UNIVERSITÉ DU QUÉBEC À MONTRÉAL

INFLUENCE DU PEUPLIER FAUX-TREMBLE SUR LA RÉGÉNÉRATION DU SAPIN BAUMIER DANS LA PESSIÈRE À MOUSSES DE L'OUEST DU QUÉBEC

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RÉSUMÉ

Dans la forêt boréale du nord-ouest du Québec (Canada), une plus grande abondance de feuillus dans la portion sud du domaine résineux pourrait créer des conditions plus favorables à l'établissement des espèces associées au domaine mixte. En effet, les propriétés du sous-bois et la réponse à divers types de perturbation sont grandement influencées par la composition des peuplements. Ainsi, la présence du peuplier faux-tremble (*Populus tremuloides* Michx.) en pessière pourrait offrir des conditions plus propices à l'établissement et à la croissance du sapin baumier (*Abies balsamea* (L.) Mill.) au nord de sa zone de dominance. L'objectif général de cette étude consiste à déterminer si la présence du peuplier faux-tremble facilite la régénération du sapin baumier au sein de la pessière à mousses de l'ouest du Québec. Pour ce faire, des sites présentant une transition au niveau du couvert, allant d'une dominance de l'épinette noire (*Picea mariana* (Mill.) BSP) à un peuplement mixte de peuplier faux-tremble et d'épinette noire, ont été sélectionnés. Des transects disposés de façon à traverser la transition entre les 2 types de peuplement ont été utilisés pour caractériser la régénération du sapin baumier et les conditions environnementales le long du gradient mixte-résineux.

Les résultats indiquent que la régénération du sapin baumier est généralement plus abondante lorsque le peuplier est présent dans la canopée. Des différences au niveau de la distribution le long du gradient des trois groupes de hauteur utilisés pour décrire l'abondance du sapin en sous-couvert (petits, < 30cm; moyens, de 30 à 100cm; grands, >100 à 300cm) suggèrent que l'établissement est probablement lié davantage à la proximité des semenciers qu'à la disponibilité des substrats. Par contre, des conditions de croissance plus favorables sous le couvert mixte augmenteraient le taux de survie des semis, ce qui expliquerait l'abondance de la régénération avancée. Cette meilleure croissance pourrait être liée au fait que la litière de peuplier, en étant facilement décomposable, ralentit le processus de paludification qui s'observe avec le temps dans les peuplements dominés par l'épinette noire de la région de la ceinture d'argile et qui crée des conditions qui nuisent au développement du sapin baumier.

Ainsi, en facilitant la régénération du sapin baumier dans le domaine résineux, la présence du peuplier faux-tremble en pessière pourrait contribuer à l'expansion nordique du domaine de la sapinière à bouleau blanc. Les résultats de cette étude témoignent de l'importance des interactions biotiques positives dans les mécanismes de succession secondaire, en particulier dans les zones où les contraintes environnementales sont plus importantes.

Mots clés : *Abies balsamea*, *Populus tremuloides*, facilitation, régénération, pessière, peuplements mixtes.

INTRODUCTION GÉNÉRALE

Problématique

La distribution des espèces végétales et la composition des communautés qui forment les écosystèmes forestiers sont modelées de façon importante par le climat (Whittaker, 1975; Woodward, 1987). La migration des espèces en réponse à d'éventuels changements climatiques pourrait mener à la création de nouveaux assemblages, et ultimement à la redéfinition des limites des grands biomes (Davis, 1981; Rizzo et Wiken, 1992; Webb et Bartlein 1992; Chapin *et al.*, 1993). Ce phénomène risque d'être particulièrement important à la limite nordique de distribution des espèces, là où les interactions compétitives sont moins intenses et les réponses au changement du milieu plus rapides (Chapin *et al.*, 2004). Certaines études présentent des modèles de migration des espèces pouvant atteindre près d'une centaine de kilomètres au cours du prochain siècle (Davis, 1989; Prentice *et al.*, 1992; Malcolm *et al.*, 2002). Par contre, les prédictions suggérant un contrôle prédominant du climat sur la distribution des végétaux sous-estiment largement l'importance des processus locaux et le rôle des interactions biotiques dans les mécanismes de migration (Loehle 1998, 2000; Brooker *et al.*, 2007; Caplat *et al.*, 2008). Par ailleurs, la dynamique de la succession et la régénération des peuplements forestiers sont grandement déterminées par le régime des perturbations naturelles (Paine *et al.*, 1998; Bond *et al.*, 2005; Jasinski et Payette, 2005). Ainsi, un changement au niveau des composantes climatiques entraînant une altération du régime des perturbations naturelles aurait probablement des conséquences bien plus importantes sur la distribution des espèces que celles prédites par les modèles n'intégrant que l'enveloppe climatique des espèces (Weber et Flannigan, 1997).

Dans les écosystèmes boréaux, la sensibilité aux variations du climat est particulièrement élevée puisque la température est un facteur limitant pour la croissance de nombreuses espèces (Kittel *et al.*, 2000; Chapin *et al.*, 2004). Les perturbations naturelles, en particulier le feu, constituent un élément de contrôle important pour la dynamique de la forêt boréale du nord de l'Amérique (Johnson, 1992; Payette, 1992). Dans le nord-ouest du Québec, des différences au niveau des paramètres du régime de feu expliqueraient en partie la position de l'écotone boréal, soit la transition entre la forêt boréale mixte et résineuse. En effet, l'abondance des essences feuillues dans le domaine mixte, couplée à la présence de nombreux lacs qui peuvent agir en coupe-feu, contribueraient à réduire la taille et la sévérité des feux (Bergeron *et al.*, 2004). Au nord, la topographie favorisant les feux de grandes superficies avantagerait les espèces comme l'épinette noire (*Picea mariana* (Mill.) BSP) et le pin gris (*Pinus banksiana* Lamb.) puisqu'elles possèdent des cônes sérotineux qui s'ouvrent sous l'effet de la chaleur (Zasada *et al.*, 1992; Greene *et al.*, 1999), alors que la rétention d'une moins grande quantité d'îlots résiduels confinerait le sapin baumier (*Abies balsamea* (L.) Mill.) à croître en plus grande abondance au sud du 49^e parallèle (Gauthier *et al.*, 2000; Bergeron *et al.*, 2004).

Au cours des dernières années, l'intensification des pratiques sylvicoles en forêt boréale a mené à une augmentation de la proportion des forêts de feuillus de lumière (Brumelis et Carleton, 1988). Dans une dynamique d'aménagement forestier, les pessières noires ponctuées de peuplier faux-tremble (*Populus tremuloides* Michx.) de la région de l'Abitibi se transforment en peuplements mixtes dominés par le peuplier faux-tremble (Grondin *et al.*, 2003). Comme le sapin baumier s'établit généralement en sous-couvert de peuplier dans la portion mixte de la forêt boréale (Bergeron et Charron, 1994), le processus d'enfeuillement des pessières noires pourrait créer des conditions plus favorables à l'établissement et la croissance du sapin dans le domaine résineux. En effet, il a été démontré que la présence du peuplier en pessière améliore les propriétés physiques et chimiques du sol (Légaré *et al.*, 2005) alors qu'un couvert de feuillus contribue vraisemblablement à diminuer la sévérité des incendies forestiers (Hély *et al.*, 2000). De plus, un éventuel réchauffement du climat entraînerait sans doute une hausse du potentiel reproductif de cette espèce au nord de sa zone de dominance (Messaoud *et al.*, 2007a).

Dans cette situation, les interactions biotiques positives pourraient jouer un rôle déterminant sur les mécanismes de succession qui influencent la vitesse de migration des espèces. Ainsi, une connaissance approfondie des facteurs qui contrôlent les limites de distribution et la dynamique de la végétation est essentielle à une meilleure compréhension de la mise en place des grands biomes dans un environnement en constante évolution. Cependant, comment se produisent ces changements et à quelle échelle spatio-temporelle peut-on les observer? C'est dans ce contexte plus global que se situe la présente étude. Puisque ce sont les propriétés de régénération qui influencent la vitesse à laquelle une espèce migre en réponse aux changements de son environnement (Chapin *et al.*, 1993), c'est principalement sur cet aspect que porte l'étude.

État des connaissances

La dynamique de la régénération du sapin baumier est bien connue dans la portion sud de la forêt boréale de l'ouest du Québec, où les peuplements de feuillus de lumière de peuplier faux-tremble et de bouleau blanc (*Betula papyrifera* Marsh.) établis après feu évoluent vers des peuplements dominés par le sapin baumier et le cèdre blanc (*Thuja occidentalis*) (Bergeron et Dubuc, 1989; Bergeron, 2000). Ce changement graduel des arbres qui forment la canopée est déterminé principalement par la tolérance à l'ombre et le taux de croissance des espèces puisque la plupart s'établissent dans les quelques années qui suivent le passage d'une perturbation majeure (Bergeron et Dubuc, 1989; Bergeron et Charron, 1994). Une série de trouées permet au sapin baumier établi en sous-couvert d'atteindre la canopée, alors que les épidémies de tordeuse des bourgeons de l'épinette favorisent le recrutement des feuillus intolérants (Kneeshaw et Bergeron, 1996; 1998). L'assemblage de ces peuplements mixtes forme le domaine de la sapinière à bouleau blanc. Au nord de ce secteur, dans le sous-domaine bioclimatique de la pessière à mousses de l'ouest, les peuplements d'épinette noire constituent le type de couvert le plus fréquent sur le territoire, accompagné par des peuplements de pin gris, de sapin baumier, de bouleau blanc et de peuplier faux-tremble (Grondin, 1996; Bergeron *et al.*, 1998). En absence de feu, les changements observés au sein de ces peuplements se situent davantage au niveau de la structure que de la composition. En effet, les pessières noires à structure équienne qui forment la première cohorte se voient progressivement remplacées par d'autres épinettes noires et l'accumulation de la matière organique au sol favorisant le marcottage entraîne le développement d'une structure plus irrégulière (Harper *et al.*, 2003; 2005).

Cette accumulation de la matière organique au sol qui s'observe avec le temps depuis la dernière perturbation mène à l'entourbement des peuplements (MacLean *et al.*, 1983). Ce processus appelé paludification est typique des peuplements forestiers anciens de la ceinture d'argile (Fenton *et al.*, 2005). Cette vaste région située de chaque côté de la frontière du Québec et de l'Ontario est caractérisée par des dépôts importants laissés par les lacs proglaciaires et possède un sol minéral riche en argile et en limon (Vincent & Hardy, 1977). Des réavancées glaciaires ont par la suite compacté ces argiles, ce qui les rend très peu perméables et qui favorise la mise en place des conditions propices à la paludification (Veillette, 1994). La dominance de l'épinette noire dans ce secteur favorise l'accumulation de la matière organique au sol par l'entremise de sa litière récalcitrante qui ralentit le processus de décomposition (Flanagan et Van Cleve, 1983), ce qui favorise l'établissement et l'expansion des sphaignes au sein de la couche de bryophytes dominée par les mousses hypnacées *Pleurozium schreberi*, *Hylocomium splendens* et *Ptilium crista-castrensis* (Taylor *et al.*, 1987; Fenton et Bergeron, 2006). Cette augmentation du couvert de sphaignes favorise la mise en place d'un environnement froid, humide et acide, ce qui réduit le taux de décomposition de la matière organique, l'activité microbienne et la disponibilité des nutriments essentiels à la croissance, notamment l'azote (N) et le phosphore (P) (Heinselman, 1981; Van Cleve et Viereck, 1981; Foster, 1985; Bisbee *et al.*, 2001; Turetsky, 2003). Dans cette situation, on assiste à une baisse de productivité des peuplements forestiers (Harper *et al.*, 2005).

La paludification peut être importante pour comprendre les changements observés au niveau de la structure et de la composition des peuplements en pessière. En effet, une étude menée par Lecomte et Bergeron (2005) dans la région de la ceinture d'argile révèle que les changements de composition au niveau du paysage sont déterminés par la tolérance des espèces à l'ombre, mais aussi par leur tolérance à l'entourbement. En absence de feu, l'épinette noire domine tous les peuplements ainsi que, pour la plupart des sites, la régénération avancée. La succession semble donc favoriser les espèces tolérantes à l'ombre. Cependant, comme les fréquences du sapin baumier et du mélèze laricin (*Larix laricina* (DuRoi) K. Koch) dans les stades avancés sont respectivement négativement et positivement corrélées au potentiel d'entourbement des sites, la tolérance à la paludification semble être un élément important de la succession en forêt boréale résineuse. Ainsi, les peuplements dominés par l'épinette noire favorisent à la fois la mise en place et le retour d'un certain type de communauté forestière. L'inflammabilité des essences résineuses, principalement l'épinette noire et le pin gris, mais aussi celle les plantes du sous-bois, les mousses hypnacées et les éricacées, favorise la récurrence des feux de forêt (Van Cleve *et al.*, 1991). Les espèces évoluant au sein de ces communautés doivent donc être bien adaptées à ce type de perturbation. L'épinette noire possède des cônes semi-sérotineux qui s'ouvrent sous l'effet de la chaleur, mais a aussi la capacité de se régénérer par marcottage (Zasada *et al.*, 1992; Greene *et al.*, 1999). Cette espèce peut donc s'établir abondamment suite au passage du feu, mais aussi se maintenir en absence de perturbation, lorsque l'épaisse couche de matière organique se développe au sol.

Depuis quelques années, il y a un intérêt grandissant pour l'étude des peuplements mixtes d'épinette noire et de peuplier faux-tremble de ce secteur. Le peuplier possède une litière facilement décomposable qui accélère le cycle des éléments nutritifs et réduit l'acidité du sol (Van Cleve et Noonan, 1975; Flanagan et Van Cleve, 1983; McClaugherty *et al.,* 1985; Bockheim *et al.,* 1991; Alban et Pastor, 1993; Paré et Bergeron, 1996; Légaré *et al.*, 2005). En plus d'augmenter la disponibilité des nutriments, un taux élevé de décomposition de la matière organique au sol serait nuisible à la croissance des mousses et sphaignes (Frego et Carleton, 1995; Saetre *et al.*, 1997; Fenton *et al.*, 2005). Par conséquent, la présence de peupliers en pessière pourrait contribuer à ralentir le processus de paludification et augmenter la productivité des peuplements (Légaré *et al.,* 2004; 2005; Fenton *et al.*, 2005). Les dépôts argileux de la région comportent des habitats mésiques propices à une dominance du sapin baumier (Bergeron et Bouchard, 1983), mais ce type de dépôt supporte souvent une importante couche de matière organique (Brumelis et Carleton, 1988; Boudreault *et al.*, 2002) ce qui limiterait l'établissement du sapin baumier dans le domaine résineux au profit de l'épinette noire (Gauthier *et al.*, 2000; Messaoud *et al.*, 2007b). Cette situation favoriserait du même coup la présence de l'épinette noire dans le paysage en facilitant son potentiel de réenvahissement suite à une perturbation au détriment du sapin baumier pour qui la recolonisation de sites se produit exclusivement à partir de semenciers résiduels (Galipeau *et al.*, 1997; Gauthier *et al.*, 2000). Par l'influence que le peuplier exerce sur son milieu, la présence de ce feuillu en pessière pourrait créer un environnement plus favorable au sapin baumier au nord de sa zone de dominance, entraînant ainsi l'expansion nordique de la sapinière à bouleau blanc.

Bien que la limite nordique de la distribution du sapin baumier se situe au-delà de la transition entre le domaine mixte de la sapinière à bouleau blanc et le domaine résineux de la pessière à mousses (Sirois, 1997), celui-ci ne réussit pas à dominer le paysage résineux. Il semble que les conditions climatiques diminueraient le potentiel reproducteur du sapin baumier dans le domaine résineux, alors que celui de l'épinette noire ne paraît pas affecté par ce gradient latitudinal (Messaoud *et al.*, 2007a). Par contre, un éventuel réchauffement du climat pourrait avantager le sapin baumier. La présence du peuplier en pessière pourrait quant à elle favoriser la régénération du sapin baumier en offrant des conditions plus favorables à son établissement et sa croissance en sous-couvert, mais aussi en augmentant la disponibilité des semences. En effet, le sapin baumier est un conifère très tolérant à l'ombre qui démontre une bonne capacité à se régénérer et à s'établir sous divers types de peuplement pour ainsi former une abondante banque de semis (Harvey et Bergeron, 1989; Frank, 1990; Côté et Bélanger, 1991; Morin et Laprise, 1997). Comme il se régénère principalement par graines, la présence de semenciers est nécessaire au réenvahissement d'un site après perturbation et sa reproduction est donc sérieusement limitée par le feu (Bakuzis *et al.*, 1965; Galipeau *et al.*, 1997). Le sapin baumier possède de grosses semences comparativement aux autres conifères, ce qui limite le potentiel de dispersion des graines (Greene *et al.*, 1999). Cependant, la présence d'espèces décidues peut vraisemblablement contribuer à réduire la sévérité du feu (Hély *et al.*, 2000), ce qui pourrait favoriser la préservation des semenciers de sapin baumier. Ainsi, la présence de peuplements mixtes de peuplier faux-tremble et d'épinette noire au sein du paysage résineux assurerait une plus grande disponibilité de semences pour le sapin baumier. De plus, le peuplier pourrait vraisemblablement altérer les conditions qui assurent le maintien des communautés dominées l'épinette noire et les bryophytes. En freinant le développement de l'environnement froid, humide et acide qui se forme au cours du processus de paludification et en assurant une plus grande disponibilité de nutriments, le peuplier pourrait créer des conditions qui faciliteraient la régénération du sapin en pessière.

Les principaux facteurs qui assurent la présence d'une espèce au sein d'un paysage forestier sont des conditions climatiques favorables à sa reproduction et sa croissance, la disponibilité de semences, la présence de sites propices à son établissement, puis une résilience aux perturbations (Major, 1951; Whittaker, 1975; Grubb, 1977; Harper, 1977; Eriksson et Ehrlen, 1992; Zasada *et al.*, 1992). Les propriétés de régénération ainsi que les conditions qui prévalent au moment de l'établissement sont donc des facteurs déterminants pour la composition des communautés. D'un point de vue démographique, l'établissement constitue une étape limitante puisque les jeunes arbres ont des besoins plus spécifiques (Clark *et al.*, 1999) et qu'ils sont confinés à des zones décrites comme étant des « habitats sécuritaires » (sensu Harper, 1977). Par conséquent, l'étude des jeunes arbres est particulièrement appropriée pour observer la réponse d'une espèce aux changements de son environnement (Gomez-Aparicio *et al.,* 2008). À l'échelle des graines et des semis, cet environnement est fortement modifié par les autres plantes (Aguiar et Sala, 1994) et les arbres qui forment la canopée exercent une grande influence sur les propriétés biotiques et abiotiques qui caractérisent l'environnement du sous-bois (Daubenmire, 1968; Harper, 1977). Évidemment, le succès de la régénération chez les arbres nécessite un établissement réussi des semis, mais aussi des taux de survie et de croissance qui assureront le recrutement subséquent (Rooney et Waller, 1998). L'effet bénéfique du peuplier sur l'établissement et la croissance du sapin baumier pourrait influencer la succession et ainsi contribuer au changement de composition des communautés forestières de cette région.

Ainsi, la présence du sapin en pessière pourrait vraisemblablement être facilitée par une plus grande abondance de feuillus dans la portion sud du domaine résineux. En écologie végétale, la facilitation est l'effet positif exercé par une plante sur une autre (Callaway, 1997). Les modèles de succession végétale reconnaissent depuis longtemps le rôle de la facilitation (Clements, 1916; Connell et Slatyer, 1977). Par contre, l'étude des interactions biotiques est largement dominée par la compétition (Brooker *et al.*, 2008). La proximité pour de nombreux chercheurs des écosystèmes plus riches où la compétition est un processus dominant est probablement à l'origine de cette concentration d'études sur le sujet (Brooker et Callaghan, 1998). Toutefois, il a été démontré au cours des dernières années que la facilitation et la compétition sont des processus qui agissent simultanément au sein des communautés végétales, et que l'effet net varie le long du gradient environnemental (Hunter et Aarssen, 1988; Bertness et Callaway, 1994; Greenlee et Callaway, 1996; Callaway et Walker, 1997; Holmgren *et al.*, 1997; Brooker et Callaghan, 1998; Kitzberger *et al.*, 2000). En effet, la compétition serait plus importante dans les zones les plus productives des écosystèmes, alors que la facilitation serait le principal mécanisme là où l'environnement est plus sévère. Ainsi, la facilitation pourrait jouer un rôle déterminant dans la succession des communautés situées dans les endroits où les contraintes environnementales sont plus importantes.

Objectifs

Dans cette situation, il est juste de se demander comment interagissent les différentes espèces au sein d'une communauté et comment les liens biologiques qu'elles développent peuvent affecter la succession du peuplement et la composition du paysage forestier. La prise en considération des processus locaux dans l'étude des mécanismes de succession, en particulier dans les zones où le stress environnemental est plus élevé, peut grandement influencer les prédictions des modèles de migration des espèces en réponse aux changements climatiques. L'objectif général de cette étude est de documenter l'importance du rôle de la facilitation dans les mécanismes de succession secondaire, en particulier chez une espèce qui se trouve à la limite de sa zone de dominance. Le premier chapitre de ce mémoire examine donc la relation entre le sapin baumier et le peuplier faux-tremble et tente de déterminer si la présence du peuplier facilite la régénération du sapin baumier au sein de la pessière à mousses de l'ouest du Québec. Pour ce faire, on évalue comment la présence du peuplier dans le couvert influence les principaux facteurs qui assurent le succès de la régénération naturelle d'une espèce; l'établissement, la croissance et la disponibilité des semences. Ainsi, on suppose que : 1) les lits de germination favorables à l'établissement du sapin baumier sont plus abondants sous le peuplier faux-tremble que sous un couvert dominé par l'épinette noire; 2) les conditions de croissance sont plus favorables pour le sapin baumier en sous-couvert de peuplier faux-tremble que sous un couvert dominé par l'épinette noire; 3) la présence de peuplier faux-tremble induit localement des feux de sévérité plus faible, protégeant ainsi les semenciers de sapin baumier lors du passage d'un incendie forestier.

CHAPITRE I

HARDWOOD ABUNDANCE FAVOURS BALSAM FIR INVASION IN THE BLACK SPRUCE-FEATHERMOSS BOREAL FOREST OF WESTERN QUEBEC (CANADA)

1.1 Abstract

In northwestern Québec (Canada), the presence of trembling aspen in black spruce dominated stands could contribute to the northward expansion of the mixedwood part of the boreal forest into the coniferous zone. By changing soil and fire conditions, two main factors that limit the invasion of the southern dominant balsam fir, aspen may facilitate balsam fir regeneration by creating conditions more favourable to the establishment and growth of this species. To evaluate the effect of aspen on balsam fir regeneration, we selected 7 sites possessing two adjacent stand types: a mixedwood stand with the heterogeneous presence of aspen and a black spruce dominated stand. Balsam fir regeneration, understory environment, and canopy composition were characterized from 531 sampling units distributed along transects that crossed the transition between the two stand types. Abundance of understory balsam fir regeneration was described using 3 height groups: seedling (<30cm), small sapling (30 to<100cm), and tall sapling (100 to 300cm). The results showed that balsam fir regeneration was generally more abundant when aspen was present in the canopy. Differences between the distribution of seedling and sapling groups along the mixedwood-coniferous gradient suggest that establishment probably occur over a wide range of substrates, but that the better growth conditions found under mixedwood stands ensure a higher survival rate for balsam fir seedlings. Balsam fir regeneration in black spruce-feathermoss forests seems to be facilitated by the presence of aspen in the canopy, thus suggesting that the increase of hardwoods in these coniferous forests, favoured by intensive management practices and climatic change, could contribute to the acceleration of the northward expansion of the mixedwood part of the boreal forest. These results provide insight on the role positive interactions play in regeneration dynamics and improve knowledge of the mecanisms involved in secondary succession.

Key words: *Abies balsamea*, *Populus tremuloides*, facilitation, coniferous boreal forest, mixedwood stands, regeneration.

1.2 Introduction

Postive interactions in plant communities, or facilitation, has long been recognized as an important factor driving ecological succession (Clements, 1916; Connell and Slatyer, 1977). However, competition has dominated consideration of functional strategies and biotic interactions within the ecological literature (Brooker *et al.*, 2008). Recent developments in plant facilitation research suggest that the net effects of competitive and facilitative interactions vary along environmental gradients, where competition is the dominant biotic interaction in more productive part of the gradient, and facilitation more important in areas with greater abiotic stress, such as those near ecotones (Hunter and Aarssen, 1988; Bertness and Callaway, 1994; Greenlee and Callaway, 1996; Callaway and Walker, 1997; Holmgren *et al.*, 1997; Brooker and Callaghan, 1998; Kitzberger *et al.*, 2000). Thus, facilitation could play a significant role in explaining the distribution and successional dynamics of forests in areas with greater abiotic stress (Holmgren *et al.*, 1997).

In northwestern Québec, the continuous boreal forest is divided into two bioclimatic domains: the southern mixedwood balsam fir (*Abies balsamea* (L.) Mill.) - paper birch (*Betula papyrifera* Marsh.) domain and the northern coniferous black spruce (*Picea mariana* (Mill.) BSP) - feathermoss forests (Saucier *et al.*, 1998). The transition between the mixedwood and coniferous boreal forests is partly explained by a combination of disturbance regime characteristics, landscape configuration, and climatic factors. The abundance of deciduous species in the mixedwood domain and the numerous lakes that can act as firebreaks both induce smaller and less severe fires, thus favouring species that require survivors to provide seeds for the reinvasion of burnt sites (e.g., balsam fir), whereas the flat topography of the northern coniferous domain promote the dominance of fire-adapted species, such as black spruce (Gauthier *et al.*, 2000; Bergeron *et al.*, 2004). Moreover a reduction in balsam fir seed production has been observed along the climatic gradient (Messaoud *et al.*, 2007a) despite the fact that its northern distribution limit is located far from the transition between its zone of dominance and the northern black spruce-feathermoss forests (Sirois, 1997).

In the absence of fire, the black spruce stands of this region are prone to paludification, i.e, an accumulation of organic matter and the expansion of a *Sphagnum spp.* cover, which creates waterlogged conditions that reduce soil temperatures, decomposition rates, microbial activity, and nutrient availability (Van Cleve and Viereck, 1981; Turetsky, 2003; Fenton *et al.*, 2005; Lavoie *et al.*, 2005; Fenton and Bergeron, 2006). This mechanism also results in a general decrease of stand productivity associated with changes in canopy structure where black spruce, originally established after fire, are progressively replaced by other black spruce originating from layering (Harper *et al.*, 2002; 2005). The increase in *Sphagnum spp.* cover thus promotes black spruce regeneration at the expense of other late successional species, such as balsam fir (Lecomte and Bergeron, 2005). These monospecific coniferous stands are also susceptible to large, severe fires (Hély *et al.*, 2001) that limit the invasion of species that require survivor seed trees to reinvade. In many southern boreal forest ecosystems, intensive management practices have supplanted fire as the main form of disturbance leading to an increase in the proportions of early successional hardwood species in comparison to a mosaic of stands shaped by natural disturbances (Brumelis and Carleton, 1988; 1989). In northwestern Quebec, black spruce stands with occurence of trembling aspen (*Populus tremuloides* Michx.) as a minor component and that are situated on fine textured soils are particularly sensitive to this process (Grondin *et al.*, 2003). Interest in understanding the dynamics of the black spruce and aspen mixedwood stands has grown over the last few years. In fact, recent studies suggest that the presence of aspen in these stands could halt the paludification process because their easily decomposable litter accelerates nutrient cycling and inhibits moss and *Sphagnum* growth (Van Cleve and Noonan, 1975; Paré and Bergeron, 1996; Légaré *et al.*, 2004; 2005; Fenton *et al.*, 2005; Laganière *et al.*, 2009).

By changing environmental conditions, the occurence of small patches of aspen within a landscape that is otherwise dominated by black spruce could favour the displacement of black spruce to the benefit of other species, such as balsam fir. Facilitation occurs when a species enhances the survival, growth, or fitness of another species (Callaway, 1997). Aspen may facilitate balsam fir regeneration in the southern part of the coniferous domain by creating conditions favourable to the establishment and growth of this species. The success of natural regeneration relies mainly on seed supply, availability of suitable seedbeds, and proper environments for germination and seedling growth (Daniel *et al.*, 1979; Caspersen and Saprunoff, 2005). The cold and acidic conditions that develop with time under black spruce are detrimental to balsam fir, a species usually associated with mesic sites (Bergeron and Dubuc, 1989; Messaoud *et al.*, 2007b), making aspen understory a more suitable place for it to establish. In addition, aspen may contribute to the preservation of balsam fir seed trees in the coniferous landscape by decreasing fire intensity, as decreases in intensity generally occur where deciduous species are abundant (Hély *et al.*, 2000). Further, stands dominated by shade intolerant species, such as aspen, generally transmit more light than those dominated by shade tolerant conifer species (Messier *et al.*, 1998); the light regime is a critical factor affecting tree growth (Lieffers *et al.*, 1999).

With ongoing global warming, major shifts in the ecological boundaries of forest ecosystem are likely to occur (Rizzo and Wiken, 1992). Therefore, facilitation could greatly influence species abilities to expand their range (Caplat *et al.*, 2008). An increase in hardwoods within the black spruce-feathermoss forest, coupled with a warmer climate, could create more favourable conditions for balsam fir regeneration, thus potentially leading to a northward expansion of mixedwood into the coniferous forests. The presence of aspen in the canopy greatly influences the understory environment, but its role in determining successional pathway is still unknown for the northern coniferous forests. The objective of this study is to assess whether or not the presence of aspen in the canopy facilitates the regeneration of balsam fir within the black spruce-feathermoss forest of northwestern Quebec. We hypothesize that understory balsam fir are more abundant when aspen is present in the canopy because the mixedwood stands not only provide suitable sites for establishment and better growth conditions, but also because the presence of deciduous species within the coniferous landscape contributes to the protection of balsam fir seed trees from fire.

1.3 Methods

1.3.1 Study area

The study area is part of the black spruce (*Picea mariana* (Mill.) BSP) – feathermoss (*Pleurozium schreberi* (Brid.) Mitt.) forest of western Quebec (Saucier *et al.*, 1998), located at the border of the Abitibi-Témiscamingue and Nord du Québec regions (49°09'N to 49°15'N, 78°44'W to 78°51'W) (Figure 1.1). This region is part of the Northern Clay Belt of Quebec and Ontario, a vast physiographic unit comprised of lacustrine deposits left by the proglacial lakes Barlow and Ojibway during the post-Wisconsin (Vincent and Hardy, 1977). The disturbance regime is characterized by large fires that kill all aboveground vegetation (Heinselman, 1981; Payette, 1992). The fire cycle length has increased from 101 years before 1850, to 398 years since 1920; the mean stand age is 148 years (Bergeron *et al.*, 2004).

The Lake Matagami Lowland corresponds to the south-western part of the black spruce-feathermoss forest. The topography is generally flat with a nearly continuous forest cover (Bergeron *et al.*, 1998). The landscape is dominated primarily by black spruce with an important component of deciduous or mixedwood stands originating from clearcuts or fire (Bergeron *et al.*, 1998). The closest meteorological station is located at La Sarre. For the 1961-1990 period, data from this station show a mean annual temperature of 0.8°C and a mean annual precipitation of 856.8mm (Environnement Canada, 1993). The length of the growing season is about 155 days (Robitaille and Saucier, 1998).

1.3.2 Sampling design and data collection

1.3.2.1 Sampling design

During the summer of 2006, seven sites possessing black spruce dominated stands adjacent to mixedwood stands containing a heterogeneous presence of aspen and natural balsam fir regeneration were selected. A stand initiation map (Bergeron *et al.*, 2004) and an ecoforestry map (MRNF, 2006) were used to choose sites with similar abiotic characteristics (surface deposits, slope, and drainage). The stands likely originated from a single fire that occurred around 90 years ago. The texture of the mineral soil has been verified through granulometric analysis (McKeague, 1978). The time since last fire was determined by coring a number of the dominant trees. At each site, two 100 meters long transects were placed in manner to cross the transition between the coniferous and mixedwood stands. To ensure that the mixedwood and coniferous stands were not associated with different deposits, a variance analysis (ANOVA) was conducted from samples taken at each extremety of the transects with the "transect" being the random factor and "type of stand" the fixed factor The analysis did not reveal any differences in clay percentages between the transects ($F = 0.0020$, $p = 0.9648$) and stand types ($F = 2.0706$, $p = 0.1014$).

Sampling points were marked systematically every 5 meters along each transect. An equivalent number of balsam fir of less than 3 meters height were also selected within a 5m wide section established along the transects. Firs were selected in a manner to maximize their distribution under the 2 stand types and to obtain a representative sampling of the firs growing in the understory with no overlap between sampling areas, thus the firs sampled were always located at a distance of at least 4m from the next selected fir. All of the fir regeneration sampled were individuals in good condition with no trunk or branch damage. At each site, 40 points and 40 firs were sampled, with the exception of one site that contained a punctuated presence of aspen where only 11 firs were present, making a total of 531 sampling units for the seven sites (280 systematic sampling points and 251 selected fir).

1.3.2.2 Canopy composition

The point-centered quarter method was used to describe the compositional characteristics of the canopy cover, where each sampling unit is considered the center point of 4 quarters oriented with the line of the transect (Cottam and Curtis, 1956). At each point, the species, diameter at breast height (DBH), and distance to the point were noted for the nearest living tree (DBH>10cm) in all four directions. A relative dominance index was calculated per species for each sampling unit using the following equation:

$$\text{Relative dominance} = \frac{\text{Total basal area of the species per sampling unit}}{\text{Total basal area of all species per sampling unit}} \times 100$$

The use of the 4 nearest trees allowed a more detailed analysis of environmental heterogeneity; environmental heterogeneity plays an important role in determining the nature of seedbeds and growth conditions for seedlings and saplings (Greene *et al.*, 1999; Pelletier *et al.*, 1999; Saetre, 1999; Légaré *et al.*, 2005). The mean distance (MD) of the four point-to-nearest-tree distances measured at each sampling unit was 2.3m. To ensure that stand densities were comparable between the different sites, we measured the absolute densities per ha (10 000m^2 / MD^2) for each transect (n=14) and performed a variance analysis (ANOVA) with the transects nested in the site factor (n=7). Absolute densities were natural log-transformed for normality. Results showed no significant differences (site: F=2.05, p=0.1812; transect: F=1.09, p=0.3719).

Sampling units possessing at least one aspen in the four nearest trees were classified as part of the mixedwood stand. The canopies were mainly composed of aspen and black spruce, but scattered individuals of jack pine (*Pinus banksiana* Lamb.), balsam fir, white birch, and tamarack (*Larix laricina* (Du Roi) Koch.) were also present. To ensure that the presence of aspen was not correlated with mineral soil properties, we tested the relationship between the mean relative dominance of aspen along the mixedwood sections of the transects with the clay percentages found at the mixedwood transect extremities using Pearson's correlation coefficient. This test revealed no significant relationships between the variables (r=0.0626, p=0.8317).

1.3.2.3 Microsite environments

The percent cover of understory species (herbs, shrubs, and bryophytes), woody debris, and deciduous litter within a 1m^2 quadrat centered on the sampling units were estimated using the following seven classes: (1) <1%; (2) [1%-5%[; (3) [5%-25%[; (4) [25%-50%[; (5) [50%-75%[; (6) [75%-95%[; (7) [95%-100%]. Woody debris were classified using 3 groups: aboveground, on the ground, and decaying. The decaying class of woody debris was defined as wood that could easily be penetrated by a pen to a depth of 3-5 cm.

The depth of the organic horizon (LFH layer) was measured for 115 systematically determined sampling units (56 sampling points and 59 selected firs). A sample of each organic horizon was brought back to the laboratory and frozen in order to determine pH, phosphorus concentration (P), and the carbon to nitrogen (C/N) ratio at a later date. The C/N ratio can be used as a general indicator of site quality where low C/N ratios correspond to sites that are rich in nutrients and possess high decomposition rates (Campbell, 1978). The forest floor pH was analyzed in distilled water (McKeague, 1978). The remainder of the samples were oven-dried at 60°C for 24h and then ground. Percent carbon and nitrogen contents were measured on the dried samples using a LECO CNS-2000 combustion analyzer (LECO Corp., Michigan, USA). Phosphorous content was extracted with a Bray II solution (McKeague, 1978) and then analyzed colorimetrically with a LACHAT flow analyzer (LACHAT Inst., Milwaukee, USA).

In August 2006, the light environments were assessed using the method validated by Parent and Messier (1996). Instantaneous measurements (Q_0) were taken at ground level and above the main understory vegetation (30cm aboveground) for each sampling unit and at the top of the selected firs using a LAI-2000 quantum sensor (Li-Cor Inc., Lincoln, USA) during completely overcast conditions. Full light conditions (Q_i) were obtained by placing a second sensor recording continuous measurements with a data logger in an adjacent clearing. Percent photosynthetic photon flux density (%PPFD = (Q_0/Q_i) x 100) represents mean daily light (400 to 700 nm) penetration under the forest canopy.

1.3.2.4 Abundance and growth of balsam fir regeneration

Balsam fir regeneration abundance was measured within a 2m diameter plot centered on each sampling unit and described using 3 height groups: seedling (<30cm), small sapling (30 to<100cm), and tall sapling (100 to 300cm).

Total height, stem diameter at ground level (measured with an electronic calliber ± 0.01mm), annual height increment, and crown morphological development were measured in the field for the 251 selected firs. Annual height increments were noted for the last 5 years (2002-2006) by precisely locating the terminal bud scars (node) left by the yearly fall of scales that protect the bud of the terminal leader (Parent *et al.*, 2002). The stem length between two nodes corresponds to an annual height increment unit, with the 2006 measurement starting from the terminal leader to the last node. A relative growth index was calculated by dividing the sum of the last 5 year's increments ($HG_{2002\text{-}2006}$) by the total height of the individual.

A mean annual increment value was obtained by averaging heigth growth for the completed growth seasons ($HG_{2002\text{-}2005}$). Lateral branches were measured for the last node in order to estimate crown morphological development with a spreading coefficient (C_s). This C_s is described with the following equation:

$$C_s = f / (\Sigma\, l_{br} / n)$$

where f is the length from terminal leader, $\Sigma\, l_{br}$, the sum of lateral branch length, and n, the number of lateral branches. This coefficient indicates the importance of terminal leader growth to lateral branch extension for the last node. It allows a rapid estimation of the actual state of the height growth of a tree with an umbrella shape indicating a suppressed state and a conical form generally characterizing a full growth state (Parent and Messier, 1995).

To understand the establishment dynamics of balsam fir within the sampled stands, we systematically sampled 95 of the 251 selected fir for age determination. The above and below ground parts were collected and brought back to the laboratory for dendrochronological analyses. Tree age is usually estimated by counting the number of annual growth rings at the ground level, i.e., at the presumed collar location (Telewski and Lynch, 1991). For trees growing in the understory, the trunk base may gradually become embedded in the humus layer, promoting the formation of an adventitious root system on the stem that can obscure the true location of the root collar (Telewski and Lynch, 1991; Parent *et al.*, 2000). This development is often accompanied by a reverse taper, i.e. a reduction in the number of growth rings towards the true collar (hypocotyl region) located below ground level (DesRochers and Gagnon, 1997). For shade-tolerant species, such as balsam fir, missing rings can also occur aboveground, likely resulting from radial growth cessation caused by a long period of growth in low light environments (Morin and Laprise, 1997; Parent and Morin, 2002). Consequently, the age of a seedling with adventitious roots can be underestimated by more than 20 years when counting rings at solely the ground level (Parent *et al.*, 2000).

To ensure that the aging would not be biased by these phenomena, successive counts on the transverse sections of both the above and belowground stem sections were performed. The strength of dendrochronological analyses relies on the ability of accurately dating the year of formation of each growth ring within a tree using the technique of cross-dating (Telewski and Lynch, 1991). Stem cross-section sampling began under the live crown, as growth rings begin forming just below, and extended downwards to ground level (Esau, 1960; Krause and Morin, 1995). Between 2 and 5 readings were performed, depending on stem height and visual aspect (more readings were made for stems displaying suppressed growth periods, where bud scars were difficult to identify). Beginning at the ground level, we tried to find the exact hypocotyl region by cutting the belowground part into 2-3cm transverse sections. The transition from stem to root was identified by the shift from the presence of a pith to a central vascular cylinder and by using pointer years from ground level (Esau, 1960; DesRochers, 1996). The cross-sections were progressively sanded (80-320 grit) and visually cross-dated using the skeleton plot method according to the procedures of DesRochers and Gagnon (1997). The ages obtained were minimal ages, as the hypocotyl regions were not exactly located, but determined as a 2-3cm region.

1.3.2.5 Search for seed trees

We searched for the presence of balsam fir seed trees (tree>10cm DBH, living or dead) within a 30m area around the transects because seed density usually follows a negative exponential decline with distance from the stem (Greene and Johnson, 1996; Greene *et al.*, 1999) and the mean height of mature trees is about 15m. We recorded the number and DBH of seed trees within this area.

1.3.3 Statistical analysis

The mean values of the different variables describing balsam fir regeneration abundance and growth were compared between the mixedwood and coniferous stands using Wilcoxon's nonparametric test, as assumptions of the variance analysis were not met.

In order to obtain an integrated representation of the abundance of the different groups of balsam fir regeneration with increasing proportions of aspen and the relative effects of environmental variables associated with the mixedwood–coniferous gradient, a canonical redundancy analysis (RDA) was performed. Response variables (abundance of seedlings, small saplings, tall saplings, and total abundance) measured within the 2m diameter plot were Hellinger transformed prior to analysis. The Hellinger transformation makes abundance and presence/absence data suitable for analysis with linear methods, such as RDA (Legendre and Gallagher, 2001). The explanatory matrix included the following variables measured for the 531 sampling units: relative dominance of aspen and black spruce, light measured at the ground level ($light_G$) and 30cm aboveground ($light_{30}$), percent cover of woody debris (aboveground, on the ground and decaying), deciduous litter, herbs (grouping all herb species), mosses (grouping mosses and lichens species), *Sphagnum spp.*, and ericaceous shrubs. Of all understory species identified, only the ones present at more than 5% of the sampling units were retained with the median value of each class being used for analyses.

The associations between balsam fir regeneration and substrates were determined using a chi-square analysis to test for differences between the observed and expected frequencies of substrates (Scherrer, 1984). Substrates were measured within a $1m^2$ quadrat and classified as deciduous litter, mosses, and *Sphagnum spp.* A qualitative substrate type was attributed to each sampling unit given the percent cover of these substrates. Instead of using abundances for the 2m diameter plot, total fir abundance (≤3m) was measured within the $1m^2$ quadrat and used to describe the occupation rate of the substrate types covering the same surface. A total of 589 firs were present in the 531 quadrats. The observed frequency (f_{obs}) was defined as the number of firs associated with a given substrate type, while the expected frequency (f_{exp}) was the number of firs associated with a substrate type with equal distribution amongst the substrates (f_{exp} = (589/531) x frequency of substrate type). A second chi-square analysis was performed to test for associations between balsam fir and woody debris (aboveground, on the ground, and decaying) representing the three decomposition stages.

An indicator species analysis was performed to identify understory species associated with the presence of balsam fir and that show a similar kind of response to the presence of aspen in the canopy using the method of Dufrêne and Legendre (1997). The computation of indicator values combined a species relative abundance (percent cover within the $1m^2$ quadrats) with its relative frequency of occurrence amongst different groups of sites. Indicator values are maximized when all individuals of a species are found in a single group of sites and occur at all sites within that group. Two types of groups were analyzed: species associated with the presence or absence of aspen in the canopy and species associated with the presence or absence of balsam fir regeneration (≤3m) in the $1m^2$ quadrat. The different species of *Carex* spp., *Dicranum* spp., *Lycopodium* spp., *Polytrichum* spp., *Pyrola* spp., *Sphagnum* spp., and *Viola* spp. were grouped to genus, while *Athyrium filix-femina*, *Dryopteris disjuncta*, and *Dryopteris spinulosa* were grouped into the *Polypodiaceae* family in order to attain the 5% level required to be included in the analysis. The statistical significance of the species indicator values were evaluated using a Monte Carlo test of significance of observed maximum indicator value for each species based on 1000 randomizations. Analyses were performed with the aid of PC-ORD (McCune and Mefford, 1999).

Another RDA was performed to illustrate the growth characteristics measured for the 251 selected firs (total height, stem diameter, mean annual increment, relative growth, and spreading coefficient) in relation to stand composition and environmental variables. Light at the top of the selected firs ($light_{top}$) was added to the matrix of explanatory variables previously described for the RDA of abundance data. Ordinations were computed with the program CANOCO Version 4.5 (ter Braak and Smilauer, 2002).

The age structure of the balsam fir regeneration was established for the 95 aged individuals. These aged individuals were grouped according to the same height classes used for abundance analyses (seedling (<30cm), small sapling (30 to<100cm), and tall sapling (100 to 300cm)). Mean ages were then compared using variance analysis (ANOVA) with Tukey's multiple comparison tests.

To determine if the abundance of understory balsam fir could be attributed to the fact that more balsam fir seed trees were found on sites with increased proportions of aspen, the total abundance of balsam fir regeneration measured per sampling unit were added to produce a measure per transect and a regression analysis between abundance of understory balsam fir and number (and basal area) of mature balsam fir was then conducted. Univariate analyses were performed using JMP IN 5.1 (SAS Institute Inc., Carry, USA).

1.4 Results

A comparison of the abundance and growth variable means for the mixedwood and coniferous stands are presented in Table 1.1. The mean values for all abundance and growth variables were significantly higher for the mixedwood stands.

The ordination plot (RDA) clearly illustrates the positions of the environmental variables and balsam fir regeneration abundance in relation to stand composition (Figure 1.2). The mixedwood part of the gradient was characterized not only by the presence of aspen and deciduous litter, but also by herbs and woody debris. At the opposite end, black spruce dominated stands were mainly associated with moss cover and to the group formed by ericaceous shrubs, *Sphagnum spp.*, and understory light (light_G and light_{30}). The position of the different groups of balsam fir regeneration along this gradient indicates an association with the mixedwood environment. The position of the total balsam fir regeneration, i.e., the sum of the three groups, indicates a positive association with litter and aspen and a negative association to spruce, moss, understory light, ericaceous shrubs, and *Sphagnum spp.* Taller saplings showed stronger correlations with herbs and decaying woody debris, while seedlings and small saplings were related more to woody debris on the ground. Seedling abundance was less associated to composition compared to the sapling groups. When forest floor properties were included in the analysis (an ordination conducted with a systematically determined subsample of 115 sampling units), higher pH and phosphorus concentrations occurred in the humus layers of the mixedwood environments, whereas high C/N ratios and humus thickness were found associated with black spruce canopy. Strong negative associations were found between high C/N ratios and the two sapling groups, deciduous litter, aspen, and decaying woody debris (results not shown).

Both the observed frequencies of total fir regeneration among the different substrates and the classes of woody debris were significantly different than the expected frequencies (Table 1.2, $p<0.001$). There were significantly more firs on deciduous litter substrates and less on moss and *Sphagnum* substrates ($p<0.05$). Positive associations were found only with substrates possessing a maximum percent cover of deciduous litter, i.e., with less than 15% cover of the other substrate types, suggesting that moss and *Sphagnum* substrates are less susceptible to be occupied by balsam fir, even if present in small proportions. Significant associations were also found for the three classes of woody debris described separately ($p<0.05$). The association was highest for decaying woody debris, followed by on-ground debris, and then negative for aboveground woody debris, indicating that fir was associated with the more advanced stages of decomposition.

Indicator species (Table 1.3) found in common with the aspen and the balsam fir groups were *Aralia nudicaulis*, *Pyrola spp.* and *Viola spp.*, while *Gaultheria hispidula*, *Carex spp.*, *Pleurozium schreberi*, *Ptilium crista-castrensis,* and *Sphagnum spp.* were commonly absent from these two groups. *Maianthemum canadense* was associated solely with fir, while *Kalmia angustifolia*, *Ledum groenlandicum*, *Hylocomium splendens* were mainly found in its absence. *Aster macrophyllus*, *Clintonia borealis*, *Cornus canadensis, Linnaea borealis*, *Lycopodium spp., Rubus pubescens*, *Trientalis borealis*, and *Polytrichum spp.* were found to be significant with the presence of aspen, whereas *Dicranum spp.* was significant with its absence.

Key characteristics of the 251 selected firs are presented in Table 1.4. The RDA biplot illustrates that higher values of growth caracteristics were all associated with the presence of aspen in the canopy and its related environmental variables (Figure 1.3). The spreading coefficient, mean annual increment ($HG_{2002\text{-}2005}$), and taller individuals (described with stem diameter and total height) were all correlated to deciduous litter cover, light measured at the top of the fir, aspen, and decaying woody debris. These response variables were also negatively associated with light measured 30cm aboveground. The position of relative growth, even if still associated to the mixedwood environment, was related more to herb cover and opposed to the presence of ericaceous shrubs.

The heights of the 95 aged individuals ranged from 16 to 243cm. The hypocotyl sections were found for 91 of the 95 trees. Cross-dating of the belowground sections added up to 17 years to the age estimates and only 15 firs were correctly dated at ground level. The age structure (Figure 1.4) shows a continuous and abundant recruitment of balsam fir seedlings. The mean ages of the 3 height groups were significantly different ($p<0.05$, n=95) according to Tukey's multiple comparisons test performed on the log-transformed data.

Mature balsam fir trees were not abundant in the stands. Seed trees were present at only 3 sites and their abundances varied greatly (5 trees at site 2, 11 at site

3, and 36 at site 5). Thus, the relationship between total fir regeneration abundance and the seed trees (abundance and basal area) was not significant (abundance: $R^2=0.2449$, $p=0.0720$; basal area: $R^2=0.2731$, $p=0.0552$).

1.5 Discussion

1.5.1 Abundance and growth of balsam fir regeneration

The results of this study indicate that balsam fir regeneration within the black spruce-feathermoss forest is generally more abundant when aspen is present in the canopy. Looking at the differences between the distributions of the three groups of balsam fir regeneration (seedlings, small saplings, and tall saplings) in relation to stand type, mixedwood or pure coniferous, reveals that seedling abundance is probably less influenced by aspen than the other groups. This suggests that seedling establishment is likely more a question of seed bearer proximity than seedbed availability. In fact, distance from a preserved zone has been identified as the most important factor explaining balsam fir regeneration density in many recruitment studies (Galipeau *et al.*, 1997; Asselin *et al.*, 2001; Caspersen and Saprunoff, 2005). Seedlings of larger-seeded species such as balsam fir are known to be resistant to various stress and generally do not require very specific seedbed types (Bakuzis *et al.*, 1965; Grubb, 1977; Greene *et al.*, 1999; Simard *et al.*, 1998; 2003). Thus, establishment could have occurred over a wide range of substrates, as offered by the sampled mixedwood-coniferous gradient. Even if seedbed conditions have changed since the germination period, the observed substrates probably correspond, to a certain degree, to the initial conditions because the main canopy species (black spruce and aspen) establish themselves simultaneously following a disturbance (Chen and Popadiouk, 2002). Moreover, in a study concerning the early seedling demography of balsam fir, Duchesneau and Morin (1999) showed that the spatial patterns of the newly emerged seedlings generally corresponded to seed dispersal, but that a few years later, the spatial pattern of the still surviving seedlings was independent of seed dispersal; seedbed types and understory light conditions were found to be the main factors explaining seedling mortality. This change in the spatial distribution of the seedlings could explain the differences observed between the three groups of balsam fir regeneration, where understory environments, mainly influenced by canopy composition, would lead to differential survival rates.

Sampling the regeneration over this range of heights is useful, as the advanced regeneration allows the identification of microsites that not only offer good germination substrates, but also growth conditions suitable for subsequent survival. Thus, the availability of microsites suitable for germination and subsequent survival would be higher under an aspen canopy, suggesting a higher mortality of the younger cohort under black spruce. Given the fact that balsam fir is a very shade tolerant species (Frank, 1990) and that it has the ability to persist for long periods in the understory and then respond with rapid growth to increases in light levels (Morin and Laprise 1997; Messier *et al.*, 1999), the negative association of seedling abundance with higher levels of understory light may suggest that seedlings are in fact individuals of lower growth. However, the results of the dendrochronological analysis showed that the smaller firs were generally younger, thus making saplings effectively older individuals experiencing better growth and higher survival rates in association with the rich aspen understory.

Deciduous litter cover is a relatively important variable associated with the presence of balsam fir regeneration. Many studies have reported the inhibitory effects of deciduous litter on conifer regeneration (Koroleff, 1954; Simard *et al.*, 1998; 2003; Parent *et al.*, 2006). In this study, most of the sampled regeneration has passed the limiting stage of germination suggesting that balsam fir could, in the long-term, benefit from the deciduous litter substrate. Moreover, the study sites presented a mixture of deciduous and coniferous species and they probably carry less litter than what was observed in some of the previous establishment studies conducted in the mixedwood part of the boreal forest. The fact that aspen litter accelerates decomposition rates and nutrient cycling (Van Cleve and Noonan, 1975; Paré and Bergeron, 1996; Légaré *et al.*, 2005) is probably responsible for the better growth observed for firs within the mixedwood stands. Indeed, the environmental variables associated with the presence of aspen in the canopy were consistent with these findings. Significant covers of deciduous litter, herbs, and woody debris were found under aspen, along with high pH and phosphorus concentrations in the humus layer. In contrast, black spruce dominated stands were characterized by the presence of bryophytes, ericaceous shrubs, thick organic layers, and high C/N ratios. The influence that individual tree species have on the understory environment vary greatly with distance from the trunk (Zinke, 1962; Lodhi, 1977; Messier *et al.*, 1998; Saetre, 1999; Légaré *et al.*, 2005; Kembel and Dale, 2006). Thus, it was possible to use the basal area of the nearest trees to detect the influence that the main canopy species have on environmental heterogeneity, which greatly affects trees growing in the understory.

Stand development in boreal mixedwood stands is characterized by a thinning stage leading to a canopy transition where pioneer tree dominance declines and shade-tolerant conifers take over the main canopy (Chen and Popadiouk, 2002). This mechanism could explain the abundance of woody debris found in the mixedwood stands. The association of fir with decaying woody debris is another indicator of the high decomposition rates that characterize the presence of aspen within these stands and likely explains the better growth observed for fir under mixedwood environments. In the southern boreal forests, stand aging enhances balsam fir regeneration through a reduction of leaf litter and herbaceous vegetation, along with increases in moist humus and rotten logs (Bergeron and Dubuc, 1989; Simard *et al.*, 1998). Aspen litter also prevents the establishment of *Sphagnum spp.*, which characterizes the development of cold, wet and acidic environments (Turetsky, 2003). In addition, the increased soil temperatures at these latitudes are likely to stimulate microbial activity and nutrient cycling (Chapin *et al.*, 1992). Thus, the higher soil temperatures associated with the presence of aspen probably constitute an advantage for balsam fir, especially north of its zone of dominance. The more acidic environment found under pure black spruce stands is also detrimental to balsam fir, particularly in the coniferous domain where the species preference for mesic sites is accentuated when compared to the mixedwood forests (Messaoud *et al.*, 2007b).

The high levels of understory light measured in the coniferous stands seems to contradict studies that found that deciduous species transmitted more light than conifer dominated stands (Messier *et al.*, 1998). In fact, the abundance of balsam fir regeneration and other understory vegetation under the mixedwood stands probably greatly reduces the light measured at the ground level and 30cm aboveground. Thus, light measured at the top of the sampled firs constitutes the most reliable measure of light available for growth. As expected, these light levels were higher with the presence of deciduous species in the canopy and highly associated with the growth of understory balsam fir. Both vertical and lateral growth were favoured by aspen cover. Moreover, balsam fir may also benefit from the absence of aspen foliage in spring and fall (Constabel and Lieffers, 1996). Furthermore, increased light and nutrients provide good conditions for the development of dense and tall understory vegetation that can hamper the establishment and growth of shade-tolerant conifers (Messier *et al.*, 1998). However, the benefits that come with this rich environment when compared to pure black spruce stands probably overcome the negative effects of abundant competitors. In fact, as previously exposed, mixedwood stands support less and less herbaceous vegetation with time as succession progresses (Simard *et al.*, 1998).

The position of the relative growth index along the mixedwood-coniferous gradient suggests that it may be less influenced by stand composition than other growth characteristics. For example, with the mean annual increment and total height, the influence of smaller firs was hidden by the effects of taller ones; their association with the presence of aspen supports the fact that taller firs were mainly found under mixedwood stands. Given the range of the sampled heights (12.2 to 297 cm, Table 1.4), the calculation of a relative growth index was a good method to obtain an overall picture of growth for all firs, without the effect of height. Thus, the position of the relative growth index on the RDA suggests that ericaceous shrubs exert a negative effect on the growth of balsam fir seedlings and saplings. In fact, ericaceous shrubs are known to be detrimental for conifer growth in general (Chapin, 1983; Titus *et al.*, 1995; Mallik, 2003). *Kalmia angustifolia* and *Ledum groenlandicum*, both members of the ericaceous family, were good indicator species for the absence of balsam fir regeneration and were found primarily in coniferous stands. Mosses (*Pleurozium schreberi*, *Ptilium crista-castrensis*) and *Sphagnum spp*. were also associated with black spruce dominance and the absence of balsam fir seedlings and saplings. Most of the indicator species associated with the presence of aspen and absence of fir (*Aster macrophyllus*, *Clintonia borealis*, *Cornus canadensis, Linnaea borealis*, *Trientalis borealis*) are species that spread with abundant light (Brumelis and Carleton, 1989). This may indicate that balsam fir is restricted to the more shaded portions of the mixedwood understory, which is in agreement with the high shade tolerance of the species.

Furthermore, mycorrhizal fungi play a major role in a number of ecological processes within the boreal forest (Read *et al.*, 2004). Simard *et al.* (1997) found a net carbon transfer from paper birch to Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco) seedlings through ectomycorrhizae, thus suggesting that mycorrhizal networks between pioneer species and shaded seedlings could promote the establishment of shade-tolerant species. In the mixedwood boreal forest of Quebec, some studies showed that mycorrhizal fungi distributions were influenced by the relative proportions of host tree species (Kernaghan *et al.*, 2003; DeBellis *et al.*, 2006). Even if no direct links between aspen, fir, and other understory species have been reported, recent work conducted on several genera of *Pyroleae* (one of the indicator species for aspen and balsam fir) found many potential fungal symbiots, which raises the possibility that these species (*Pyrola spp.*) may contribute to broader linkages with different host species within the forest community (Massicotte *et al.*, 2008).

1.5.2 Regeneration dynamics

We could not find evidence that the presence of aspen contributed to the preservation of balsam fir from fire, as we did not find sufficient mature firs within the sampled area to explain the abundance of regeneration. This could be due to the fact that this study was designed to evaluate the effect of canopy composition at the scale of the tree, whereas the presumed effect of aspen on fire severity acts more at the stand level (Hély *et al.*, 2000). A landscape study of the spatial distribution of mature balsam fir trees along with the mixedwood stands would be more appropriate to answer this question. The presence of natural regeneration requires seeds from living trees, as the dispersed seeds of balsam fir cannot survive more than one year (Houle, 1992). Although most of the seeds fall directly beneath the tree, the maximum dispersal capacity of an adult balsam fir is known to be about 160m (Sims *et al.*, 1990) and studies conducted in northwestern Quebec have found even found greater dispersal distances (Béland and Bergeron, 1993; Galipeau *et al.*, 1997). The seedling bank present at the sampled sites may have originated from trees that experienced some kind of protection during the last disturbance and that have since died or may have come from living trees found beyond the sampled area. In both cases, if we assume that the seed bearers proximity partly explains the regeneration abundance

(Galipeau *et al.*, 1997; Asselin *et al.*, 2001) and that this regeneration is more abundant under the mixedwood stands, we can still hypothesize that more seed bearers were present in the area surrounding the mixedwood stands.

The age structure obtained was typical of delayed postfire recruitment, as observed in other studies of balsam fir establishment (Bergeron and Charron, 1994; Galipeau *et al.*, 1997). However, we cannot compare recruitment during the initial phase of succession because we only sampled firs up to 3m in height. The absence of fire adaptations for balsam fir explains its late recruitment following disturbance (Bergeron, 2000). Furthermore, as it depends on living seed trees to colonize a site, the delay may be even longer in the black spruce-feathermoss domain than for the mixedwood forests because of balsam fir's lesser abundance in the landscape (Messaoud *et al.*, 2007a).

1.5.3 Conclusions

Our results suggest that the presence of aspen in black spruce-feathermoss forests facilitates balsam fir regeneration through enhanced growth conditions that ensure a higher survival rate for balsam fir seedlings. The easily decomposable aspen litter accelerates nutrient cycling and hinders the development of a thick forest floor layer, thus greatly altering conditions that otherwise provide a competitive advantage to black spruce. This natural process, coupled with warmer temperatures and industrial logging, could accelerate the northward expansion of the mixedwood bioclimatic domain into the coniferous forests. Investigating some of the mechanisms by which aspen facilitates balsam fir regeneration constitutes the first step for a global understanding of a long-term process that could lead to a shift in species dominance and to the redistribution of bioclimatic domain limits. Moreover, this study acknowledges the role of positive interactions on regeneration dynamics where abiotic stress is important. Improved understanding of facilitation process has direct relevance to the prediction of species response to climate change and to the development of strategies for maintaining the diversity and functional integrity of boreal forest ecosystems.

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Figure 1.1 Map of the study area showing the location of the 7 sampling sites.

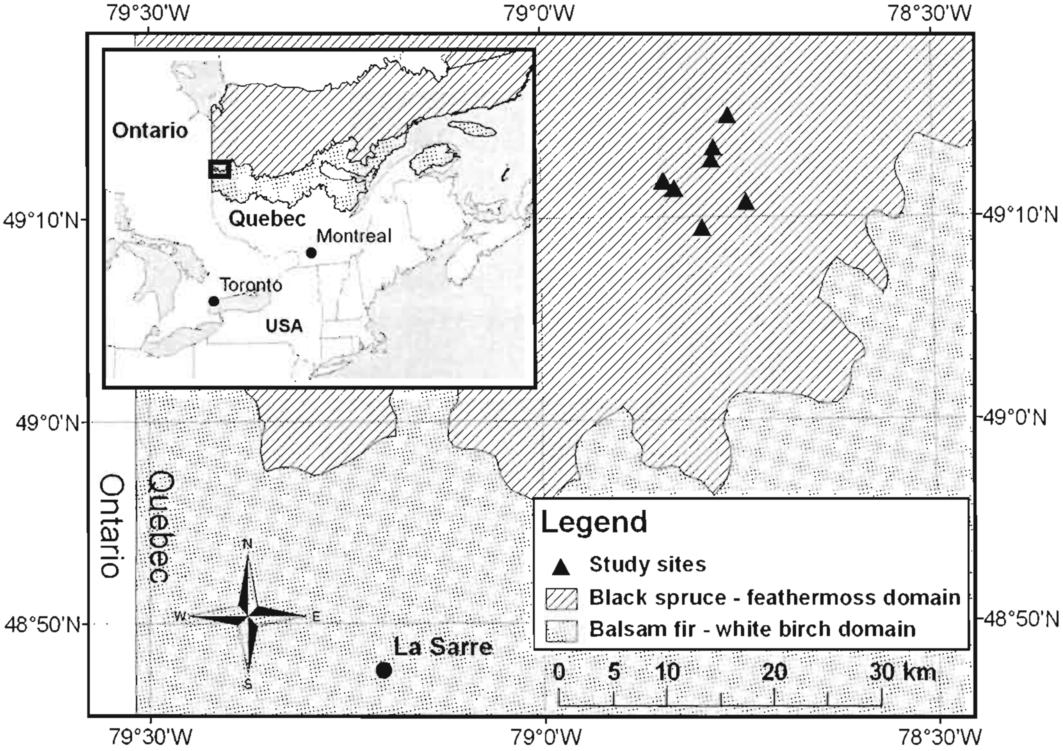

Figure 1.2 RDA correlation biplot of balsam fir regeneration abundance (dashed arrows) and environmental variables (solid arrows). *Seedling*: abundance of balsam fir seedlings (< 30cm); *Small sap.*: abundance of balsam fir saplings (from 30cm to <100cm); *Tall sap.*: abundance of balsam fir saplings (from 100cm to 300cm); *BF total*: total abundance of balsam fir (≤3m); *Aspen*: relative dominance of aspen; *Spruce*: relative dominance of black spruce; *Wood G*: woody debris on the ground; *Wood A*: woody debris aboveground; *Wood D*: decaying woody debris; *Light G*: %PPFD at ground level; *Light 30*: %PPFD 30cm aboveground. Percentage of variance in the data explained by ordination axes I and II: 17.2%, n=531.

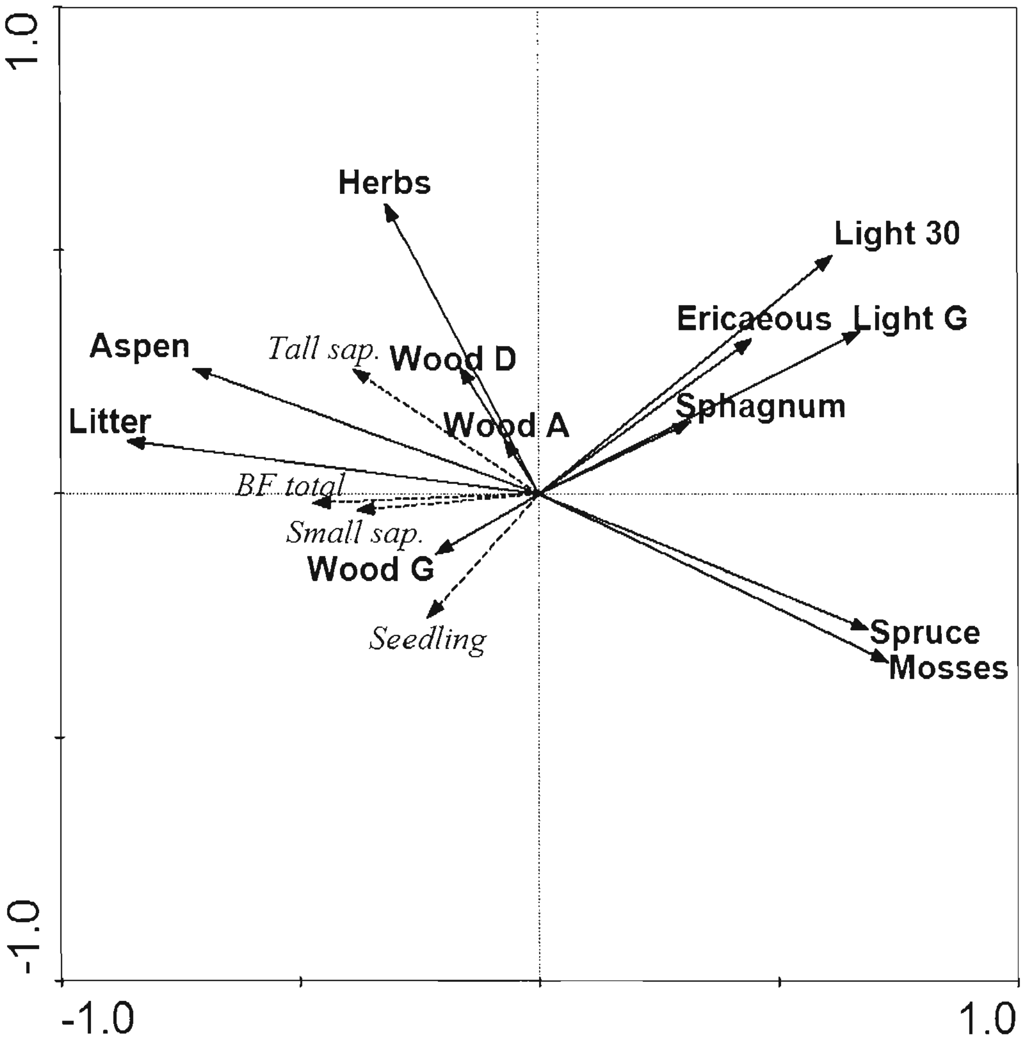

Figure 1.3 RDA correlation biplot of balsam fir regeneration growth characteristics (dashed arrows) and environment variables (solid arrows). *Aspen*: relative dominance of aspen; *Spruce*: relative dominance of black spruce; *Wood G*: woody debris on the ground; *Wood A*: woody debris aboveground; *Wood D*: decaying woody debris; *Light G*: %PPFD at ground level; *Light 30*: %PPFD 30cm aboveground. Percentage of variance in the data explained by ordination axes I and II: 61.8%, n=251.

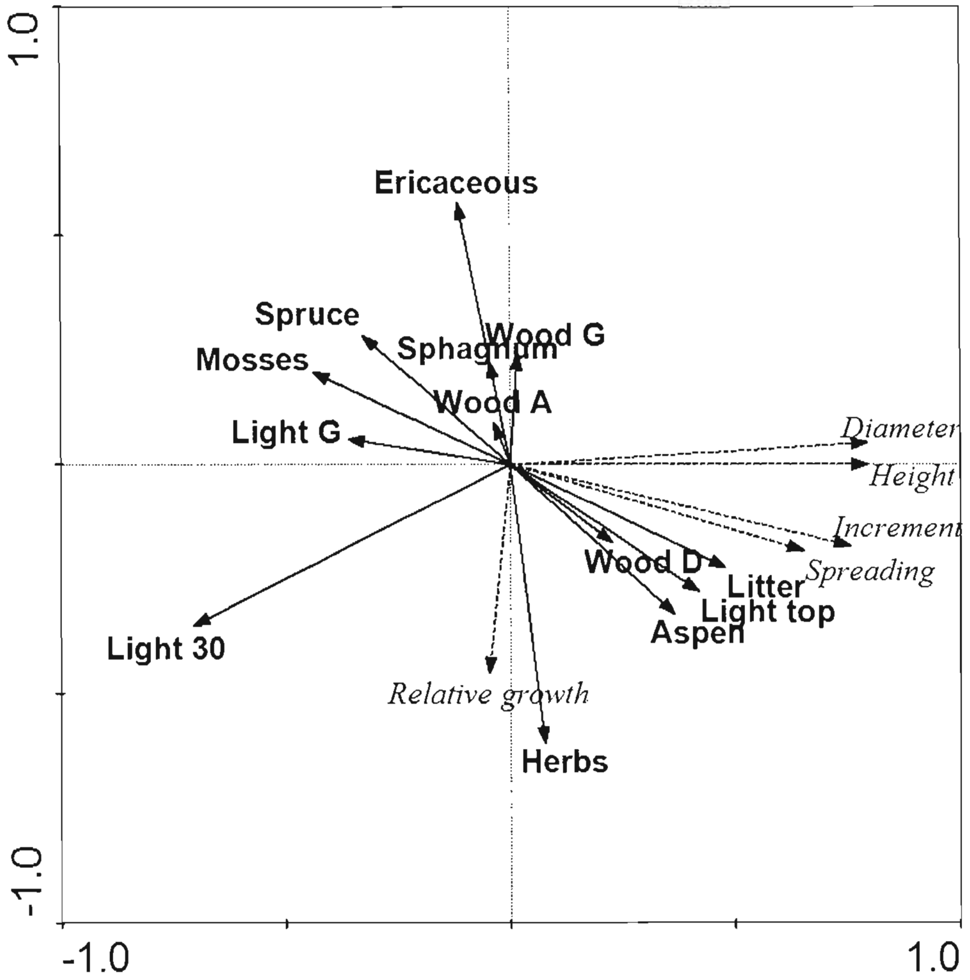

Figure 1.4 Age structure of balsam fir regeneration (≤3m) estimated by the dendrochronological analysis of a subsample of 95 firs.

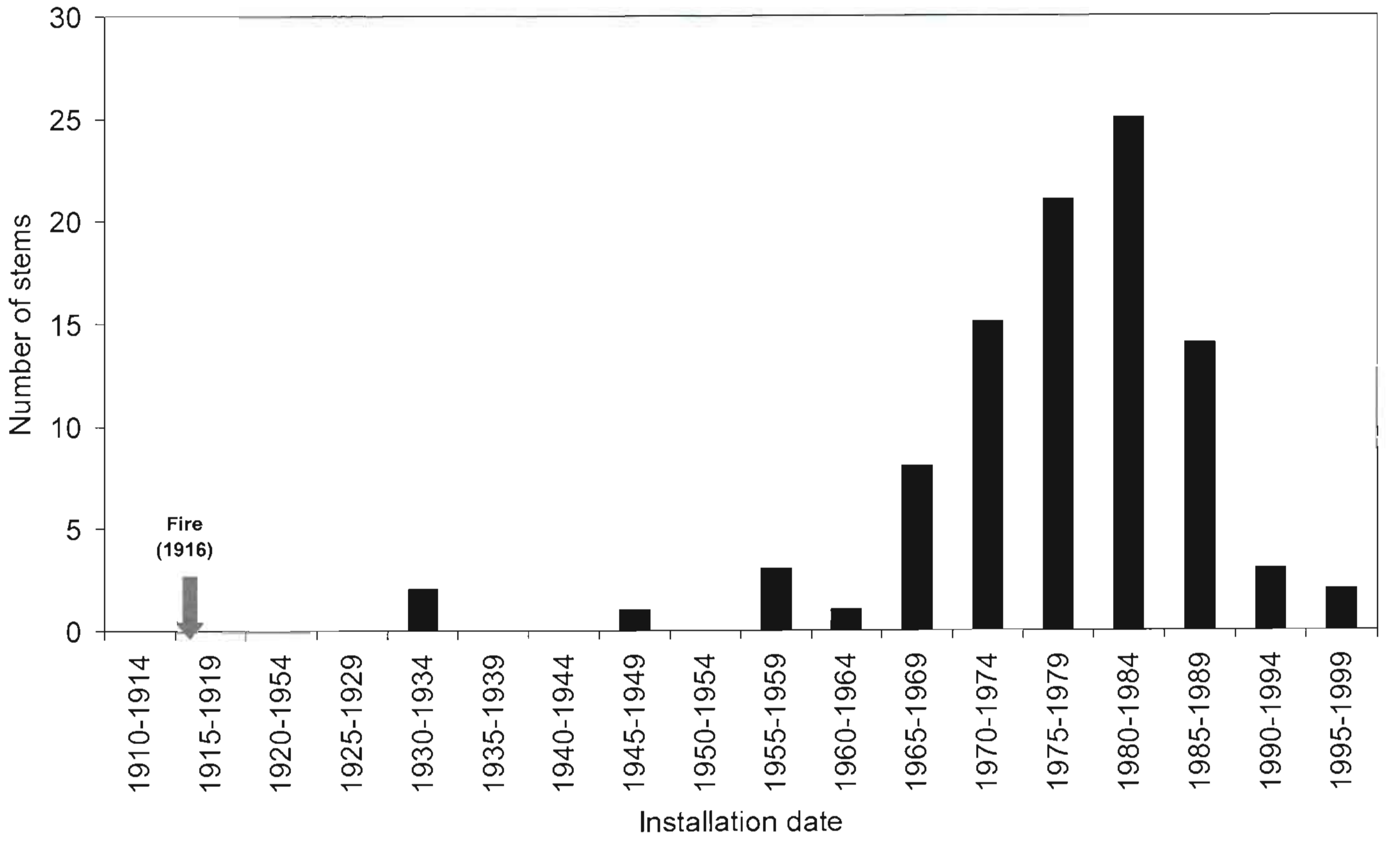

Table 1.1 Comparison of balsam fir seedling and sapling abundance and growth values between mixedwood and coniferous stands using the Wilcoxon test.

	Mean values (S.D.)*		S	*p*
	Mixedwood	Coniferous		
Abundance (n=531)				
Seedlings	2.16 (0.15)	1.19 (0.20)	42261	<0.0001
Small saplings	2.63 (0.15)	0.67 (0.20)	36721.5	<0.0001
Tall saplings	1.67 (0.11)	0.60 (0.14)	37316	<0.0001
Total	6.47 (0.32)	2.45 (0.43)	35715	<0.0001
Growth (n=251)				
Total height (cm)	108.53 (4.16)	63.01 (7.76)	4437.5	<0.0001
Diameter (mm)	16.65 (0.61)	10.49 (1.13)	4660	<0.0001
Mean annual increment (cm)	9.45 (0.37)	5.04 (0.70)	4146.5	<0.0001
Relative growth	0.46 (0.01)	0.41 (0.02)	5924	0.0181
Spreading coefficient	3.07 (0.11)	1.97 (0.20)	4659	<0.0001

*S.D.: standard deviation

Table 1.2 Chi-square analysis of associations between balsam fir regeneration (≤3m), substrates, and woody debris. Bold values are significant at $p<0.05$.

	Case observed	Case expected	Residuals	χ^2	*p*
Substrate					
Deciduous litter	251	170.8	80.2	**37.634**	
Deciduous litter and mosses	275	307.3	-32.3	3.386	
Deciduous litter, mosses, and *Sphagnum*	24	32.2	-8.2	2.074	
Deciduous litter and *Sphagnum*	13	15.5	-2.5	0.412	
Mosses	7	32.2	-25.2	**19.691**	
Mosses and *Sphagnum*	18	24.4	-6.4	1.680	
Sphagnum	1	6.7	-5.7	**4.806**	
Total	589			69.682	<0.001
Woody debris					
Aboveground	75	96.5	-21.5	**4.791**	
On the ground	66	51.0	15.0	**4.395**	
Decaying	61	37.7	23.3	**14.378**	
Above and on the ground	117	118.7	-1.7	0.024	
Above and decaying	22	21.1	0.9	0.041	
On the ground, and decaying	11	6.7	4.3	2.836	
Decaying, above, and on the ground	12	10.0	2.0	0.407	
No woody debris	225	247.4	-22.4	2.021	
Total	589			28.894	<0.001

Table 1.3 Indicator values (IV) of understory species showing positive (+) or negative(-) associations with balsam fir (≤ 3m) and with the presence of aspen in the canopy. Bold values are significant at $p<0.05$.

	Balsam fir		**Aspen**	
	IV	Association	IV	Association
Gaultheria hispidula	**36.8**	-	**55.3**	-
Kalmia angustifolia	**7.2**	-	3.2	-
Ledum groenlandicum	**17.0**	-	13.1	-
Vaccinium angustifolium	18.5	-	18.8	-
Vaccinium myrtilloides	13.5	+	15.8	+
Aralia nudicaulis	**6.6**	+	**6.6**	+
Aster macrophyllus	7.2	+	**12.9**	+
Carex spp.	**10.7**	-	**8.9**	-
Clintonia borealis	12.8	+	**23.2**	+
Coptis groenlandica	11.4	-	12.8	-
Cornus canadensis	44.1	+	**52.4**	+
Polypodiaceae	5.1	-	4.3	+
Goodyera repens	14.3	+	13.5	-
Linnaea borealis	37.4	+	**42.7**	+
Lycopodium spp.	18.4	+	**32.2**	+
Maianthemum canadense	**42.6**	+	36.5	+
Petasites palmatus	9.3	-	9.2	+
Pyrola spp.	**17.0**	+	**15.1**	+
Rubus pubescens	10.5	+	**22.0**	+
Trientalis borealis	26.3	+	**38.1**	+
Viola spp.	**29.2**	+	**44.3**	+
Dicranum spp.	21.2	-	**32.4**	-
Hylocomium splendens	**7.6**	-	5.0	-
Pleurozium schreberi	**59.4**	-	**70.2**	-
Polytrichum spp.	25.5	+	**45.9**	+
Ptilium crista-castrensis	**33.6**	-	**44.4**	-
Sphagnum spp.	**24.9**	-	**35.9**	-

Table 1. 4 Characteristics of the 251 selected firs.

	Minimum	**Maximum**	**Mean (S.D.)***
Total height (cm)	12.2	297	98.4 (61.0)
Diameter at trunk base (mm)	1.88	41.4	15.3 (8.8)
Height growth in 2006 (cm)	0.0	31.2	7.8 (7.3)
Mean annual height increment for 2002-2005 (cm)	0.83	25.0	8.8 (5.3)
Spreading coefficient	0.14	9.67	2.8 (1.6)
% PPFD at the top	3	22.7	9.0 (3.5)

*S.D.: standard deviation.

CONCLUSION GÉNÉRALE

Le principal objectif de cette étude était de mettre en évidence la relation entre deux espèces, un arbre feuillu qui forme la canopée et un conifère qui évolue en sous-couvert. Les interactions entre les différentes espèces arborescentes qui forment un écosystème forestier sont nombreuses et démontrer l'effet facilitateur d'une espèce pionnière sur une espèce de fin de succession peut être complexe, particulièrement lorsque les deux espèces sont relativement abondantes. La rareté des études expérimentales sur ce thème s'explique sans doute par la durée de vie des arbres et la difficulté de manipuler des individus adultes sur le terrain (Michalet *et al.*, 2008). Un certain nombre d'études portant sur la facilitation examinent effectivement les liens qui se créent au sein des communautés végétales entre des espèces de différents stades de développement, mais les communautés étudiées se situent souvent dans des environnements sujets à d'importants stress (Aguiar et Sala, 1994; Callaway et Walker, 1997; Hacker et Gaines, 1997; Tewksbury et Lloyd, 2001). De plus, le remplacement des espèces au cours de la succession peut être perçu comme étant le résultat des interactions positives et négatives entre les espèces (Connell et Slatyer, 1977), mais aussi comme étant déterminé simplement par les caractéristiques écologiques de ces espèces et les propriétés de l'habitat (Bazzaz, 1990). Ainsi, le défi consiste à établir dans quelle mesure la coexistence de deux espèces dans un peuplement est le fruit d'une relation positive entre celles-ci.

Les résultats de cette étude contribuent aussi à documenter le déplacement de la limite nordique de la sapinière à bouleau blanc dans l'ouest du Québec en examinant la relation entre l'espèce dominante de ce domaine mixte, le sapin baumier, et l'espèce qui pourrait vraisemblablement jouer un rôle clé dans ce processus, le peuplier faux-tremble. Un changement de dominance au sein du paysage forestier s'effectue principalement par des transitions de la voie successionnelle à l'intérieur des peuplements qui se distribuent dans le temps et dans l'espace (Chapin *et al.*, 2004) et c'est la raison pour laquelle on choisit d'observer d'abord les mécanismes à l'échelle du peuplement pour étudier les phénomènes qui se produisent à plus grande échelle. L'utilisation des 4 arbres les plus près pour détecter la variation des conditions du sous-bois en fonction du changement des espèces du couvert a permis d'observer une réponse au niveau de la régénération du sapin baumier. En effet, une étude effectuée par Légaré *et al.* (2005) révèle que l'influence du peuplier faux-tremble sur les propriétés du sol est observée principalement à l'intérieur d'une zone de 7 m autour du tronc. Ainsi, puisque la distance moyenne des arbres au point d'échantillonnage dans notre étude était de 2,3 m, l'utilisation de la surface terrière relative des espèces du couvert semble constituer une mesure adéquate du microenvironnement du sous-bois qui détermine le potentiel d'établissement de la régénération (Greene *et al.*, 1999). Par contre, cette approche semble avoir été plus efficace pour identifier les facteurs qui influencent la croissance plutôt que l'abondance du sapin. En effet, la composition des communautés est influencée à la fois par la variabilité des conditions de l'environnement à petite échelle et par les processus qui se déroulent à l'échelle du peuplement (Collins et Good, 1987; Beckage et Clark, 2003). Une approche située davantage à l'échelle du peuplement permettrait probablement de mieux reconnaitre les facteurs qui déterminent l'abondance de la régénération avancée. Toutefois, l'objectif ici était plutôt de comparer la réponse du sapin sous les 2 types de couvert, ce qui a été atteint.

La présence du peuplier faux-tremble dans le couvert accélère la cycle des éléments nutritifs, réduit l'acidité du sol et nuit au développement des mousses et des sphaignes (Van Cleve et Noonan, 1975; Flanagan et Van Cleve, 1983; Bockheim *et al.,* 1991; Alban et Pastor, 1993; Frego et Carleton, 1995; Paré et Bergeron, 1996; Saetre *et al.*, 1997 Légaré *et al.*, 2005). Ceci contribue vraisemblablement à freiner le processus de paludification observé dans les pessières noires avec le temps depuis la dernière perturbation (Fenton *et al.*, 2005). Comme la présence du peuplier faux-tremble dans une matrice autrement dominée par l'épinette noire exerce une grande influence sur les propriétés du milieu, l'abondance du sapin baumier dans ces peuplements mixtes pourrait être attribuable à son caractère opportuniste qui prend avantage des conditions de croissance favorables retrouvées sous le peuplier comparativement à l'environnement moins productif des peuplements dominés par l'épinette noire. Toutefois, la relation positive observée entre l'abondance et la croissance du sapin baumier en sous-couvert et la présence du peuplier semble illustrer un effet bénéfique réel du peuplier sur le sapin. Par sa litière riche et la lumière transmise sous sa canopée, la présence du peuplier crée un environnement de croissance favorable qui assure une meilleure survie des semis de sapin baumier. Ainsi, la présence du peuplier faux-tremble en pessière pourrait faciliter la régénération du sapin baumier au nord de sa zone de dominance. Deux hypothèses écophysiologiques sont proposées pour expliquer ces résultats; tout d'abord, un bilan annuel de lumière plus élevé sous le peuplier permettrait au sapin baumier d'obtenir un meilleur rendement photosynthétique, ensuite, la litière de peuplier, en empêchant l'établissement des sphaignes, aurait un effet positif sur la température du sol, ce qui favoriserait encore plus la photosynthèse, et du même coup la croissance du sapin baumier en sous-couvert de peuplier.

Ainsi, cette facilitation de la régénération du sapin baumier par le peuplier faux-tremble constitue probablement un processus naturel qui pourrait éventuellement mener à l'expansion nordique du domaine mixte à long terme. Par contre, ce processus risque d'être accéléré avec une intensification des coupes et un réchauffement du climat. La relation entre ces deux espèces pourrait être approfondie par l'étude des liens biologiques qui se forment au niveau du sol à l'intérieur des communautés, principalement par les mycorhizes, et par l'influence du peuplier sur le rendement photosynthétique du sapin baumier. En effet, les réseaux mycorhiziens qui se développent entre les espèces semblent être une avenue intéressante pour l'étude des facteurs qui favorisent la coexistence de certaines espèces (Booth, 2004). Les effets de la présence de ces peuplements mixtes sur la sévérité du feu et sur la préservation d'arbres semenciers à l'intérieur du territoire résineux pourraient aussi être examinés.

Implications pour l'aménagement

Dans le contexte actuel de changements climatiques et de gestion écosystémique, il apparaît essentiel de bien comprendre la dynamique naturelle des écosystèmes forestiers afin de développer des stratégies d'aménagement forestier durable. En ce basant sur une connaissance approfondie des systèmes naturels, il est alors possible de maintenir les fonctions essentielles (ex. productivité, résilience) et la biodiversité des écosystèmes sous aménagement (Johnson *et al.*, 1999; Bergeron *et al.*, 2002; Burton *et al.*, 2006). Les peuplements mixtes de peuplier faux-tremble et d'épinette noire font partie de la diversité du paysage forestier du nord-ouest québécois. Certains auteurs proposent de pratiquer de l'aménagement mixte en pessière afin de maintenir la productivité des peuplements (Légaré *et al.*, 2004; 2005; Fenton *et al.*, 2005). En effet, les interventions forestières qui ne perturbent pas l'épaisse couche de matière organique qui se développe avec le temps dans les peuplements dominés par l'épinette noire peuvent nuire à la croissance des jeunes arbres (Lavoie *et al.*, 2007). La présence d'une certaine proportion de peuplier faux-tremble pourrait limiter ce phénomène (Légaré *et al.*, 2004). Ainsi, le fait que ce type d'aménagement soit proposé dans les régions susceptibles à la paludification vient appuyer l'intérêt de bien étudier leur dynamique naturelle.

Au cours des prochaines années, un réchauffement du climat imputable aux émissions anthropogéniques de gaz à effet de serre est à prévoir (IPCC, 2007). Cette situation engendrera de profondes transformations au niveau de la distribution et de la composition des écosystèmes forestiers (Rizzo et Wiken, 1992). Le fonctionnement d'un écosystème étant déterminé principalement par les espèces qu'on y retrouve, l'étude de la migration des espèces constitue un élément essentiel à la compréhension de la réponse des écosystèmes face à ces changements (Johnstone et Chapin, 2003). De plus, le processus de facilitation semble être un élément clé permettant de mieux comprendre, donc de mieux prédire, le comportement de ces espèces en milieu naturel (Brooker *et al.*, 2008). Par ailleurs, puisque le feu constitue la principale perturbation naturelle en forêt boréale (Johnson, 1992; Payette, 1992), l'interaction entre le changement du climat et le régime d'incendies pourrait être beaucoup plus important que les effets directs du réchauffement global sur les espèces (Weber et Flannigan, 1997). De plus, une espèce comme le sapin baumier est particulièrement sensible aux variations du climat puisque l'étude de sa distribution historique suggère que l'essor et le déclin de ses populations en forêt résineuse soient déterminés par un changement du régime d'incendies (Ali *et al.*, 2008). Les connaissances fondamentales sont donc indispensables à une meilleure compréhension de la réponse de la végétation dans un environnement en constante évolution.

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