreal mixedwood tree growth on contrasting soils and disturbance types. Can. J. For. Res. 36: 986-995.

Messaoud, Y., Bergeron, Y., and Leduc, A. 2007a. Ecological factors explaining the location of the boundary between the mixedwood and coniferous bioclimatic zones in the boreal biome of eastern North America. Global Ecol. Biogeogr. 16: 90-102.

Messaoud, Y., Bergeron, Y., and Asselin, H. 2007b. Reproductive potential of balsam fir (Abies balsamea), white spruce (Picea glauca), and black spruce (P. mariana) at the ecotone between mixedwood and coniferous forests in the boreal zone of western Quebec. Am. J. Bot. 94: 746-754.

Nigh, G.D., Ying, C.C., and Qian, H. 2004. Climate and productivity of major conifer species in the interior of British Columbia, Canada. For. Sci. 50: 659-671.

OMNR. 2003. Silviculture guide to managing spruce, fir, birch, and aspen mixedwoods in Ontario's boreal forest. Version 1.0. Ontario Ministry of Natural Resources, Queen's Printer for Ontario.

Payette, S. 1993. The range limit of boreal tree species in Québec-Labrador: an ecological and palaeoecological interpretation. Rev. Palaeobot. Palynol. 79: 7-30.

Payette, S., and Delwaide, A. 1994. Growth of black spruce at its northern range limit in Arctic Québec, Canada. Arctic Alpine Res. 26: 174-179.

Payette, S., Delwaide, A., Morneau, C., and Lavoie, C. 1994. Stem analysis of a long-lived black spruce clone at treeline. Arctic Alpine Res. 26: 56-59.

Pigott, C.D. 1992. Are species distributions determined by failure to set seed? In Fruit and seed production. Aspects of environmental physiology and ecology. Edited by C. Marshall and J. Grace, Cambridge University Press, Cambridge, UK, 203-216.

Richards, F.J. 1959. A flexible growth function for empirical use. J. Exp. Bot. 10: 290-300.

Saucier, J.-P., Grondin, P., Robitaille, A., and Bergeron, J.-F. 1998. Les zones de végétation et les domaines bioclimatiques du Québec. Comité sur la carte des régions écologiques (3e version). Gouvernement du Québec, Québec, Canada.

Sirois, L. 1997. Distribution and dynamics of balsam fir (Abies balsamea (L.) Mill.) at its northern limit in the James Bay area. Ecoscience 4: 340-352.

Sirois, L. 2000. Spatiotemporal variation in black spruce cone and seed crops along a boreal forest – tree line transect. Can. J. For. Res. 30: 900-909.

Tremblay, M. F., Bergeron, Y., Lalonde, D., and Mauffette, Y. 2002. The potential effects of sexual reproduction and seedling recruitment on the maintenance of red maple (Acer rubrum L.) populations at the northern limit of the species range. J. Biogeogr. 29: 365-373.

Ung, C.H., Bernier, P.Y., Raulier, F., Fournier, R.A., Lambert, M.C., and Régnière, J. 2001. Biophysical site indices for shade tolerant and intolerant boreal species. For. Sci. 47: 83-95.

Veillette, J.J. 1994. Evolution and paleohydrology of glacial lakes Barlow and Ojibway. Quatern. Sci. Rev. 13: 945-971.

Wang, G.G. 2004. Height growth pattern of lodgepole pine in relation to natural subregions in Alberta. Western J. Appl. For. 19: 154-159.

Wang, G.G., and Huang, S. 2000. Height growth pattern of white spruce in natural subregions in Alberta, Canada. For. Ecol. Manage. 134: 271-279.

Wang, G.G., Huang, S., Monserud, R.A., and Klos, R.J. 2004. Lodgepole pine site index in relation to synoptic measures of climate, soil moisture and soil nutrients. For. Chron. 80: 678-686.

Zarnovican, R. 1985. Analyse de tige : une méthode à redécouvrir. Nat. can. 112: 253-260.

4.9. Table captions

Table 4.1. Comparisons of age (years), DBH (cm), height (m), and site index (m) between forest types and between species. The letters at right of each number indicate similar (same letter) or different (different letters) values for the different species (lower case letters) and forest types (capital letters) (Tukey test) at $\alpha = 0.05$. Numbers in parentheses indicate standard deviation from the mean.

Table 4.2. Comparisons of potential site index at 50 years (m) between forest types and between species for the three site types (MRNFQ data, Grondin et al. (2000)). Standard deviation from the mean is also shown. The letters at right of each number indicate similar (same letter) or different (different letters) potential site index values between forest types (capital letters) and between species (lower case letters) for each site type (Tukey test at $\alpha = 0.05$). N = 65 for balsam fir, 20 for white spruce, 136 for black spruce.

4.10. Figure captions

Figure 4.1. Study area showing the four sampled sites (A: lake Montalais, B: lake Duparquet, C: Cochrane, D: Muskuchii) and the distribution of the MRNFQ sampling plots from which complimentary field data were obtained (Grondin et al., 2000). Also shown is the location of the boundary between the mixedwood and coniferous forests in western Québec (after Saucier et al. (1998)) and in northeastern Ontario (approximate, after Mackey et al. (1996) and OMNR (2003)).

4.11. Appendices

Appendix 3. Relationship between height and age for balsam fir, white spruce and black spruce in the four sites sampled in this study across the ecotone between mixedwood and coniferous forests.

Table 4.1. Comparisons of age (years), DBH (cm), height (m), and site index (m) between forest types and between species. The letters at right of each number indicate similar (same letter) or different (different letters) values for the different species (lower case letters) and forest types (capital letters) (Tukey test) at $\alpha = 0.05$. Numbers in parentheses indicate standard deviation from the mean.

Dataset	Species	Variables	Mixedwood forest	Coniferous forest
This study	*Abies balsamea* N = 36	Age	70.67^{Aa} (11.50)	72.78^{Aa} (25.63)
		DBH	24.86^{Aa} (4.18)	23.65^{Aa} (3.33)
		Height	15.91^{Aa} (3.12)	15.27^{Aa} (3.16)
		Site index[1]	9.73^{Aa} (2.37)	9.57^{Ab} (2.29)
	Picea glauca N = 36	Age	71.39^{Aa} (17.80)	87.39^{Bab} (21.99)
		DBH	24.75^{Aa} (3.85)	25.04^{Aa} (4.55)
		Height	15.50^{Aa} (3.08)	15.20^{Aa} (3.63)
		Site index[1]	9.88^{Aa} (2.54)	8.09^{Aab} (2.57)
	Picea mariana N = 34	Age	89.53^{Ab} (18.70)	99.82^{Ab} (23.54)
		DBH	24.75^{Aa} (3.62)	24.24^{Aa} (4.00)
		Height	16.40^{Aa} (2.57)	15.14^{Ba} (2.65)
		Site index[1]	7.92^{Aa} (2.70)	6.78^{Ba} (2.05)
MRNFQ	*Abies balsamea* N = 65	Age	68.18^{Aa} (14.53)	71.03^{Aa} (21.63)
		DBH	23.91^{Aa} (4.57)	21.91^{Aa} (5.24)
		Height	17.13^{Aa} (1.66)	15.07^{Ba} (2.67)
		Potential site index[2]	17.93^{Ab} (1.39)	17.06^{Ab} (1.95)
	Picea glauca N = 20	Age	75.33^{Aab} (36.39)	107.73^{Ab} (38.94)
		DBH	35.21^{Ab} (11.91)	34.48^{Ab} (11.21)
		Height	18.65^{Aa} (3.72)	19.99^{Ac} (5.13)
		Potential site index[2]	19.04^{Ab} (2.82)	16.17^{Bb} (2.34)
	Picea mariana N = 136	Age	91.81^{Ab} (34.64)	95.37^{Ab} (32.49)
		DBH (cm)	21.66^{Aa} (4.62)	22.35^{Aa} (5.29)
		Height (m)	17.15^{Aa} (2.37)	16.92^{Ab} (3.22)
		Potential site index[2]	14.15^{Aa} (2.91)	13.36^{Aa} (2.65)

[1] Site index after 25 years of free growth.

[2] Potential site index at 50 years according to the Chapman-Richards model function (Grondin et al., 2000).

Table 4.2. Comparisons of potential site index at 50 years (m) between forest types and between species for the three site types (MRNFQ data, Grondin et al. (2000)). Standard deviation from the mean is also shown. The letters at right of each number indicate similar (same letter) or different (different letters) potential site index values between forest types (capital letters) and between species (lower case letters) for each site type (Tukey test at α = 0.05). N = 65 for balsam fir, 20 for white spruce, 136 for black spruce.

	FS		MM		CX	
	Mixedwood	Coniferous	Mixedwood	Coniferous	Mixedwood	Coniferous
Abies balsamea	$18.37^{Ab} \pm 1.36$	$16.74^{Bb} \pm 2.12$	N.A.	$18.90^{b} \pm 0.56$	$17.28^{Ab} \pm 1.22$	$17.18^{Ab} \pm 1.62$
Picea glauca	$19.77^{Ab} \pm 2.20$	$15.85^{Bab} \pm 2.56$	N.A.	N.A.	$16.85^{Aab} \pm 4.31$	$15.72^{Aab} \pm 1.49$
Picea mariana	$14.83^{Aa} \pm 2.68$	$13.66^{Aa} \pm 2.70$	N.A.	$14.15^{a} \pm 1.67$	$12.75^{Aa} \pm 2.93$	$12.50^{Aa} \pm 2.68$

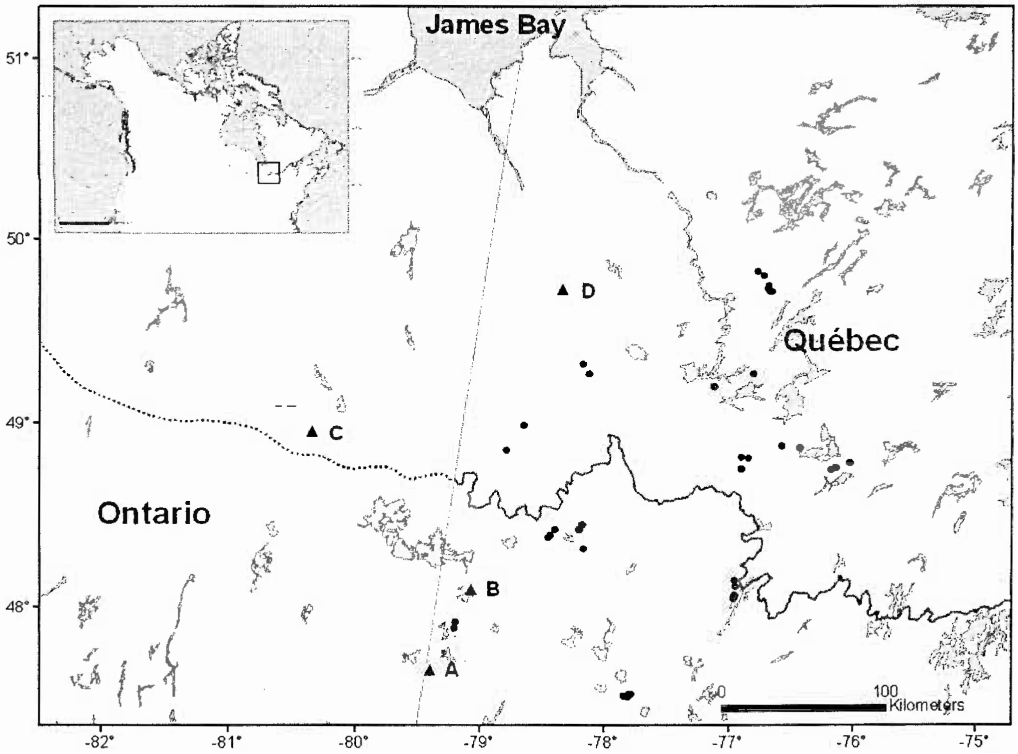
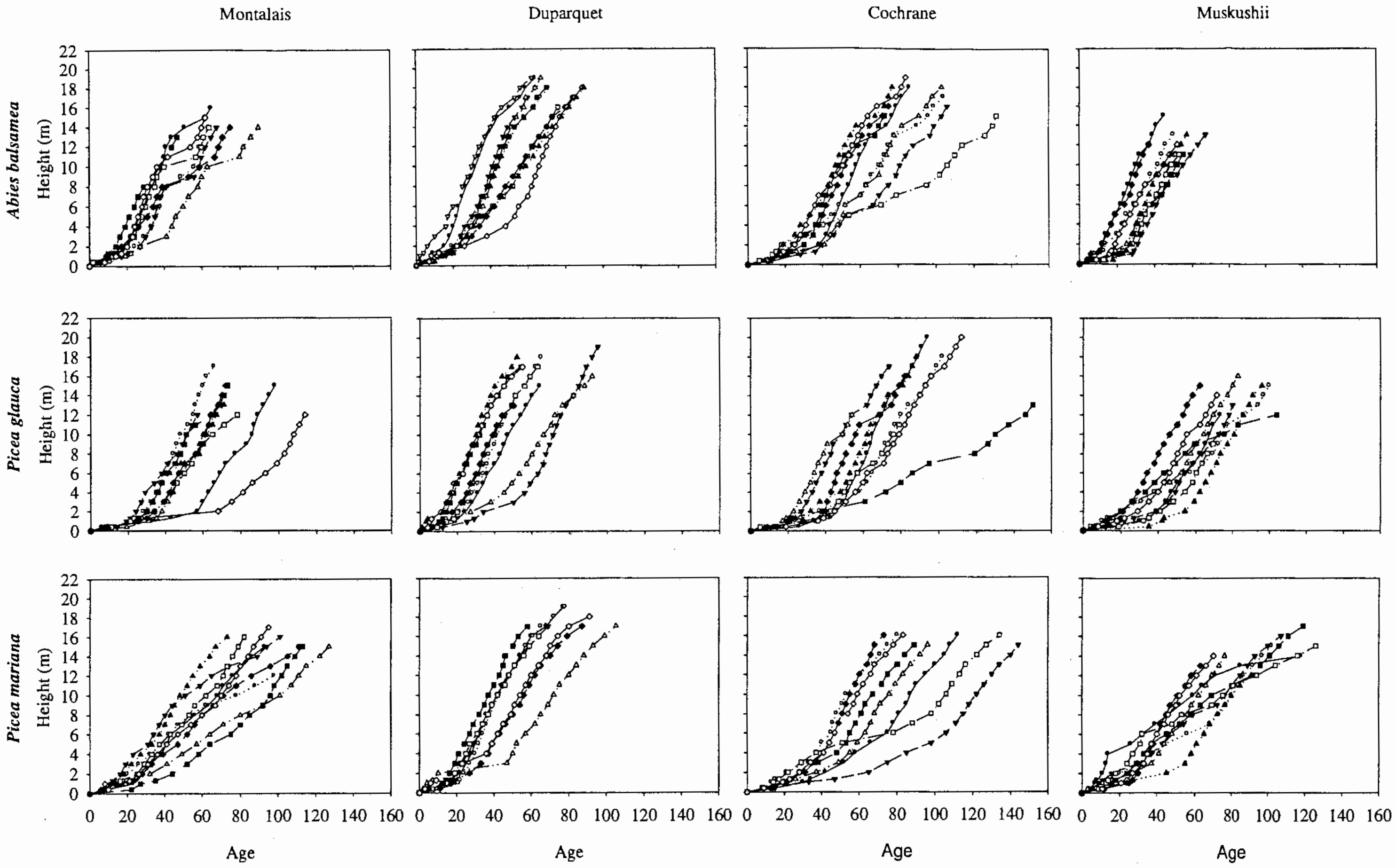

James Bay
Québec
Ontario
A
B
C
D
0
100
Kilometers
51°
50°
49°
48°
-82°
-81°
-80°
-79°
-78°
-77°
-76°
-75°

Figure 4.1.


Montalais
Duparquet
Cochrane
Muskushii
Abies balsamea
Picea glauca
Picea mariana
Height (m)
0
2
4
6
8
10
12
14
16
18
20
22
0
20
40
60
80
100
120
140
160
Age

Appendix 4.1.

CONCLUSION GÉNÉRALE

La dynamique de l'écotone forêt mixte/forêt coniférienne représentée par un changement de dominance du sapin baumier vers l'épinette noire dans la zone boréale du nord-est américain nous a permis de mettre en évidence l'importance et la complexité des facteurs écologiques ainsi que la dynamique des espèces dominant dans cette région pouvant être responsables de la localisation de cet écotone. Pour cela, nous avons dégagé plusieurs points essentiels repris dans les sections suivantes.

1. Les facteurs écologiques

La limite nordique de la forêt mixte communément appelée la sapinière est en partie contrôlée par la rareté des conditions écologiques favorisant son établissement et son développement dans la forêt coniférienne communément appelé pessière i.e. altitude, dénivelé, respectivement à l'échelle locale et paysage. Dans ce type de forêt, les facteurs non favorables sont plutôt abondants i.e. épaisseur de la matière organique à l'échelle locale, et un district riche en dépôt organique à l'échelle du paysage. Ces facteurs et d'autres cités dans le chapitre I déterminent les sites propices aux sapinières. Ceux-ci deviennent plus rares dans la forêt coniférienne. De plus, les populations de sapins situées dans la forêt coniférienne semblent incapables de saturer même les sites qui présentent des conditions propices. Cependant, tous ces facteurs n'expliquent qu'en partie la présence de l'écotone. Les populations situées sur des sites non propices dans la forêt coniférienne pourraient témoigner d'une abondance plus marquée dans le passé. Par conséquent, la partie inexpliquée pourrait provenir d'autres facteurs comme l'histoire postglaciaire de la végétation et à un deuxième degré les perturbations (feux). Le climat, longtemps considéré comme le principal facteur contrôlant la distribution des communautés végétales, agit plutôt de manière indirecte sur cet écotone à travers la qualité des sites et les régimes de perturbations.

2. Performance des espèces

Dans cette deuxième partie, l'objectif de l'étude était de voir si la performance (reproduction, régénération et croissance en hauteur) pouvait elle aussi expliquer la localisation de l'écotone. Cette performance a été comparée entre les deux types de forêt de part et d'autre de l'écotone. Les résultats ont indiqué que la capacité reproductive (sapin et épinette blanche) ainsi que la régénération (sapin) étaient plus faibles alors que la capacité reproductive de l'épinette noire était presque similaire dans la forêt coniférienne. Ceci explique aussi en partie que la présence de l'écotone à de si basse latitude (49°N). En effet, la production de cônes, la qualité des graines ainsi que leur germination étaient dans l'ensemble plus faibles dans la forêt coniférienne. En plus, le nombre de paisson pleine (forte production de cônes) est également plus faible. Ceci va grandement affecter négativement la régénération du sapin au départ puisque non seulement il y a moins de graines disponibles, mais en plus le renouvellement de cette régénération est plus espacée et le ré-envahissement des sites dans la forêt coniférienne est moins fréquent puisque pour le sapin seules les paissons pleines favorisent la dispersion des graines vers d'autres sites. En plus, la densité de cette régénération diminue à partir des jeunes semis jusqu'au stade gaulis du à un fort taux de mortalité, ce qui indique que le sapin est moins compétitif, (moins abondant) que l'épinette noire plus adaptée et dominant. Cette dernière n'étant pas affecté par les conditions climatiques dans la forêt coniférienne, produisant annuellement des cônes et ayant des graines plus petites que celles du sapin lui permet d'envahir plus rapidement les sites (disponibilité de graines et se dispersant à de plus grandes distances). Ceci confère à l'épinette noire un avantage prépondérant dans la compétition aussi bien à l'échelle locale que du paysage.

Par contre, la croissance en hauteur des trois espèces n'indique pas dans l'ensemble de différences marquées aussi bien entre les espèces qu'entre les deux types de forêt. Dans ce cas, il s'est avéré que les conditions édaphiques semblent jouer un rôle prépondérant qui pourrait masquer l'effet direct des conditions climatique sur la croissance. Dans la forêt coniférienne, le sapin et l'épinette blanche peuvent croître aussi bien que l'épinette noire à condition que les conditions de site soient favorables.

3. Quelles seraient les conséquences des changements climatiques à l'interface forêt mixte-forêt coniférienne?

Au niveau de l'écotone forêt mixte/forêt coniférienne, on s'attend à ce que le réchauffement climatique (hausse des températures avec une augmentation plus moins importante des précipitations; Plummer et al., 2006) puisse améliorer la capacité reproductive du sapin ainsi que de l'épinette blanche dans la forêt coniférienne (tableau 1; tableau 3 du chapitre II), alors que les changements pourraient être comparativement mineurs pour l'épinette noire.

Une meilleure production de cônes pourrait s'accompagner de paissons pleines plus fréquentes. Ceci permettra au sapin et à l'épinette blanche de disperser ses graines plus fréquemment pour ré-envahir les sites propices. Par conséquent, la régénération sera plus abondante au départ et cette augmentation de la fréquence (nombre de paisson pleine) permettra le réapprovisionnement en espèces sur ces nouveaux sites. En plus, on observera une diminution de la mortalité des semis, ce qui permettra de maintenir plus ou moins l'abondance de cette régénération.

Par contre, le succès de re-établissement dépendra de plusieurs facteurs. En effet, nous avons montré que pour le sapin la proximité des sites de ré-envahissement (puits) par rapport à ceux d'où émanent les graines (source) en provenance aussi bien de la forêt mixte en deçà de l'écotone que les populations situées dans la forêt coniférienne est déterminant puisque ses graines sont plus grosses que celles de l'épinette noire et que ce dernier est dominant à l'échelle du paysage. Ce qui confère au sapin un désavantage par rapport à l'épinette noire.

Tableau 1 : Effet du réchauffement climatique sur la reproduction et la dissémination à la limite nordique de distribution d'une espèce donnée selon deux scénarios : période humide (élévation de manière concomitante des températures et des précipitations) et sèche (température élevée et précipitations constantes ou plus faibles).

Stade	Limite nordique	
	Période humide	Période sèche
Induction florale	-/+	-/+
Floraison	-	+
Fructification	+	-
Dissémination	-	+

Ceci nous amène à dire qu'il faudra un certain temps pour que la forêt mixte devienne plus abondante dans la forêt coniférienne et qu'à plus long terme l'écotone progresse vers le nord d'où la notion de "time lag" pour les espèces dont la migration est plus lente et à plus long terme et à plus grande échelle (Woodward, 1987; Masek, 2001). En plus, ce "time lag" pourrait être plus important puisque l'écotone sépare deux types de forêt où la compétition interspécifique est plus importante que dans le cas d'un écotone entre une forêt coniférienne et une toundra (Kullman (1986-2002) et Payette (1975-2002).

En plus, en dépit des conditions climatiques favorables, les conditions de sol peuvent être défavorables s'il y a surplus d'eau (augmentation des précipitations plus importantes que celles des températures). Ce qui pourrait compromettre l'établissement du sapin et de l'épinette blanche sur certains sites (chapitre IV; Rizzo & Wiken, 1992; Malcolm et *al.*, 2002). Notons que les sols mettent plus de temps à évoluer que le climat. Ce dernier agit directement sur l'espèce ou la population (performance: reproduction et régénération). Cependant, il agit indirectement à travers les conditions édaphiques (voir chapitre I) et microclimatiques i.e. présence de feuillus versus pessière pure (voir chapitre I).

Sykes & Prentice (1996) ont simulé la dynamique forestière à l'écotone entre la forêt feuillue dominée par le hêtre commun (*Fagus sylvatica*) et la forêt coniférienne dominée par l'épinette de Norvège (*Picea abies*) suite à un réchauffement climatique. Cet écotone est situé au sud de la Suède dans le parc national de Norra Kvill. En estimant la biomasse des deux espèces dominantes sur une période de temps de 1000 ans, ils ont établi deux scénarios : l'un sans les perturbations majeures naturelles et l'autre avec perturbations. Les résultats indiquent que la hêtraie va envahir la pessière mais à un rythme plus lent vu que les deux espèces sont très tolérantes à l'ombre. Cependant, les perturbations naturelles vont accélérer cette invasion, puisque le hêtre va saturer les sites libérés par la pessière. De ce fait, la hêtraie va remplacer la pessière plus rapidement. Cependant, il faut noter que ce changement de dominance va quand même s'opérer après plusieurs siècles car il s'agit des arbres dont la longévité est plus grande notamment pour les deux espèces.

Cette étude pourrait être un bon exemple pour prédire la dynamique de l'écotone forêt mixte/forêt coniférienne. Les sapinières situées près de l'écotone ainsi que celles dans la forêt coniférienne seront les sources de dispersion des graines. Cependant, la dynamique spatio-temporelle future de ces sapinières va dépendre également de deux scénarios selon qu'on se dirige vers une période humide ou sèche (Fig. 1). En effet, les perturbations naturelles (feux), qui dépendent elles aussi du climat, pourraient influencer grandement selon que celles-ci seront plus fréquentes et de taille réduite (période humide) ou seront plus fréquentes et de taille plus grande (période plus sèche). Dans le premier scénario, les feux auront un effet bénéfique sur deux plans :

1. les populations reliques de sapinières dans la pessière ne seront pas détruites et pourront se maintenir,
2. ces feux de plus faibles intensités vont être favorables aux sapinières de part l'ouverture des pessières, ce qui facilitera l'invasion du sapin baumier (espèce plus tolérante à l'ombre).

C'est dire que ces petits feux vont peut être accélérer l'augmentation des sapinières dans la forêt coniférienne.

Dans le second scénario, les feux auront un effet plutôt négatif car ceux-ci seront plus dévastateurs provoquant ainsi une extinction locale de certaines de ces sapinières dans la pessière qui seront graduellement remplacées par des espèces plus adaptées aux feux i.e. épinette noire ou pin gris. On s'attendrait à ce que ce soit plus l'épinette noire à cause de sa dominance et sa plus grande capacité d'envahir les sites récemment brûlés dans la pessière à mousse. Le pin gris pourrait envahir certains sites à condition que ces derniers soient très proches des populations sources, que les conditions de sol soient favorables pour l'espèce (sols sablonneux) et que les feux soient assez récurrent (100 ans) pour que ces populations établies se maintiennent car le pin gris est une espèce intolérante à l'ombre. Par contre, d'autres sapinières situées dans des zones refuges (proximité des lacs et rivières; Messaoud et al., 2007) pourraient envahir des sites non loin de ces refuges qui sont actuellement non favorables à leur établissement comme les sols trop humides très abondants dans la pessière, une fois que ces grands feux aient brûlés et fait disparaître la matière organique et que ces sols s'assèchent.

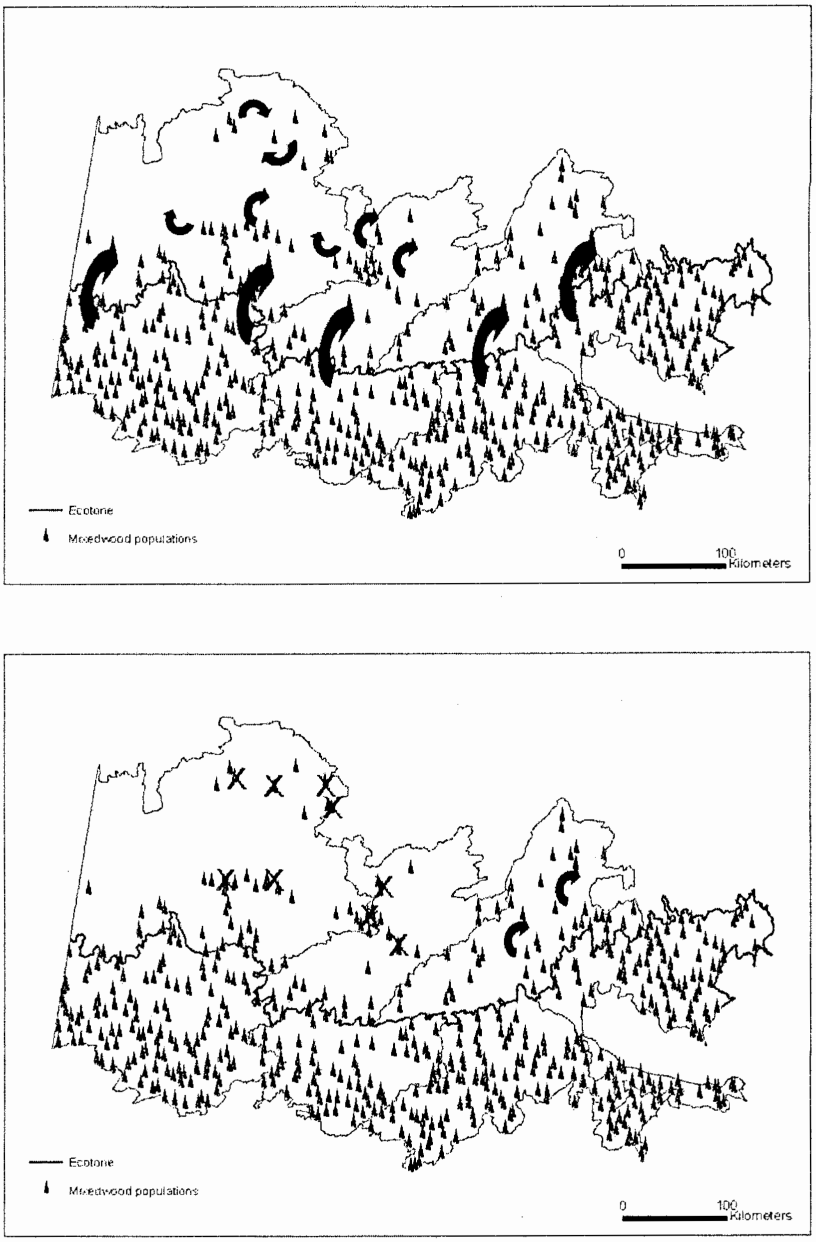


Figure 1. Scénario de la dynamique future des métapopulations de sapinières de part et d'autre de l'écotone suite à un changement climatique plus chaud et plus humide (A) ou plus chaud et plus sec (B). Flèche bleue et la croix rouge indique respectivement l'établissement et l'extinction à l'échelle locale.

4. Aménagement forestier

Considéré comme une perturbation anthropique, cette pratique semble avoir un effet additif sur l'expansion du sapin baumier. En effet, cet aménagement reposant notamment sur la méthode de CPRS (coupe avec protection de régénération et des sols) ouvre le peuplement forestier notamment les peuplements d'épinette noire, espèce très demandée dans l'industrie i.e. pâte à papier et protège la régénération qui dans le futur favoriserait l'établissement du sapin baumier à condition que les sites soient favorables (Brumelis & Carleton, 1988).

D'une manière globale, la migration de la forêt mixte vers la forêt coniférienne semble être inéluctable suite aux changements climatiques. On s'attend donc à un déplacement de l'écotone vers le nord. Cependant, on peut supposer que l'abondance de cette forêt mixte reposera notamment sur les deux scénarios de perturbations naturelles. Cette dynamique spatio-temporelle se maintiendra à condition que le réchauffement climatique se poursuive et demeure constant et que les conditions édaphiques le permettent. En effet, à l'échelle du paysage, il subsistera encore de grandes pessières situées dans des sites encore non favorables (sols trop humides ou peu perturbés; Mccune & Allen, 1985). On pourrait déduire que si la forêt coniférienne serait graduellement remplacée par la forêt mixte, cette dernière pourrait ne pas ressembler à celle qui prévaut actuellement dans la forêt mixte (Richard, 1993). Les espèces migrant individuellement vers le nord et les conditions édaphiques et topographiques différentes dans la forêt coniférienne que dans celles de la forêt mixte impliqueront une composition spécifique à l'échelle du paysage qui pourraient être différente (Bergeron et al., 2004). Dans ce cas, les modèles de simulation à l'échelle de la communauté et du paysage doivent tenir compte de tous ces facteurs qui jouent un rôle important sur la présence de la forêt mixte. Ceci permettra de mieux prédire la localisation des deux types de forêt ainsi que leur écotone.

5. Références citées dans l'introduction et la conclusion générale

Ammari, Z. 2001. Facteurs contrôlant la limite nord de la forêt mixte dominée par le sapin dans l'ouest du Québec. Mémoire MSE, Université du Québec à Montréal.

Arris, L.L. & Eagleson, P.S., 1989. Evidence of a physiological basis for the boreal-deciduous forest ecotone in North America. Vegetatio, 82: 55-58.

Bakusis, E.V. & Hansen, H.S. 1965. Balsam fir: a monographic review. The university of Minnesota Press, Minneapolis.

Barnosky, C.W., 1987. Response of vegetation to climatic changes of different duration in the late Neogene. Tree, 2: 247-250.

Barras, N. & Kellman, M. 1998. The supply of regeneration micro-sites and segregation of tree species in a hardwood/boreal forest transition zone. Journal of biogeography, 25: 871-881.

Béland, M. & Bergeron, Y. 1993. Ecological factors affecting abundance of advanced growth in jack pine (*Pinus banksiana* lamb.) stands of the boreal forest of Northwestern Quebec. The forestry chronicle, 69: 561-567.

Bérard, J.A. 1996. Manuel de foresterie. Ordre des ingénieurs forestiers du Québec. Québec, Presses de l'université Laval, 1428 p.

Bergeron, Y., Bouchard, A. & Massicotte, G. 1985. Gradient analysis in assessing differences in community pattern of three adjacent sectors within Abitibi, Quebec. Vegetatio, 64: 55-65.

Bergeron Y. & Gagnon, D. 1987. Age structure of red pine (*Pinus resinosa* Ait.) at its northern limit in Quebec. Canadian Journal of Forest Research, 17: 129-137.

Bergeron, Y. & Dubuc, M. 1989. Succession in the southern part of the Canadian boreal forest. Vegetatio, 79: 51-63.

Bergeron, Y. & Archambault, S.1993. Decreasing frequency of forest fires in the southern boreal zone of Québec and its relation to global warming since the end of the 'Little Ice Age'. The Holocene, 3: 255-259.

Bergeron, Y. & Brisson, J. 1994. Effect of climatic fluctuations on post-fire regeneration of two pine and red pine populations during the twentieth century. Géographie physique et quaternaire, 48: 145-149.

Bergeron, Y., Gauthier, S., Flannigan, M. & Kafka, V. 2004. Fire regimes at the transition between mixedwood and coniferous boreal forest in northerwestern Quebec. Ecology, 85, 1916-1932.

Black, R.A. & Bliss, L.C. 1980. Reproductive ecology of *Picea mariana* (Mill.) BSP., at tree line near Inuvik, Northwest Territories, Canada. Ecological monographs, 50: 331-354.

Brumelis, G. & Carleton, T.J. 1988. The vegetation of postlogged black spruce lowlands in central Canada. I. Trees and tall shrubs. Canadian journal of forest research, 18: 1470-1478.

Brubaker, L.B. 1986. Responses of tree populations to climatic change. Vegetatio, 67: 119-130.

Burns & Honkala, 1990. Silvics of North America. Washington, D.C., U.S. Department of Agriculture, 654 p.

Cappuccino, N., Lavertu, D., Bergeron, Y. & Régnière, J. 1998. Spruce budworm impact, abundance and parasitism rate in a patchy landscape. Oecologia, 114: 236-242.

Colombo, S.J. 1998. Climatic warming and its effect on bud burst and risk of frost damage to white spruce in Canada. The forestry chronicle, 74 : 567-577.

Dale, V.H., Joyce, L.A., McNulty, S. & Neilson, R.P. 2000. The interplay between climate change, forests, and disturbances. The science of the total environment, 262: 201-204.

Damman, A.W.H. 1979. The role of vegetation analysis in land classification. The forestry chronicle, 55: 175-182.

Earle, CJ. 1993. Ribbon forest development in the forest-tundra of Wyoming : Differing roles of trees establishing by layering of from seed. Bulletin of the ecological society of America, 74 (2 suppl.).

Flannigan, M.D. & Bergeron, Y. 1998. Future wildfire in circumboreal forests in relation to global warming. Journal of Vegetation Science, 9: 469-476.

Flannigan, M.D., Bergeron, Y., Engelmark, O. & Wotton, B.M. 1998. Future wildfire in circumboreal forests in relation to global warming. Journal of Vegetation Science, 9: 469-476.

Gagnon, R. 1989. Maintien après feu de limites abruptes entre les peuplements d'épinettes noires (*Picea mariana*) et des formations de feuillus intolérants (*Populus* *tremuloides* et *Betula papyrifera*) dans la région du Saguenay-lac Saint-Jean (Québec). Naturaliste canadien, 116: 117-124.

Galipeau, C., Kneeshaw, D. & Bergeron, Y. 1997. White spruce and balsam fir colonization of a site in the southeastern boreal forest as observed 68 years after fire. Canadian Journal of Forest Research, 27: 139-147.

Greene, D.F. & Johnson, E.A. 2000. Tree recruitment from burn edges. Canadian journal of forest research, 30: 1264-1274.

Harvey, B. D. & Bergeron, Y., 1989. Site patterns of natural regeneration following clear-cutting in northwestern Quebec. Canadian journal of forest research, 19: 1458-1469.

Hofgaard, A., Kullman, L. & Alexandersson, H. 1991. Response of old-growth montane *Picea abies* (L.) Karst. forest to climatic variability in northern Sweden. New Phytologist, 119: 585-594.

Hogg, E.H. 1994. Climate and the southern limit of the western Canadian boreal forest. Canadian Journal of Forest Research, 24: 1835-1845.

Hogg, E.H. & Schwarz, A.G. 1997. Regeneration of planted conifers across climatic moisture gradients on the Canadian prairies : implications for distribution and climate change. Journal of Biogeography, 24: 527-534.

Houle, G. & Filion, L. 1993. Interannual variations in the seed production of *Pinus banksiana* at the limit of the species distribution in northern Québec, Canada, American Journal of Botany, 80: 1242-1250.

Huntley, B. & Webb, T. 1989. Migration : species' response to climatic variations caused by changes in the earth's orbit. Journal of Biogeography, 16: 5-19.

Kullman, L. 1986. Late Holocene reproductional patterns of *Pinus sylvestris* and *Picea abies* at the forest limit in central Sweden. Canadian journal of botany, 64: 1682-1690.

Kullman, L. 1993. Pine (*Pinus sylvestris* L.) tree-limit surveillance during recent decades, central Sweden. Arctic and Alpine Research, 25: 24-31.

Kullman, L. 1993. Tree limit dynamics of *Betula pubescens* ssp. *Tortuosa* in relation to climate variability: evidence from central Sweden. Journal of Vegetation Science, 4: 765-772.

Kullman, L. 1995. New and firm evidence for mid-holocene appearance of *Picea abies* in the Scandes Mountains, Sweden. Journal of Ecology, 83: 439-447.

Kullman, L. 1996. Norway spruce present in the Scandes mountains, Sweden at 8000 BP: new light on Holocene tree spread. Global Ecology and Biogeography Letters, 5: 94-101.

Kullman, L. 1996. Rise and demise of cold-climate *Picea abies* forest in Sweden. New Phytologist, 134: 243-256.

Kullman, L. 2001. Immigration of *Picea abies* into North-central Sweden. New evidence of regional expansion and tree-limit evolution. Nordic Journal of Botany, 21: 39-54.

Kullman, L. 2002. Rapid recent range-margin rise of tree and shrub species in the Swedish Scandes. Journal of Ecology, 90: 68-77.

Langvall, O. & Örlander, G. 2001. Effect of pine shelterwoods on microclimate and frost damage to Norway spruce seedlings. Canadian Journal of Forest Research, 31: 155-164.

Langvall, O., Nilsson, U. & Orlander, G. 2001. Frost damage to planted Norway spruce seedlings-influence of site préparation and seedling type. Forest ecology and management, 141: 223-235.

Larsen A.J. 1980. The boreal ecosystem. New York ; Toronto: Academic Press, 500 p.

Lavoie, C. & Payette, S. 1994. Recent fluctuations of the lichen-spruce forest limit in subarctic Québec. Journal of ecology, 82: 725-734.

Loehle, C. 1998. Height growth rate tradeoffs determine northern and southern range limits for trees. Journal of Biogeography, 25: 735-742.

Loehle, C. 2000. Forest ecotone response to climate change: sensitivity to temperature response functional forms. Canadian Journal of Forest Research, 30 : 1632-1645.

Luckman, B. 2000. Impact of climate fluctuations on mountain environments in the Canadian Rockies. 29 : 371-380.

McCune, B. & Allen, T.F.H. 1985. Will similar forests develop on similar sites?. Canadian Journal of Botany, 63: 367-376.

MacLean, D.A. 1980. Vulnerability of fir-spruce stands during uncontrolled spruce budworm outbreaks: a review and discussion. Forestry chronicle, 56: 213-221.

MacLean, D.A. 1984. Effects of spruce budworm outbreaks on the productivity and stability of Balsam fir forests. Forestry chronicle, 60: 273-279.

Malcolm, J.R., Markham, A., Neilson, R.P. & Michael Garaci. 2002. Estimated migration rates under scenarios of global climate change. Journal of Biogeography, 29: 835-849.

Masek, J.G. 2001. Stability of boreal forest stands during recent climate change: evidence from landsat satellite imagery. Journal of Biogeography, 28: 967-976.

Messaoud, Y., Bergeron, Y. & Leduc, A. 2007. Ecological factors explaining the location of the boundary between the mixedwood and coniferous bioclimatic zones in the boreal biome of eastern North America (in Press).

Morin, A. & Laprise, D. 1997. Seedling bank dynamics in boreal balsam fir forests. Canadian journal of Forest Research, 27: 1442-1451.

Nikolov, N. & Helmisaari, H. 1992. Silvics of the circumpolar boreal forest tree species *in* A systems analysis of the global boreal forest, Cambridge: Cambridge University Press, 565 p.

Paré, D. & Bergeron, Y. 1996. Effect of colonizing tree species on soil nutrient availability in a clay soil of the boreal mixedwood. Canadian journal of forest research, 26: 1022-1031.

Paulsen, J. Weber, U.M. & Korner, Ch. 2000. Tree growth near treeline: abrupt or gradual reduction with altitude? Arctic, Antarctic, and Alpine Research, 32: 14-20.

Payette, S., Deshaye, J. & Gilbert, H. 1982. Tree seed populations at the treeline in rivière aux feuilles area, northern Quebec, Canada. Arctic and Alpine Research, 14: 215-221.

Payette, S & Filion, L. 1985. White spruce expansion at the tree line and recent climatic change. Canadian journal of Forest Research, 15: 241-251.

Payette, S., Filion, L., Gauthier, L. & Boutin, Y. 1985. Secular climate change in old-growth tree-line vegetation of northern Quebec. Nature, 315: 135-138.

Payette , S. 1993. The range limit of boreal tree species in Québec-Labrador : an ecological and palaecological interpretation. Review of Palaeobotany and Palynology, 79: 7-30.

Pellatt, MG. 2000. Holocene treeline and climate change in the subalpine zone near Stoyoma Mountain, Cascade Mountains southwestern British Columbia, Canada. Arctic antarctic and alpine research, 32 : 73-83.

Plummer, D.A. Caya, D., Frigon, A., Côté, H., Giguère, M., Paquin, D., Biner, S., Harvey, R. & de Elia, R. 2006. climate and climate change over North America as simulated by the Canadian RCM. American Meteorological Society, 19: 3112-3132.

Pouliot, 1994. Le Québec dans le monde nordique. Le Naturaliste Canadien, 45-53.

Raitio, H. 1987. Site elevation differences in frost damage to Scots pine (*Pinus sylvestris*). Forest ecology and management, 20 : 299-306.

Richard, P.J.H. 1993. Origine et dynamique postglaciaire de la forêt mixte au Québec. Review of Paleobotany and Palynology, 79: 31-68.

Ritchie, J.C. & Hare, F.K. 1971. Late quaternary vegetation and climate near the arctic tree-line of Northwestern North America. Quat. Res. N.Y. 1: 331-342.

Rizzo, B. and Wiken, E. 1992. Assessing the sensitivity of Canada's ecosystems to climatic change. Climatic Change, 21: 37-55.

Rochefort, RM & Peterson, DL. 1992. Effects of climate and other environmental factors on tree establishment in subalpine meadows of Mount Rainier National Park. Bulletin of the ecological society of America (73 (2 suppl.) : 326.

Rupp, T.S., Starfield, A.M. & Chapin, F.S. 2000. A frame-based spatially explicit model of subarctic vegetation response to climatic change : comparison with a point model. Landscape ecology, 15: 383-400.

Rupp T.S., Chapin, F.S. & Starfield, A.M. 2001. Modeling the influence of topographic barriers on treeline advance at the forest-tundra ecotone in northwestern Alaska. Climatic change, 48: 399-416.

Sirois, L. 1997. Distribution and dynamics of balsam fir (*Abies balsamea* (L.) Mill. at its northern limit in the James Bay area. Ecoscience, 4: 340-352.

Sirois, L., Bégin, Y. & Parent, J. 1999. Female gametophyte and embryo development of black spruce along a shore-hinterland climatic gradient of a recently created reservoir, northern Quebec. Canadian Journal of Botany, 77: 61-69.

Sirois, L. 2000. Spatiotemporal variation in black spruce cone and seed crops along a boreal forest-tree transect. Canadian journal of forest research, 30: 900-909.

Stohlgren, T.J. & Bachand, R.B. 1997. Lodgepole pine (*Pinus contorta*) ecotones in Rocky Mountain National Park, Colorado, U.S.A. Ecology, 78: 632-641.

Sykes, M.T. & Prentice, I.C, 1996. Climate change, tree species distributions and forest dynamics: a case study in the mixed conifer/northern hardwoods zone of northern Europe. Climatic Change, 34: 161-177.

Van Wagner, C.E. 1971. Fire and red pine. Proc. 10th annu. Tall timbers fire ecol. Conf. Pp. 221-224.

Walter, H. 1973. Vegetation of the earth in relation to climate and the eco-physiological conditions. London: English Universities Press, 237 p.

Weaver & Clements, 1938. Plant ecology. New York: McGraw-Hill, 601 p.

Weisberg, P.J. & Baker, W.L. 1995. Spatial variation in tree seedling and krummholz growth in the forest-tundra ecotone of Rocky mountain national park, Colorado, USA. Arctic and Alpine Research, 27: 116-129.

Whittaker, R.H. 1970. Communities and ecosystems. Macmillan of Canada, 158 p.

Woodward, F.I., 1987- Climate and plant distribution. New York: Cambridge University Press, 174 p.

Woodward, A., Silsbee, G., Schreiner, E.G. & Means, J. 1994. Influence of climate on radial growth and cone production in subalpine fir (*Abies lasiocarpa*) and mountain hemlock (*Tsuga mertensiana*). Canadian Journal of Forest Research, 24: 1133-1143.

Zasada, J.C. 1971. Frost damage to white spruce cones in interior Alaska. USDA forest service, Portland (Oregon), PNW-149: 1-7.

Zasada, J.C., Foote, M.J., Deneke, F.J. & Parkerson, R.H. 1978. Case history of an excellent white spruce cone and seed crop in interior Alaska: cone and seed production, germination, and seedling survival. USDA forest service, PNW-65: 1-53.