UNIVERSITÉ DU QUÉBEC À MONTRÉAL

CARACTÉRISATION DU PATRON DE MORTALITÉ DU PEUPLIER FAUX-TREMBLE ET DE L'ÉPINETTE BLANCHE DE LA FORÊT BORÉALE AU QUÉBEC

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AVANT-PROPOS

Les résultats obtenus lors de ce travail de maîtrise sont regroupés à l'intérieur d'un chapitre. Ce chapitre présente à la caractérisation de la mortalité du stade adulte du peuplier faux-tremble et de l'épinette blanche au sud de la forêt boréale québécoise, en Abitibi. Le texte est conforme à un article soumis à la « revue canadienne de recherche forestière ». La totalité des références du mémoire est présentée à la section Bibliographie.

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RÉSUMÉ GÉNÉRAL

Trois facteurs contrôlent la dynamique forestière : le recrutement, la croissance et la mortalité. Ce dernier est directement responsable du contrôle de la dynamique des peuplements. Il élimine les individus moins compétitifs, détermine la dominance spécifique et permet la remise en circulation des éléments nutritifs. Ainsi, la croissance et le recrutement des arbres sont étroitement reliés à la mortalité. Malheureusement, très peu d'information sur les facteurs causant la mort des arbres est disponible en ce qui concerne la forêt boréale. Certains facteurs tels que le stade de développement de l'arbre (semis, gaule ou adulte), la taille, l'espèce, l'effet des herbivores et les conditions environnementales semblent avoir un effet direct sur cette mortalité. Afin d'améliorer nos connaissances sur la dynamique forestière, cette étude s'est penchée sur le patron de mortalité temporel et spatial du stade adulte du peuplier faux-tremble (*Populus tremuloides*) et de l'épinette blanche (*Picea glauca*), au sud-ouest de la forêt boréale du Québec. Ces deux espèces ont été choisies en fonction de leurs nombreuses disparités. La première espèce, le peuplier, est intolérante à l'ombre, possède une large couronne située au-dessus de la canopée ainsi qu'un profond système de racine. La seconde espèce, l'épinette blanche, est considérée tolérante à l'ombre, possède un système de racine de faible profondeur ainsi qu'une longue et étroite couronne. Les hypothèses de travail sont : (1) la mortalité du peuplier faux-tremble est fortement dominée par des facteurs de type endogène, induisant une importante hausse de la mortalité à la sénescence du peuplement; (2) contrairement au peuplier, la mortalité de l'épinette blanche est majoritairement induite par des facteurs exogènes, provoquant ponctuellement une hausse de la mortalité. Le ratio de la mortalité (mort / total) démontre l'effet inverse. Des analyses dendrométriques ont permis d'identifier l'année de la mort des arbres. Les résultats ont permis d'observer une hausse importante de la mortalité chez le peuplier faux-tremble, en 1974, due probablement à la livrée des forêts (*Malacosoma disstria*). Cette hausse de la mortalité a été ressentie jusqu'en 1983. La mortalité des peupliers faux-tremble a été majoritairement observée chez les jeunes arbres (40 à 60 ans), avec un second sommet entre 110 et 155 ans. Chez l'épinette blanche, la mortalité a été observée de façon ponctuelle entre les années 1991 à 1999. La grande proportion des arbres qui meurent debout (>60%) et la caractérisation de la structure du bois au point de fracture, en plus des données météorologiques, ont permis de rejeter l'hypothèse que le vent soit une cause importante de la mortalité. Par contre, les épinettes retrouvées sur le sol démontrent une susceptibilité accrue au vent provenant du nord-ouest. Contrairement au peuplier, l'épinette blanche meure majoritairement à un âge avancé (110 à 150 ans). La position dans la canopée s'est avérée un facteur important pour prédire la mortalité des deux espèces. Les arbres intolérants à l'ombre (peuplier faux-tremble) démontrent un taux élevé de mortalité pour les individus dominé et co-dominants (15,5% et 11,5% respectivement). La variation du taux de mortalité en fonction de la position dans la canopée est moins importante pour l'épinette, qui est tolérante à l'ombre (opprimés 6,6%, co-dominants 5,5% et dominants 3,4%), que pour le peuplier. Étonnamment, les individus dominants des deux espèces possèdent des taux de mortalité comparables (peuplier 3,2%, épinette 3,4%). Les résultats obtenus pourront être utilisés pour valider les modèles théoriques ou de simulation de la dynamique de peuplements, tel que SORTIE ou tout autres modèles où la mortalité est un processus sous-jacent à la dynamique de peuplement.

INTRODUCTION GÉNÉRALE

La mortalité des arbres est un élément important de la dynamique des écosystèmes forestiers. Sa compréhension permet une meilleure prédiction de la dynamique et de la productivité des peuplements et l'anticipation des réactions des arbres face aux stress environnementaux (Franklin et al 1987, Miner et al. 1988, Pederson 1998). Même si leur importance a déjà été démontrée antérieurement, les facteurs contribuant à la mort des arbres sont, à ce jour, peu connus (Franklin et al. 1987, McCune et al. 1988, Mueller-Dombois 1993, Pederson 1998).

Bien que l'étude de la mortalité soit un sujet de recherche récent, certaines zones du globe, telles que la forêt tropicale et le Centre Ouest des États-Unis, possèdent plus de connaissance sur ce sujet. Plusieurs des recherches provenant de ces pays résultent d'événements catastrophiques (chablis, épidémie d'insectes, feu, vent excessif, anthropique, etc.) (Veblen et al. 1992, Condit et al. 1995, Dyer et Baird 1997, Pederson 1998, Villalba et Veblen 1998). La vaste mortalité induite par ce type de facteurs permet aux chercheurs de déterminer de fortes relations entre la cause et l'effet (Innes 1992, Clinton et al. 1993, Pederson 1999). Cette facilité à identifier les facteurs de mortalité est fortement réduite lorsque les peuplements sont régis par des facteurs endémiques (ou non-catastrophiques) (Harcombre et Marks 1983, Franklin et al. 1987, McCune et Henkel 1993, Pederson 1999). Dans ce cas, la mortalité est provoquée par une multitude de facteurs qui interagissent, rendant leur identification et leur quantification difficiles (Franklin et al. 1987, Pedersen 1998, Villalbat et Veblen 1998) particulièrement lorsqu'une période de temps importante s'écoule entre la cause de la mort et son effet perceptible par l'humain.

En forêt boréale, les facteurs de perturbations les plus importants sont le feu et les épidémies d'insectes (MacLean 1984, Cogbill 1985, Baskerville 1986, Bergeron et al. 2001). Cependant, depuis le dernier siècle, la récurrence des feux de forêt dans l'Est de l'Amérique du Nord a diminué (Archambault et Bergeron 1992, Bergeron et al. 2001), permettant aux perturbations dites secondaires de prendre de l'importance. Malheureusement, la mortalité en période inter feu est très peu documentée, particulièrement lorsque la mortalité n'est pas relié à des événements majeurs tels les épidémies d'insectes. En période non épidémique, la mort des arbres est principalement reliée aux facteurs de mortalité extrinsèque (e.g. sécheresse) et intrinsèque (e.g. sénescence) (Pederson 1998).

Parmi les facteurs extrinsèques, le vent est cité comme la plus importante cause de mortalité (Runkle 1990, Dyer et Baird 1997). Son impact sur les peuplements forestiers est différent de tout autres agents de perturbation. Les arbres ne sont affectés que localement, c'est à dire qu'une partie d'un peuplement peut être dévastée tandis que la portion annexe est intacte (Glitzenstein et Harcombe 1988, Veblen et al. 1989, Matlack et al. 1993, Dyer et Baird 1997).

Bien que les recherches au nord-ouest de l'Amérique du Nord soient souvent associées aux événements extrêmes tels que les grands orages, les ouragans, les cyclones extra tropicaux et, moins fréquemment, les tornades (Canham et al. 2001), le vent est aussi responsable de perturbations de plus faible ampleur (Ulanova 2000). Selon les caractéristiques physiques de l'arbre, et particulièrement la taille, la probabilité de chute varie. Ainsi, les arbres de classes intermédiaires démontrent une plus grande tendance au bris et au déracinement que les arbres sous la canopée (Glitzenstein et Harcombre 1988, Peterson et Pickett 1991, Dyer et Baird 1997). Étonnamment, les arbres surpassant la canopée ne sont pas affectés de façon disproportionnelle. Puisqu'ils occupent une position dominante et qu'ils sont exposés davantage aux grands vents, ces arbres ont développé un système d'encrage et de résistance plus efficace contre l'action éolienne. Le stade de développement du peuplement s'avère aussi un facteur important. Frangi et Lugo (1991) ont observé que les peuplements au stade transitionnel démontrent une plus grande sensibilité au vent que les peuplements jeunes ou âgés. Tandis que Everham et Brokaw (1996) et Ruel et al. (2001) ont identifié l'exposition de l'arbre comme facteur prépondérant. Les arbres situés au sommet de montagnes, à proximité de coupes forestières ou près d'ouvertures naturelles sont plus assujettis aux chutes.

Les caractéristiques morphologiques propres à l'espèce pourraient aussi être responsables du risque de chute. Par exemple, les conifères ont une plus grande sensibilité au vent que les arbres à feuillage caduque (Foster 1988, Veblen et al. 2001). Les conifères ont plus de chance d'être déracinés en période hivernale, lorsque le sol est gelé et que les arbres à feuillage caduque ont perdu leurs feuilles. D'autres chercheurs ont avancé que les conifères étaient plus vulnérables en raison de leur plus grande emprise au vent (Foster 1988).

Les caractéristiques propres aux individus, tel le système de racines, est un important facteur influençant la résistance. Les arbres provenant de rejets ou possédant de profondes racines détiennent un meilleur encrage dans le sol et diminuent leur sensibilité au déracinement. L'architecture de la couronne possède aussi un effet direct. Les arbres possédant une large ou haute couronne sont plus exposés au vent et ont plus de risque d'être brisés. Par contre, à cause de la grande variabilité de la densité du bois, de l'architecture et du système de racines racinaire il est à présent difficile de tirer des généralisations. Peterson et Pickett (1991) ont, eux, observé que l'action du vent est davantage reliée à la grandeur de l'arbre plutôt qu'à l'espèce. L'humidité du sol peut aussi jouer un rôle important. Le déracinement a souvent été observé sur des sols à mauvais drainage ou lorsque le vent est accompagné par de fortes pluies (Everham et Brokaw 1996).

Plusieurs autres facteurs extrinsèques, de seconde importance, peuvent aussi causer la mort. Ainsi ces arbres sains qui sont blessés ou écrasés suite à la chute d'arbres de plus grandes tailles (Frangi et Lugo 1991) ou la contamination par des agents parasitaires; ce dernier facteur cause souvent une mort graduelle qui rend difficile l'identification de l'agent pathogène. On peut aussi observer la diminution et l'arrêt de l'absorption des éléments nutritifs. Différentes causes climatiques telles que la sécheresse (Betancourt et al. 1993), les gelées printanières (Jenkins et Pallardy 1995) et les températures extrêmes (Jenkis et Stephen 1995) peuvent en constituer l'origine.

Le taux de mortalité des espèces arborescentes est une importante caractéristique pour connaître le taux de remplacement des espèces en forêt. Grâce à cette information, nous pouvons évaluer la dominance d'une espèce à l'intérieur d'un peuplement et mieux comprendre la dynamique forestière. Malgré la quasi inexistence de cette information en forêt boréale, nous savons que plusieurs facteurs sont susceptibles d'influencer le taux de mortalité des deux espèces étudiées. Parmi ceux-ci, mentionnons la taille des individus, l'âge du peuplement, l'espèce, la composition en espèce dans le peuplement, la présence d'herbivores et les conditions environnementales (Manokoran et Kochummen 1987, Condit et al. 1995, McCormick 1995, Bergeron 2000).

La tolérance à l'ombre est l'un des plus importants facteurs intrinsèques régissant la mortalité des arbres. Plusieurs chercheurs ont travaillé à caractériser et à modéliser la tolérance à l'ombre des semis à l'intérieur de la forêt boréale (Horn 1971, Bormann et Likens 1979, Shugart 1984, Glitzenstein et al. 1988, Burns et Honkala 1990, Pacala et al. 1994, Kobe et al. 1995, Kobe 1996, Kobe et Coates 1997, Peter et Clark 2000, Lin et al. 2001). Le consensus est que la mortalité est principalement induite par l'incapacité à survivre à l'ombre ; ainsi, les semis disposant de peu de lumière subissent une grande mortalité. Selon Manokoran et Kochummen (1987), on peut observer un patron similaire pour les arbres adultes. Les individus situés sous la canopée montrent un taux de mortalité supérieur à ceux dans la canopée.

Attribuable à la dégénérescence métabolique, la sénescence peut être responsable d'une réduction importante du nombre d'individus d'une cohorte (Noodén 1988, Noodén et Leopold 1988, Lugo et Scatena 1996). Suite à une perturbation majeure, tel que le feu, la nouvelle cohorte possède une grande dominance d'âge (forêt équienne) (Lugo et Scatena 1996). Tard dans le développement, lorsque les individus de cette cohorte deviennent vieux, la sénescence généralisée induit une forte augmentation de la mortalité dans le peuplement. Selon leur durée de vie, les espèces sont affectées à différents moments.

La plus importante application de l'étude de la mortalité est l'amélioration des méthodes de calcul servant à prédire la dynamique forestière. Depuis quelques années, les modèles impliquant la mortalité se sont multipliés. Parmi les plus récents modèles, notons ceux de Hamilton (1990), Kobe et al. (1995), Kobe et Coates (1997), Pedersen (1998), Dobbertin et Biging (1998) et Monserud et Sterba (1999). Malheureusement, ces modèles sont trop spécifiques (à une espèce, une classe de hauteur, de DHP ou pour une région donnée) pour pouvoir être directement appliqués à de nouvelles régions. Leur adaptation nécessite de nouvelles connaissances. Par exemple, SORTIE (Kobe et Coates 1997) est un modèle de dynamique forestière qui prédit, entre autres, la mortalité des semis et des gaulis en fonction des paramètres de croissance. Mais, ce modèle ne tient pas compte, présentement, de la croissance radiale pour prédire la mortalité chez les arbres adultes. Ainsi, un taux de mortalité aléatoire commun est utilisé pour tous les individus adultes d'une même espèce, ce qui semble peu réaliste.

Malgré la grande superficie de la forêt boréale, sa diversité végétale demeure relativement pauvre. Seules neuf espèces arborescentes dominent communément les peuplements de l'Amérique du Nord : *Pinus banksiana, Larix laricina, Abies balsamea, Picea mariana, Picea glauca, Betula papyrifera, Populus tremuloïdes, Populus balsamifera* et *Thuya occidentalis* (Takhtajan 1986) . L'objectif global de cette recherche est de caractériser le patron de mortalité naturelle au stade adulte de deux de ces espèces. La première est le peuplier faux tremble (*Populus tremuloides*), le plus important arbre à feuillage caduque de la forêt boréale de l'Amérique, à la fois écologiquement et commercialement. Cette espèce est considérée intolérante à l'ombre, possède une large couronne située au-dessus de la canopée, ainsi qu'un profond système de racines (Burns et Honkala 1990). La seconde espèce est l'épinette blanche (*Picea glauca*). Elle possède aussi un grand intérêt économique (pour la fabrication de la pâte à papier et le bois de charpente) et est considérée tolérante à l'ombre. Ce conifère possède un système de racines de faible profondeur ainsi qu'une longue et étroite couronne. Le patron de mortalité de ces deux espèces est comparé en fonction de critères spatiaux, temporaux et structuraux.

Deux hypothèses sont avancées pour chacune des espèces.
Pour le tremble les facteurs endogènes sont présumés responsables de la mort des arbres :

- Les arbres adultes situés sous la canopée (i.e. sous dominants et dominés) ont une mortalité plus élevée en raison du manque de lumière.
- Une forte mortalité se produit lors de la sénescence de la première cohorte de trembles après environ 100 à 120 ans.

Pour l’épinette blanche, les facteurs exogènes sont présumés responsables de la mort des arbres:

- Le vent est responsable de l’essentiel de la mortalité.
- La mortalité est plus importante à proximité d’une lisière (et ceci même si la lisière est un lac, donc permanente) en raison d’une exposition plus importante au vent.

La possibilité d’utiliser la croissance radiale pour prédire la mortalité des arbres adultes sera évaluée afin de raffiner, ultérieurement, le sous-modèle de mortalité dans SORTIE. Ainsi l’approche développée par Kobe et al. (1995) et Kobe et Coates (1997) pour la prédiction de la mortalité des semis, sera testée chez les arbres adultes. Selon cette approche, les individus ayant une faible croissance auront tendance à de mourir.

Par contre, cette technique peut ne pas fonctionner si la croissance radiale n’est pas reliée à la mort. Particulièrement dans le cas de l'épinette blanche où les facteurs exogènes sont présumés responsables de la mort de cette espèce. Ainsi la mortalité risque de ne pas être associée à une réduction de croissance puisque la mort est induite de façon quasi instantanée et indépendante de cette croissance. Ce problème ne devrait pas se poser pour le peuplier. Si l’on admet que la sénescence est vraisemblablement la principale cause de mortalité, une baisse considérable de croissance sera constatée dans les années précédant la mort.

Une cinquième hypothèse, applicable surtout au tremble (mais aussi tester pour l’épinette), est donc proposée.

- Les individus présentant une croissance de moyenne à supérieure auront une faible probabilité de mourir.

CHAPITRE I

Patterns of aspen and white spruce mortality in Quebec's Boreal Forest

1.1 ABSTRACT

Temporal, spatial and structural patterns of adult aspen (*Populus tremuloides*) and white spruce (*Picea glauca*) mortality were studied in intact stands in the south-western boreal forest in Quebec, Canada. Mortality was analysed in relation to two hypotheses: (1) aspen mortality is more directly related to endogenous factors (i.e. old age mortality and shading) which induces pulses of high mortality at senescence and in suppressed trees and (2) spruce mortality should be more closely related to exogenous factors such as wind. Spatially, distributions of trees (dead and live) of both species were found to be high near a lake edge and to decrease towards the interior of the stand. Aspen mortality was high within the first 30 meters of the shoreline due to beaver activity. Without taking beaver activity into consideration, both tree species have a declining ratio of dead to total trees with increasing distance from the lake. Tree-ring analyses were conducted to identify the year of mortality of each individual. Results demonstrate a significant increase in aspen mortality around 1974 due to a forest tent caterpillar (*Malacosoma disstria*) outbreak, followed by a slow decrease until 1983. Aspen mortality occurred in adult trees of all ages, but with a clear peak between 40 and 60 years of age and a smaller peak between 110 and 155 years of age. Spruce, on the other hand, showed only one peak in mortality, between 110 and 150 years of age, with clear yearly peaks between 1991 and 1999. The high proportion of trees that die standing (>60%) and the characterization of wood structure at the breakage point, supported by meteorological data, led us to reject windthrow as an important cause of mortality. Position below or within the dominant canopy was found to be an important predictor of mortality for aspen only. Shade intolerant aspen had a high mortality rate for suppressed and co-dominant trees (15.5% and 11.5% respectively) compared to dominant trees (3.2%). Surprisingly, dominant individuals of both species had similar mortality rates (aspen 3.2%, spruce 3.4%). These results can be used to validate both theoretical and simulation models of stand dynamics, like SORTIE, or other models in which mortality is an underlying process driving stand dynamics.

KEY WORDS: tree mortality, mortality rate, aspen, white spruce, tree falls.

1.2 RÉSUMÉ

Le patron de mortalité temporel, spatial et structurel au stade adulte fut établi à la fois pour le peuplier faux-tremble (*Populus tremuloides*) et l'épinette blanche (*Picea glauca*), au sud-ouest de la forêt boréale du Québec. La mortalité fut analysée en fonction de deux hypothèses: (1) la mort du peuplier faux-tremble est largement dominée par les facteurs de types endogènes, induisant une importante hausse de mortalité à la sénescence du peuplement, tandis que (2) la mortalité de l'épinette blanche est majoritairement induite par les facteurs exogènes, provoquant ponctuellement une hausse de mortalité. Le patron spatial démontre que la fréquence totale des arbres (vivants et morts) est plus élevée près du lac et décroît vers l'intérieur du peuplement chez les deux espèces. De plus, le peuplier faux-tremble indique une hausse de mortalité marquée à l'intérieur des 30 premiers mètres du lac, attribuable à l'effet du castor. Outre l'effet du castor, le taux de mortalité des deux espèces démontre une baisse de la mortalité liées à l'augmentation de la distance au lac. Des analyses dendrométriques ont permis identifier l'année de mort des arbres. Les résultats ont permis d'observer une hausse importante de mortalité chez le peuplier faux-tremble, en 1974, dû à la livrée des forêts (*Malacosoma disstria*). Cette hausse de mortalité à été ressentie jusqu'en 1983. La mortalité des peupliers faux-tremble fut majoritairement observée chez les jeunes arbres (40 à 60 ans), avec un second sommet entre 110 et 155 ans. Chez l'épinette blanche la mortalité fût observée de façon ponctuelle entre les années 1991 à 1999. La grande proportion des arbres qui meurent debout (>60%) et la caractérisation de la structure du bois au point de fracture, supportées par les données météorologiques, ont permis de rejeter l'hypothèse que le vent soit une cause importante de mortalité. Contrairement au peuplier, l'épinette blanche meurt majoritairement à un âge avancé (110 à 150 ans). La position dans la canopée s'est avérée un facteur important pour prédire la mortalité des deux espèces. Les arbres intolérant à l'ombre (peuplier faux-tremble) démontrent un haut taux de mortalité pour les individus dominés et co-dominants (15.5% et 11.5% respectivement). La variation du taux de mortalité en fonction de la position dans la canopée est moins importante pour l'épinette, tolérante à l'ombre (dominés 6.6%, co-dominants 5.5% et dominants 3.4%), que chez le peuplier. Étonnamment, les individus dominants des deux espèces possèdent des taux de mortalité comparables (peuplier 3.2%, épinette 3.4%). Les résultats obtenus pourront être utilisés pour valider les modèles soit théoriques, soit de simulation de dynamique de peuplements, tel que SORTIE, ou tout autres models où la mortalité est un processus sous-jacent à la dynamique de peuplement.

MOTS CLÉS: mortalité des arbres, taux de mortalité, peuplier, épinette blanche, chute des arbres.

1.3 INTRODUCTION

With the increasing number of scientific publications on tree mortality, there is an increased awareness that tree mortality is a critical factor controlling stand dynamics in forest ecosystems (Harcombe 1987, Maser et al. 1988, Whitmore 1989). The composition, structure and dynamics of forests can be attributed, in part, to processes that kill trees and create particular conditions for different successional pathways (Lugo and Scatena 1996). An understanding of the rates and causes of tree mortality is essential in order to predict forest growth and its response to environmental stresses (Franklin et al. 1987, Miner et al. 1988, Pedersen 1998). At this time, however, the pattern of mortality of adult trees is poorly understood with most of the research having been conducted in tropical forests. Literature on adult mortality in intact boreal forests of North America is extremely rare (Yao et al. 2001). This is particularly true for background tree mortality (i.e. not caused by large disturbances) where death occurs at relatively low rates (Harcombe and Marks 1983, Pedersen 1998).

In the boreal forest of North America, large-scale disturbance is largely due to fire and insect outbreaks (MacLean 1984, Cogbill 1985, Baskerville 1986, Bergeron et al. 2001). However, in eastern Canada over the last century, intervals between fires have increased and the effects of fire have been reduced (Archambault and Bergeron 1992, Bergeron et al. 2001). Secondary disturbances, including individual or group tree mortality, are much more important when fire return intervals are long. Although our understanding of mortality processes has advanced in recent years, there has been little interest until quite recently in studying natural single or multiple tree mortality in natural forests whose age (or time since burning) exceeded the average life-span of the tree (Kneeshaw and Gauthier accepted). During these transitional periods, individual tree mortality is principally related to exogenous (e.g., drought) and endogenous (e.g., genetic) factors (Pederson 1998).

Wind, one of the most important exogenous factors contributing to mortality, has been evaluated in many regions of the globe (Dyer and Baird 1997, Jalkanen and Mattila 2000, Gardiner and Quine 2000, Ruel 2000, Ulanova 2000, Skatter and Kucera 2000, Dunham et

Cameron 2000, Canham et al. 2001). In some case, windthrow may lead to patch dynamics whereas in many other cases wind affects trees only locally (Dyer and Baird 1997, Frelich 2002). There has been much research to show that topography and topographic positions are important factors affecting susceptibility to windthrow (Everham and Brokaw 1996, Ruel et al. 2001). In situations where topography is not an important factor, other factors such as tree species, tree size and edge exposure may be more important factors to consider (Dunn et al. 1983, Harcombre and Marks 1983, Glitzenstein and Harcombe 1988, Dyer and Baird 1997, Veblen et al. 1989, Foster and Boose 1992, Dyer and Baird 1997, Veblen et al. 2001, Canham et al. 2001).

Morphological characteristics of species are also related to susceptibility to wind damage (stem breakage, bending or uprooting). The root system is an especially important factor affecting resistance to wind. Trees with deep root systems or those originating from root suckers, such as aspen, possess a better anchorage in the soil which greatly decreases their susceptibility to uprooting. On the other hand, trees with large or tall crowns are more exposed to wind. The literature suggests that conifers are generally more affected by wind than deciduous angiosperms (Webb 1988, Peterson and Pickett 1991, Veblen et al. 2001). Wind also has less of an impact on deciduous broadleaf trees during the winter when trees are leafless and soils are frozen (Veblen et al. 2001), but the large variability in wood density, tree architecture and root system, does not easily permit generalizations within taxonomic groups.

Amongst intrinsic or autogenic factors affecting mortality, shade tolerance has been identified as one of the most important factors to consider among species (Horn 1971, Bormann and Likens 1979, Shugart 1984, Burns and Honkala 1990, Pacala et al. 1994, Kobe et al. 1995, Lin et al. 2001). In the boreal forest, research to date on shade tolerance demonstrates that growth and mortality of seedlings and saplings are strongly related to light availability (Horn 1971, Bormann and Likens 1979, Shugart 1984, Glizenstein et al. 1986, Kobe et al. 1995, Lin et al. 2001). Heavy shading leads to higher seedling and sapling mortality for shade intolerant species especially. This phenomenon is poorly documented for adult trees, but Manokoran and Kochummen (1987) reported that adult tree mortality was also linked to light availability. They found that within species, individuals located under the canopy had a higher mortality than dominant individuals.

Senescence may also be responsible for much of the mortality attributable to endogenous and metabolic degeneration and this can be observed in major reductions in the number of individuals in a cohort (Noodén 1988, Noodén and Leopold 1988). After a large disturbance event, like fire, a new even aged cohort is often dominant (Lugo and Scatena 1996). Late in development, when all individuals in the cohort are ageing, senescence of trees induces a peak in mortality in the stand. Such old-age mortality is known to vary greatly among tree species.

The demography of adult trees, particularly their mortality rate, is a key factor governing the structure of boreal forest communities. Yet, to date, few studies have investigated the patterns of tree mortality in these forests. This study examines the differences in the pattern of mortality at the adult stage for two contrasting species in the boreal forest. The first species, aspen (*Populus tremuloides* Michx.), is the most important deciduous tree species in the North American boreal forest, both ecologically and commercially. This species is considered shade intolerant, with adult trees having a wide crown found at the top of a long bole and a root system deeper than many competing species (Burns and Honkala 1990). The second species, also an important commercial tree for both pulpwood and lumber, is the shade tolerant white spruce (*Picea glauca* (Moench) Voss). It is coniferous with a shallow root system and a long narrow tree crown.

The spatial, temporal and structural patterns of mortality of these two species were investigated. One hypothesis tested was that adult aspen mortality, due to its shade-intolerance, its wind firmness and its short life span, is largely driven by endogenous factors (e.g. senescence and shade intolerance). This would suggest a peak in mortality as trees approach their reported longevity and that understory trees would have a greater probability of dieing than overstory trees. In contrast, it was hypothesized that the mortality of adult white spruce is mainly by exogenous factors (e.g. wind) since spruce is recognized to live longer, be more tolerant and more susceptible to wind than aspen (Nienstaedt and Zasada 1990).

1.4 MATERIAL AND METHODS

1.4.1 Study area

The study sites are in The Lake Duparquet Research and Teaching Forest (FERLD) surrounding Lake Duparquet in , located south of Lake Abitibi in northwestern Quebec (79°1′ W, 48°30′ N). The geomorphology of this region is characterized by the influence of a postglacial lacustrine phase that formed the Northern Clay belt, covering a vast area in east-central Canada (Vincent and Hardy 1977). The closest meteorological station to the study area is at LaSarre, ~ 42 km to the north. The climate is cold and temperate with a mean (1961-1990) annual temperature of 0.8°C, a mean annual precipitation of 856.8mm and an annual frost-free period of 64 days (Environment Canada 1993). Most liquid precipitation falls during the growing season but evaporation can limit plant growth in both June and July. The temperatures can reach below zero during the entire growing season. The maximum annual mean daily temperature is 6.7°C and the minimum is –5.5°C. Lake Duparquet is located in the southeastern boreal forest within Rowe's (1972) Missinaibi-Cabonga forest section. Balsam fir and aspen are the dominant species; black spruce (*Picea mariana*), white spruce (*Picea glauca*) and paper birch (*Betula papyrifera*) are the co-dominant species. Stands of pioneer species, such as jack pine, aspen, and paper birch, occupy large areas following a disturbance (Bergeron and Bouchard 1984).

The periodic occurrence of fire since the end of the last glaciation has been documented from lake sediments (Richard 1993). The fire regime during the last 300 years has been reconstructed by Dansereau and Bergeron (1993). The mainland fire regime is characterized by high intensity fires covering large areas, especially in flat topography (Bergeron 2000). The fire cycle has been shown to be increasing in recent centuries, reaching a cycle of more than 120 years after 1870. Three major spruce budworm (*Choristoneura fumiferana*) outbreaks occurred during 1919-1929, 1930-1950 and 1970-1993 (Morin et al. 1993). The forest tent caterpillar (*Malacosoma disstria*) is another major insect attacking deciduous stands, and severe outbreaks were reported in the area during the 20th century (Bergeron and

Charron 1994). Kneeshaw and Bergeron (1998) have shown that gap dynamics are active and important in these forests. To standardize for the effects of soil, all study sites were located on clay deposits with a moderate moisture regime (Brais and Camiré 1992).

1.4.2 Methods

Aspen and white spruce adult tree mortality was evaluated in 3 different mixedwood stands. The age of these stands is approximately 150 years and corresponds to the time of last fire. Studied stands were dominated by aspen and balsam fir, although white spruce is also present in the canopy but not in large proportions.

Three to five transects were established in each of the three stands. The starting point of the transect was located at the first aspen and spruce tree nearest to the lake and the orientation was perpendicular to the lake. At each site, transects were parallel to each other. In the case of a sudden change in forest composition, the transect was stopped and another started 50-100m away, parallel to the first one. Each transect was 10 m wide while the length varied from 100 to 480 meters. All trembling aspen (N=892) or white spruce (N=303) greater than 7 cm DBH were measured. For both dead and live trees the following data was collected: DBH, distance of each tree to the lakeshore, distance of each tree to the center of the transect line, tree canopy position as either dominant (in canopy), co-dominant (located in the canopy but clearly under dominant trees) or suppressed (very clearly well under the canopy), and a notation of wounds and distinctive signs (insect, disease, presence of fungus, cracks, etc.).

To estimate canopy position, visual estimates were made for snags whereas log length was compared to canopy height for downed trees. Time since mortality, may have led to some bias in the estimation of canopy class for trees which had been dead for many years since surrounding living trees may have continued to grow. A correction was applied to determine the correct class for co-dominant trees. A dead tree that was classified as dominant at the time of sampling would also have been dominant at any given time in the past as the surrounding canopy would have been smaller, we applied a similar logic to small suppressed trees. To make corrections for co-dominants (N=119), the year of death was verified as determined from dendroecological analyses (see below). The radial growth of surrounding trees was substracted for the number of years since tree death. For example, if tree X died 14 years ago, then 14 years of growth as subtracted from the surrounding live trees. Canopy position was then corrected by re-assigning the dead tree a canopy class based on its diameter and the diameter of surrounding species in each of the three canopy classes. For example, if tree X, which died 14 yrs ago, had a DBH of 32 cm, and the DBH of dominant trees is now > 34 cm DBH, then tree X would be re-classified from co-dominant to dominant because the DBH was probably only 28 cm at the time of the tree's death.

Each dead tree was categorised into one of five classes; 1- Broken after dead (a downed snag that died upright and fell after death); 2- Snags (dead trees that are still standing); 3- Bowed or snapped (trees that were broken when alive); 4 Uprooted (trees that blew over exposing their root systems); and 5- Crushed (trees killed when a larger tree fell on them). Since trees in class 1 and 3 may be difficult to categorize, their assignment to a class is based on our best knowledge of wood structural differences at the point of breakage. Errors would be greater for older dead trees in which physical characteristics at the point of breakage would be the hardest to identify. Thus our estimation of the numbers of trees that snapped while alive would be an underestimation for older trees. Trees that were snapped while alive presented some of the following conditions: presence of fine branches and leaves, splintering at the point of breakage, jagged break-points that were unequal in height around the trunk of the tree, points of attachment, no discolored wood, etc. Dead trees were also classified by decay conditions (0 = dead leaves still present to 5 = dead tree incorporated into the soil) according to McCune et al. (1988) methodology. Finally indices on reason of death and orientation for fallen trees are also noted.

1.4.3 Dendrochronological analysis

For live aspen, each third specimen was systematically selected and two cores were taken at the base. Since the base of trunks may be oval, the first core is taking on the longest axis and a second one is taken at 90 degree to the first core (usually a short radius). Due to the low frequency of white spruce, all trees were cored. For dead aspen and spruce, each dead tree was cut at the base and a disk was collected. If trunks were rotten, the disk was collected higher along the stem to a maximum of 2 meters. If trunks are still rotten at 2 meters, the sample wasn't retained.

The techniques used for measuring tree rings in cores and disks were the same as that used in previous dendroecological research in the same area (Archambault and Bergeron 1992, Dansereau and Bergeron 1993, Bergeron 2000). Tree-ring widths were measured using a Henson incremental measuring stage to a precision of 0.01 mm. Two radii were measured per sampled disk. The first radius was measured on the longest axes of the disk and the second was measured at 90 degrees to the first one. If a measured radius reached a rotten part of disk (this often occurred at the periphery), the radius was displaced until it felt on solid, non-rotten wood (if possible). Later on, each chronology was cross-dated with a master chronology from living trees to identify the year of mortality and the age of the dead tree. Cross-dating accuracy was verified using the COFECHA program (Holmes 1983).

1.4.4 Data analysis

The effect of distance to an opening (the lake) as a function of the ratio of dead trees to all trees (dead and live) for white spruce and aspen, was examined using a polynomial quadratic regression by the procedure :

$$[1] \quad ? = ?^{o} + a? + b?^{2} .$$

To test the effect of canopy position on mortality, an ANOVA was used. The mortality ratio was compared amongst the three different canopy classes in separate tests for each of the two species. A post-hoc Tukey test was used to determine which groups were different when the ANOVA proved to be significant. The letters a and b are used in figure 2 to identify statistically different groups.

Logistic regression models were developed to evaluate predictors of mortality. The response variable was the probability of a tree being dead. Explanatory variables included in the model were position in the canopy, DBH (at 1.3m height) and annual diameter increment during each of the last five years (complete years of growth) preceding death. The response variable ? is a binary variable indicating whether a tree is dead (? = 1) or alive (? = 0). The logistic model was formulated as follows:

$$[2] \quad p = \frac{1}{1 + e^{-(b_o + b_1 x_1 + \ldots + b_k x_k)}}$$

where ß = ($b_o, b_1, \ldots, b_k$) are unknown parameters. The stepwise procedure was used in selecting independent variables at a significance level of $P < 0.05$.

All of the above statistical analyses were conducted using SAS v8 (SAS Inc. 2000)

The probability of tree mortality based on radial growth was tested with the model developed by Kobe and Coates (1997). In this model, a maximum likelihood test, also provides a quantitative estimation of shade tolerance. The model uses the annual diameter increment of live and dead tree for a specific species and calculates the probability of mortality as the product of the density function of prior growth rates for dead individuals and the density function of prior growth rates for live individuals (see Kobe and Coates 1997 for a more detailed explanation). The model used had the form $m(g) = p(\text{death} | \text{growth}) = e^{-Cg}$. Where $m(g)$ is the probability of mortality as a function of growth, and C is a parameter to be calculated and has the biological interpretation of species shade tolerance. Lower C values indicate less tolerant species.

1.5 RESULTS

1.5.1 Pattern of mortality as a function of distance to lake (forest edge)

Both aspen and spruce were found to be more abundant (both living and dead stems) close to the lake, with the overall density of these trees decreasing with distance from the lake to the end of our transects. The mortality ratio (dead / total) was used to eliminate any possible effects of tree density on the results. This ratio illustrates a pattern that we do not observe using only relative frequencies (the relative distribution of dead trees along a transect, where the number of dead equals 100%) of dead trees along the transects (Figure 1a). For aspen, mortality was the highest near the lake (0.69), decreasing rapidly in the first 40 meters (0.27) and then increasing with distance after 180 meters. Higher mortality close to the lake was due to beaver activity. Our study suggests that beavers are responsible for cutting down 31.5% of all aspen in the first 30 meters, with beaver caused mortality increasing to close to 45% in the first 10 m. Up to 50 meters, some lives trees showed scars caused by beavers, but no beaver killed trees are observed between 30-50m.

Spruce displays a similar overall pattern as aspen as the relative frequency of spruce (both dead & live) was the highest near the lake and decreases with distance away from the lake. The mortality ratio is, however, lower near the lake (0.27) and increases with distance away from the lake (to 0.75 at 180 meters) (Figure 1b).

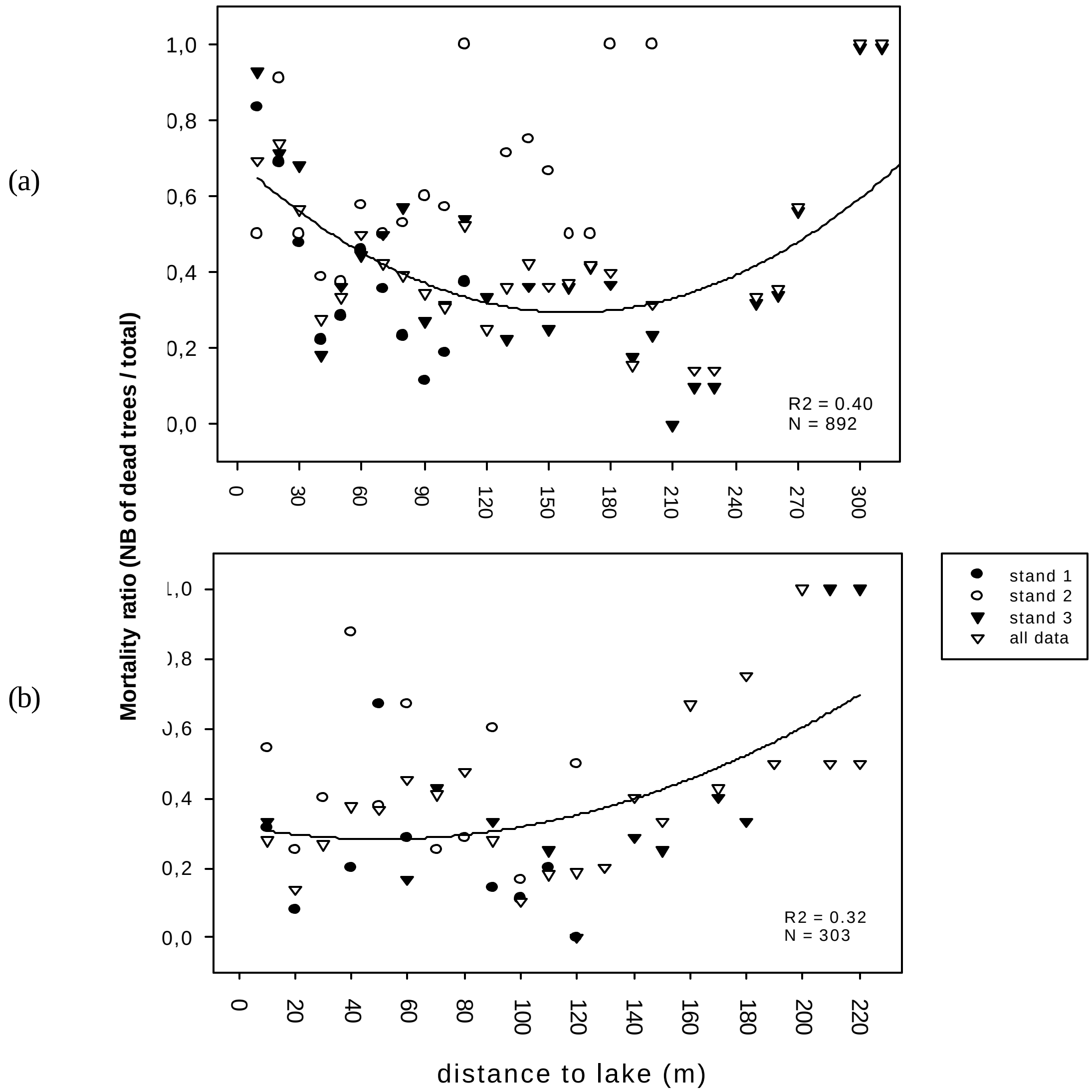


Figure 1. Aspen (a) and white spruce (b) mortality (NB of dead / total) as a function of distance to lake (m). Solid line represents tendency of all data.

1.5.2 Mortality related to structural characteristics

The position of the tree in the canopy is a important factor that contributes to mortality (Figure 2). Suppressed individuals are more susceptible to die, particularly for aspen. The mortality ratio (dead / total frequency) reveals that aspen located beneath the main canopy (ratio of 0.83) had more than 2 times greater chance of dieing than individuals considered to be in the dominant class (ratio of 0.30). Co-dominant aspen (ratio of 0.73) also had a mortality ratio much more elevated than individuals in the dominant class. Canopy position had much less of an effect on spruce mortality. Suppressed trees continue to have a higher mortality ratio than the other classes (a mortality ratio of 0.49 compared to dominants with a ratio of 0.25 and co-dominants with a ratio of 0.37) but in contrast to aspen, none of the classes were statistically different from each others.

The standardization of annual increment (increment of year X / increment of year X-1) used in the logistic regressions to detect the effect of growth, was identified as an important variable in predicting mortality. For aspen, the canopy position of the tree as well as the last complete year of radial growth before death were found to be very highly ($Pr < 0.0001$, $R^2=0.17$) significant predictors of the probability of mortality:

$$\text{Prob (dead Aspen)} = 1 / [\ 1 + \exp^{-(2.3239\ +\ 0.7618*\text{canopy position}\ -\ 0.0661*\text{DHP(cm)}\ -\ 1.0339*\text{growth\_1}\ -\ 1.3006*\text{growth\_2})}]$$

where canopy position corresponds to dominant (1), co-dominant (2) or suppressed (3) tree classes, DBH is in cm, growth_1 corresponds to the last year of radial growth in mm and growth_2 to the year before growth_1. Results for spruce were not similar as recent radial growth was not found to be an important predicting factor:

$$\text{Prob (dead Spruce)} = 1 / [\ 1 + \exp^{-(-0.5765\ -\ 0.9906*\text{canopy position}\ -\ 1.1578*\text{growth\_3})}]$$

where growth_3 corresponded to growth three years before dead, surprisingly growth_1 and growth_2 were not significant. The white spruce model was also very highly significant ($Pr< 0.0001$, $R^2=0.07$).

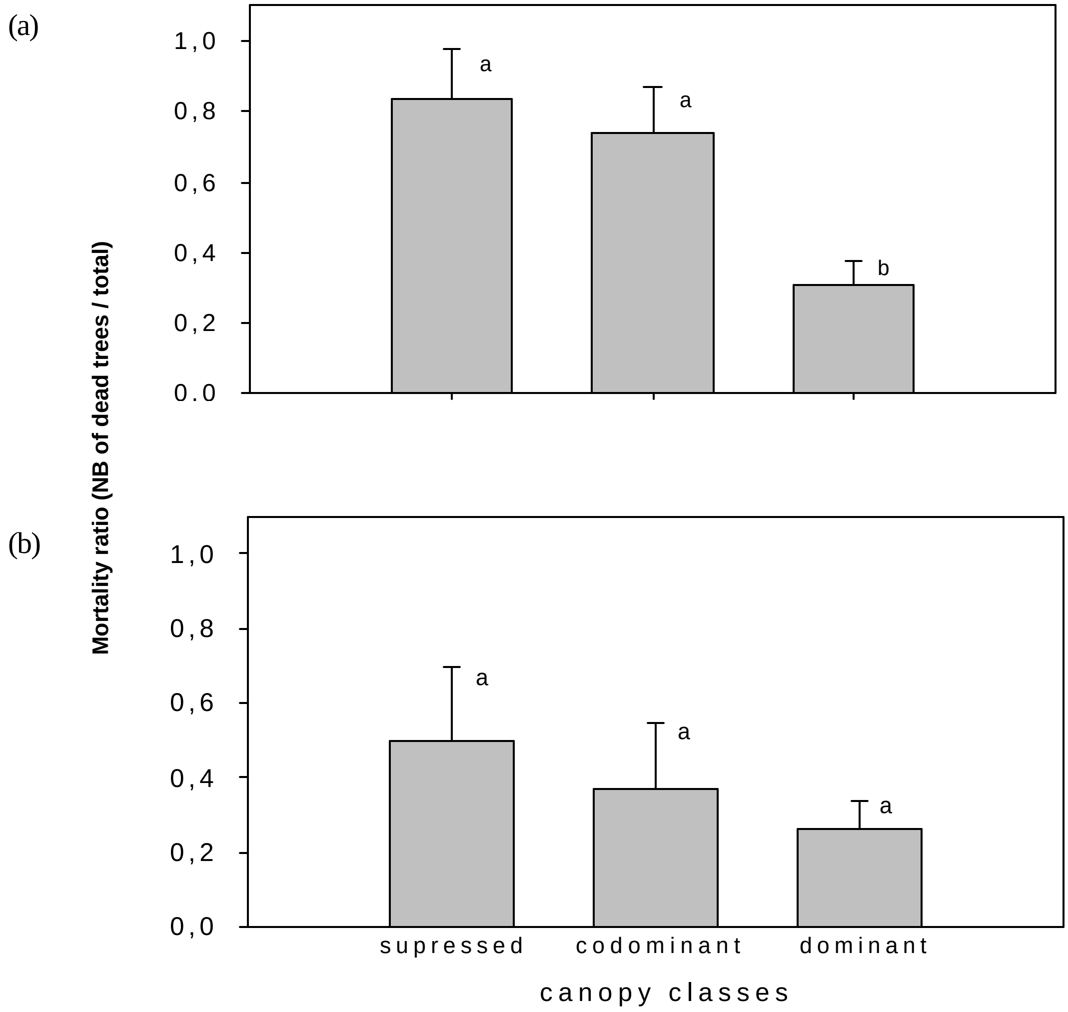


Figure 2. Aspen (a) and white spruce (b) mortality (NB dead / total) as a function of current canopy position (suppressed, codominant or dominant). Error bars are standard errors based on sampling in three stands. Different letters denote groups that are significantly different ($P<0.05$).

Characterization of the observed type of mortality revealed a similar overall pattern between spruce and aspen with most dead trees being observed 1) standing, followed by 2) those that died standing and were subsequently snapped, 3) those that were snapped while alive, 4) uprooting and 5) crushing (Figure 3). There is some variation between species, former snags now found on the ground due to windfall are higher for aspen (27%) than spruce (21%). The proportion of dead individuals observed to be snags are quite similar for both species, 67% for aspen and 65% for spruce. There is more uprooted spruce (3.1%) than aspen (0.7%) while the proportion of crushed trees are similar for both species (0.26% for spruce and 0.61% for aspen). The biggest difference was in bent trees (those trees that were alive when snapped). Spruce deaths from this type of windfall (9.9%) occur approximately 4 times more often than aspen (2.3%).

1.5.3 Temporal patterns of mortality

Dendrochronological analysis, performed only on specimens with an exterior growth ring (i.e. the outer portion of the disk could not be rotten), were used to characterize past aspen and white spruce mortality. Aspen possesses a mortality pattern that has a wave form (Figure 4a). The upper “part of the wave” corresponds to a major increase in mortality in 1974. Mortality decreases gradually afterwards until 1983 when mortality returns to a constant level that could be associated with background mortality. Unfortunately, we are not able to reconstruct mortality patterns into the past far enough to be able to observe other “waves”. Although mortality of trembling aspen was dated back until 1957, such individuals were rare due to rot. There is however a relatively high frequency of individuals that was dated to have died since the late 1960’s. Such frequencies are similar to those observed over the last decade and thus we suggest that mortality can effectively be dated back 30-35 years.

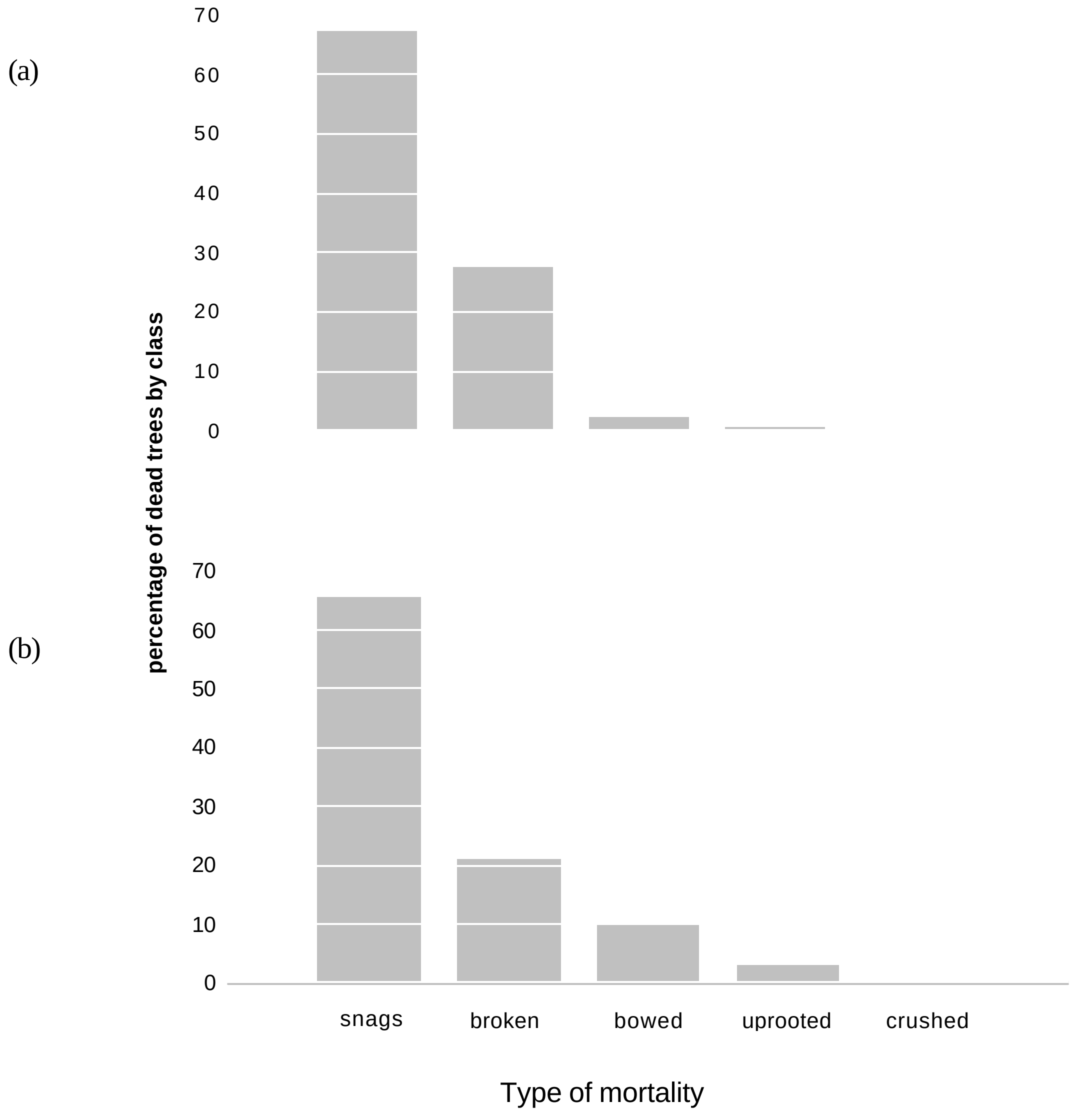


Figure 3. Observed type of mortality (snags, broken, bent, uprooted or crushed) for dead aspen (a) and white spruce (b).

White spruce, on the other hand, demonstrated another pattern (Figure 4b). Unlike the wave form mortality observed for aspen, spruce showed a more sporadic pattern of mortality with distinct years of high mortality. Years with high levels of mortality can be identified in 1991, 1995, 1997 and 1999. We analyses inter year daily variability in wind speed to see if there was any difference between years that could explain our observed yearly peaks in spruce mortality. No clear pattern was observed (prob<0.938).

Aspen and white spruce have contrasting patterns with respect to the age at which mortality occurs. Aspen dies in high numbers at a younger age than spruce. The largest number of aspen were observed to die between 40 and 60 years in age. A second peak, though less important, showed a number of individuals dying between 110 and 155 years. The relationship between age and DBH is also interesting (figure 5). As expected the younger dead individuals were in the smaller size classes; 59.1% of individuals that were under 60 years at their time of death were less than 20 cm DBH. The largest individuals (> 40cm DBH) accounted for 22.4% of the dead individuals greater than 100 yrs at time of death.

White spruce demonstrates the inverse pattern, with mortality being more important at an older stage. The highest period of mortality occurred when white spruce trees were between 110 and 150 years with a lower number dieing between 45 and 65 years. No trees that were dead were found to be larger than 40 cm although most live trees were also below this size class. No clear relationship between age and DBH class was observed. Individuals from both classes (7 to 20cm and 20 cm to 40 cm) were found across the full spectrum of ages at time of death. As an example, a tree with a DBH under 20cm is found to have died at an age of 156 years.

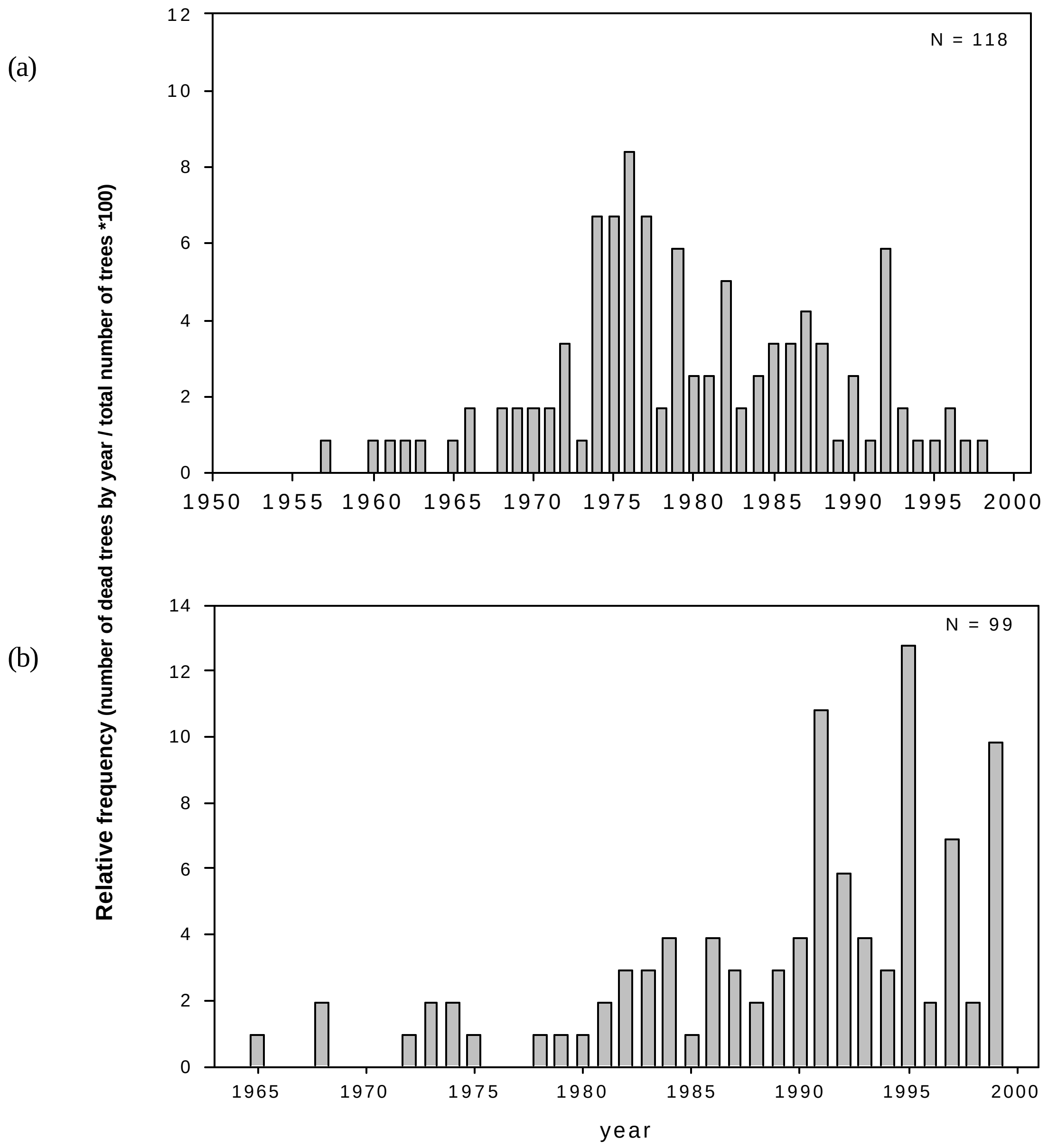


Figure 4. Year of mortality for aspen (a) and white spruce (b) evaluated by interdatation.

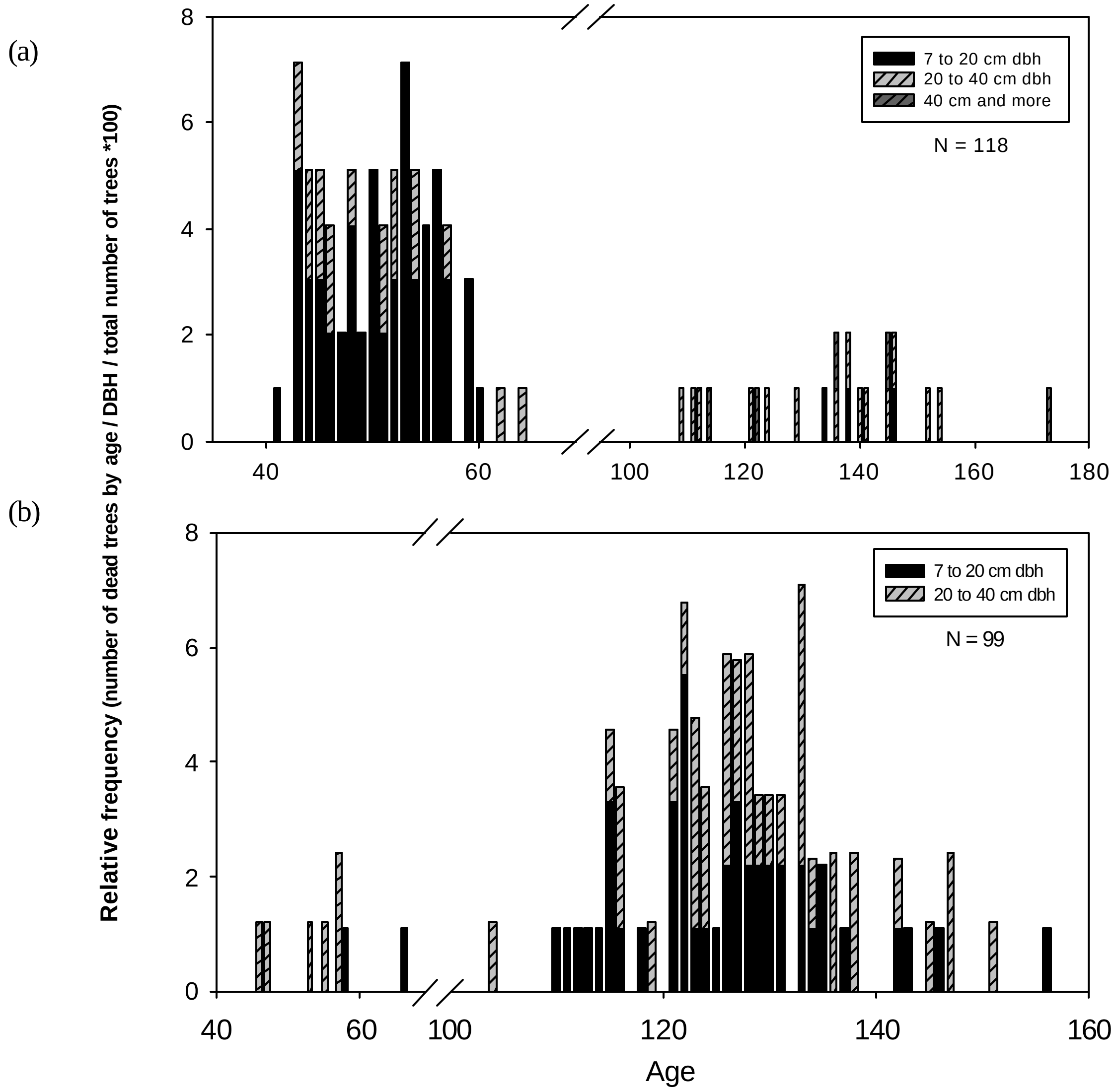


Figure 5.Age of aspen (a) and white spruce (b) mortality as a function of DBH (7 = DBH > 20 cm, 20 = DBH > 40cm and DBH = 40 cm).

Annual mortality rates (dead / total density / year) of the studied species were clearly related to canopy position (table 1). This is particularly true for aspen. Suppressed and co-dominant specimens have high average annual mortality rates, 15.5% and 11.5% respectably. However, the mortality rate drops to 3.2% for dominant aspen. For spruce, canopy position had a reduced impact on the annual rate of mortality. Although trees that were located beneath the canopy had a higher average annual mortality rate (6.6%) than larger individuals the difference was small (co-dominant spruce (5.5%) and dominant spruce (3.4%), no statistical differences were found. Differences between the species were thus most important for the suppressed and co-dominant classes. Annual mortality rates for the dominant class were quite similar to the overall average annual mortality rates, but dominant spruce (4.0%) were slightly lower than dominant aspen (5.9%).

The maximum likelihood analysis developed by Kobe and Coates (1997) for predicting mortality from radial increments of seedlings, demonstrates a lower result for aspen (3.4) than for spruce (4.2). As with the annual mortality rate, this result shows a lower shade tolerance for aspen. The results for white spruce however are much lower than for seedlings of the same species suggesting perhaps that adult trees need more light than young individuals to survive (Givnish 1988).

The relationship between canopy position and tree age was different between aspen and white spruce. For aspen, dominant individuals accounted for most of the dead trees that died between 110 to 155 years (fig.6a). No canopy class alone was found to account for the mortality peak that was observed when aspen were 40 to 60 years in age. In contrast with old individuals younger individuals came from all canopy class. White spruce that died at an advanced age (110-150 years) were also principally composed of dominant trees, however some co-dominants and a few suppressed trees were observed (fig. 6b). Surprisingly, young dead spruce (55-65 yrs) did not come from the suppressed canopy class but rather were made up entirely of trees from co-dominant and dominant positions.

Table 1 . Summary of trembling aspen and white spruce mortality ratios and mortality rates as a function of canopy class

SPECIES / Canopy class	**Mortality ratio (dead / total)**	**Annual mortality rate**	**Likelihood analysis**
ASPEN			
Suppressed	0.82	15.5%	
Co-dominant	0.67	11.5%	
Dominant	0.27	3.2%	
Overall	0.43	5.9%	3.4*
SPRUCE			
Suppressed	0.44	6.6%	
Co-dominant	0.35	5.5%	
Dominant	0.24	3.4%	
Overall	0.40	4.0%	4.2*

* = significant difference ($p<0.05$)

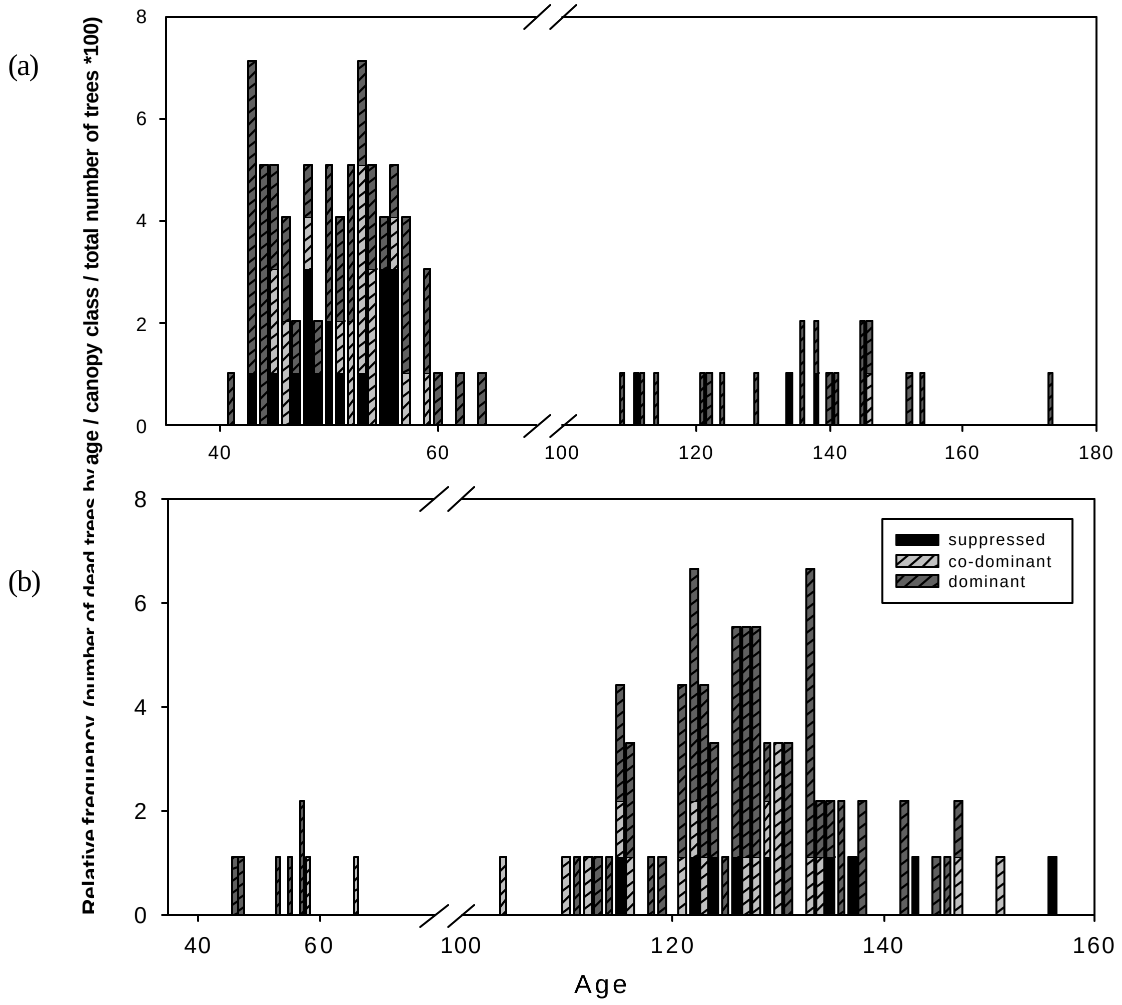


Figure 6. Age of aspen (a) and white spruce (b) as a function of canopy position (suppressed, co-dominant and dominant).

1.6 DISCUSSION

1.6.1 Endogenous mortality

Shade tolerance is central concept of forest dynamics (Kobe et al. 1995; Messier et al. 1999). Much research has identified seedling and sapling mortality in understory conditions to be related to periods of suppressed growth (Canham 1990, Kobe et al. 1995). If we assume relatively homogenous levels of below ground resources along our transects, our results can be interpreted to show that shade tolerance related mortality is also applicable to adult trees. The pattern of adult mortality that is observed among different classes is in agreement with previous studies of young trees. That is, the risk of mortality is higher for smaller individuals of shade intolerant aspen as they are presumably in the shade of the dominant trees. Statistically, individuals of the shade tolerant spruce survives equally well in all canopy classes. Aspen trees having not yet attained the canopy have a risk of mortality nearly 2 times that of white spruce. Although this finding is in agreement with that of Yao et al. (2001) in Alberta, these authors also found that this pattern was observed in all size classes with large aspen having a greater probability of mortality than large white spruce. Other authors have also suggested that mortality should be observed to be the highest for the largest trees while intermediate and smaller trees will be more vigorous and therefore less prone to die (Goff and West 1975, Harcombe 1987). However, we found that for trees in the canopy there is surprisingly little difference in mortality between the two species. The lack of agreement of our study with that of Yao et al. (2001) may be related to stand structural, site or age differences. The pattern of larger and old trees dieing at a greater rate than small and young trees has also been questioned by Runkle (2000) and our data show, although based on a relatively small number of old aspen per transect, that the larger and older trees have a smaller (for aspen) or equal (for spruce) incidence of mortality.

1.6.2 Exogenous mortality

Previous research have observed that proximity to an open area increases a tree’s exposure to wind and therefore windthrow mortality (Coates 1997, Huggard et al. 1999, Ruel 2000). Following the opening of a forest, such as after clear-cutting, species that are vulnerable to wind have a high probability of uprooting or breaking. The two species studied allow a nice comparison between a wind-tolerant species (aspen) and a wind-susceptible species (white spruce). Researchers have demonstrated that the vulnerability of white spruce comes from its superficial rooting, its long persistent crown, combined with a low wood density (Edmons et al. 1993, Bergeron 2000). Aspen on the other hand is less vulnerable due to its greater rooting system (it has both a tap root and an extensive superficial root system), deciduous crown and also its wood properties. Aspen is the species with the lowest maximum tensile strength (230 Psi), a measure of resistance to forces which tend to split the wood (Dyer and Baird 1997). We had therefore hypothesized that mortality of white spruce should be related to the distance to the lake-edge whereas aspen should be much less influenced.

Although the total number of dead spruce and aspen is higher near the lake, due to a greater total density of these species close to the lake, the ratio "number of dead trees / number of total trees" was negatively related to the proximity of the lake edge. The difference between this research and earlier research in which spruce had a greater probability of being killed by wind near edges (Stacey et al. 1994, Gardiner et al. 1997) may be explained by the permanence of the edge opening or the time since the opening was created. Earlier research has focused on proximity to edge in recently opened forests, like following burns or clear-cutting (Huggard et al. 1999, Ruel et al. 2001). In such situations, trees are not wind-firm and are thus more susceptible to being exposed to the effects of wind. Alternatively, in the situation where there is a permanent open edge, trees are wind-trained and thus less at risk to damage or mortality (Peterson and Pickett 1991, Dyer and Baird 1997). In stand interiors, canopy trees have been found to be more susceptible to strong winds than sub-canopy (protected) or super-canopy (wind-trained) trees (Peterson and Pickett 1991). Our results may thus be reflecting the lack of wind-training of interior canopy trees and their infrequent exposure to strong winds.

Contrary to our hypothesis for white spruce, windthrow does not seem to be a major cause of mortality since most trees of both white spruce and aspen died standing (>60%). We characterized all visual signs observable on trees that could be related to mortality. Three main causes of mortality stand out. First, wood-boring insects are responsible for a minor portion of mortality of spruce and aspen (near 0.5% for each species). Contrary to high mortality that occurs during spruce budworm (Blais 1981) or forest tent caterpillar (Hogg et al. 2002) outbreaks, insect impact is low in non-outbreak periods and due to insects other than the budworm or the forest tent caterpillar. Previous research in outbreak periods has also shown that SBW impacts are reduced in mixed stands (Bergeron et al. 1995, Su et al. 1996).

Secondly, fungus and disease were observed on a very small proportion of the snags. White spruce demonstrated higher signs of fungus than aspen, 3% vs 0.8% respectably. But this evaluation reflects a lower evaluation of the real portion of dead aspen affected. Canker type fungus is not always visible externally and thus a complementary wood dissection is often necessary. Thirdly, lengthwise cracks were more frequently observed on spruce snags (7.9%) than on aspen (3.8%). Splits in the wood, in majority due to frost-crack and wind-crack, increase the susceptibility of tree to disease (Silva et al. 1998). In many cases, cracks become more important during winter following their formation and increase susceptibility to disease. A lower frequency of observed splits for aspen may be linked to its higher density of wood.

1.6.3 Temporal patterns in mortality

Annual mortality rates have not been calculated or reported for most adult boreal tree species in intact forests. Most studies to date have focussed either on a specific agent of mortality, such as the SBW (Blais 1981, Morin 1994, Bergeron et al. 1995, Maclead and Mackinnon 1997), wind (Dyer and Baird 1997, Peltola et al. 1999, Ruel et al. 2001), drought (Elliott and Swank 1994, Condit et al. 1995, Jenkins and Pallardy 1995) or disease (James et al. 1984, Lewis and Lindgren 2002). Other studies such as Yao et al. (2001) developed models based on tree growth, tree diameter at breast height, etc or focussed on regenerating stems in the seedling and sapling size class (Kobe et al. 1995, Kobe and Coates 1997). In our study, aspen had a higher overall mortality rate than spruce, 5.9% and 4.0% respectively. However when broken down by size class or canopy class, the highest mortality rate for aspen is found in the co-dominant and suppressed positions. Such an observation may be a reflection of its shade intolerance and thus the difficulty in surviving beneath other individuals. Earlier work (Kobe 1996, Kobe and Coates 1997) has shown that the probability of mortality explained by recent growth is directly related to shade tolerance ranking. Results from a maximum likelihood analysis (Kobe and Coates 1997) showed that aspen has a much lower value of C (estimates of the generalized mortality function based on likelihood ratio test) than spruce, suggesting that it is indeed less shade tolerant. For adult trees the difference between aspen and spruce were found to be less than many authors have suggested for seedlings and saplings. Such decreasing differences in shade tolerance with increasing size or even reversal of shade tolerance is believed to be common in adult trees (Clark and Clark 1999) and this may be in part due to the ability of larger trees to store large amounts of carbon reserves (Canham et al. 1999) which make them less susceptible to mortality induced by low light availability.

We hypothesised that aspen mortality would be the greatest in the period associated with senescence of the stand (i.e. at the average longevity of the species which is expected between 80 to 120 years (Nienstaedt and Zasada 1990). Both Bergeron (2000) and Cumming et al. (2000) suggested that stand break-up may be responsible for creating open patches that are large enough to lead to the recruitment of a second cohort of the shade intolerant aspen. Our data, from mixedwood stands that have not burned in 150 to 185 years, does not show a sudden synchronised period of mortality related to senescence. Instead most trees died young (<60 years). Furthermore, our results show a break in the period of mortality from about 65 years until almost 110 years, with a secondary peak in mortality occurring in old aspens around 140 years. The hypothesised period of stand break-up between 80 to 120 years is therefore not observed in our stands, perhaps because many of the trees have already died and decayed. For aspen, we were able to reconstruct mortality for a period of up to thirty years, which means that we should be at the limit of the hypothesised period of stand break up in the studied 153 year-old stands. Though, the presence of this second cohort of aspen and of a stand break-up period may be deduced from the high mortality of aspen that recruited 40 to 60 years earlier. This recruitment would have occurred while the stand was 90-110 years old and may have been due to a period of canopy opening. Kneeshaw and Bergeron (1998) noted that mortality of aspen in groups of a few individuals may be sufficient to permit some aspen to recruit as a second cohort to the canopy, especially in the absence of well established conifer regeneration (Kneeshaw and Bergeron 1996, Kelly et al. 2002). This cohort may thus be due to a stand break up period that occurred across a period of more than twenty years. This relatively gradual break-up may help explain why researchers have had difficulty in locating stands that are clearly breaking up. Our data show also that some individuals survive at the period of break up and live up to 173 years. These old growth trees represent a marginal part of the forest with a high capacity to survive which may reflect genetic traits for longevity.

Temporally, we also observed a peak in aspen mortality from 1974 to 1979. This recent peak may be related to a forest tent caterpillar outbreak that was reported to have occurred in the area between 1971-73 (Camiré 1997). Researchers have noted that the forest tent caterpillar is an important agent of mortality for aspen and that mortality may continue for many years following an outbreak (Hogg et al. 2002).

A SBW outbreak has also been reported in the area between 1970-1987 (Morin et al. 1993). This outbreak led to the mortality of approximately half of the balsam fir in the area. Most of this mortality occurred in the early 1980's (Kneeshaw et al. In-Prep). Bergeron et al. (1995) observed little white spruce mortality in their data set. This concurs well with our observations that spruce did not sustain a higher-than-normal mortality in the 1980's. Peaks in spruce mortality instead occurred in a series of single years: 1991, 1995, 1997 and 1999. Although these trees may have been weakened by the outbreak, it is unlikely that these high mortality peaks occurring so many after the end of the outbreak are related to it. Our initial hypothesis was that these peaks were related to single years wind events since our data show that most of the trees died standing in these years. However, we did not find any evidence from the meteorological data (Environment Canada 2002) that these yearly peaks in mortality are in fact related to unusual years of high winds. Further studies are therefore required to explain these single-year high peaks in spruce mortality.

1.7 CONCLUSIONS

Contrary to our hypothesis, most adult aspen mortality occurred many years before (40 to 60 years) the hypothesised stand breakup period (between 80 to 120 years). This was explained by the fact that most mortality occurred in the sub-dominant classes of younger aspen that recruited long after the initial post-fire establishment phase. However, the presence of this wide-age range second cohort of aspen may be related to a period of high mortality corresponding to aspen canopy breakup occurred between 93 to 113 years.

Another interesting result was that adult mortality rate for the dominant aspen was not statistically different than that of white spruce, although as predicted sub-dominant spruce had a much lower mortality rate than sub-dominant aspen. However, we did not find any statistical differences in adult spruce mortality between suppressed, co-dominant and dominant trees. Unlike other regions, where there is presumably wind funnelling, we did not find any evidence that adult white spruce mortality was mainly due to windthrow as most trees die standing in this relatively flat part of the boreal forest

Finally, we found great inter annual variability in adult mortality rates. Some of this variability can be easily explained and even provides further evidence for the stress hypothesis (the high tree mortality in suppressed and co-dominant aspen following a recent forest tent caterpillar outbreak), but others (high recent peaks in adult white spruce) are more difficult to explain. Our results can also be used to validate and parameterise simulation models of stand dynamics. SORTIE (Pacala et al. 1994), for example, is such a spatially-explicit simulation model that is mainly driven by single tree mortality that causes changes in light availability to understory trees. Currently, SORTIE uses a constant mortality rate for trees greater than 10 cm. Our data clearly show that, while this might be correct for shade tolerant species such as white spruce, it is not adequate for shade inte species such as aspen. Data such as those presented in this study can therefore be u better fine tune adult tree mortality in such models.

CONCLUSION GÉNÉRALE

Bien que la mort des arbres soit un éléments important du processus de dynamique forestière, nos connaissances actuelles ne nous permettent pas d'apprécier toute la complexité de cette mortalité. Dans le but d'apporter de nouvelles informations sur ce processus, notre étude a identifié certains facteurs responsables de la mort des arbres.

Contrairement à d'autres régions, nous n'avons aucune preuve évidente que le vent soit une importante cause de mortalité chez l'épinette blanche adulte, puisque la plupart des arbres morts ont été observés debout. La caractérisation externe (présence ou non de fissure, maladie, etc.) des chicots n'a pu permettre d'identifier avec précision la cause de mortalité. Les fissures, les champignons et les insectes semblent tous, en partie, responsables de cette mortalité. Des études futures axées sur l'identification des causes de mortalité des chicots sont donc nécessaires. Ainsi l'effet de nouvelles causes de mortalité, telles que la sécheresse ou encore une caractérisation plus poussée des causes déjà observées, devra être vérifié.

On aurait pu penser que la proximité du lac était un facteur important en raison de l'action du vent. Cette action s'avère négligeable. Ce critères de proximité demeure néanmoins important dans l'analyse de la mortalité du peuplier faux-tremble. En fait, son impact provient majoritairement de l'action des castors. Bien que certaines recherches aient négligées ce facteur, nos résultats démontrent que le castor est la plus importante cause de mortalité pour les arbres localisés près du lac. Il apparaît, dans certains cas, est responsable de la mort de près de la moitié de tous les peupliers.

Tel que démontrée chez les semis, la tolérance à l'ombre est un important concept pour la mortalité des arbres adultes. Chez les espèces intolérantes à l'ombre, soit le peuplier, une grande différence est observable entre les individus dominés et les individus dominants. Cette différence est toutefois peu importante chez les individus tolérants comme l'épinette.

Une grande différence de mortalité est perceptible en fonction de la taille. En fait, le deux espèces étudiées démontrent des patrons de mortalité inverse. Tandis que, chez le peuplier faux-tremble, on constate une grande mortalité chez les individus de faible diamètre, on trouve chez les épinettes blanches, une mortalité accrue chez les individus de grands diamètres.

À l'inverse de nos hypothèses, la majorité des trembles morts ont été observés en bas âge et non à l'intérieur de la période prévue de sénescence. Ces individus sont trop jeunes pour correspondre à la première cohorte et proviennent, en fait, d'une seconde cohorte. De plus, l'âge de ces arbres suggère que l'événement qui à affecté ces nouveaux individus est survenu lorsque le peuplement avait entre 93 et 113 ans. Ces observations supportent en fait notre hypothèse suggérant que le tremble possède une forte mortalité, entre 80 et 120 ans, suite à la sénescence de la première cohorte.

Finalement, une grande variabilité inter-annuelle fut observée pour le taux de mortalité des arbres adultes. Une partie de cette variabilité est expliquée en fonction de nos hypothèses (ainsi la grande mortalité pour les arbres dominés ou co-dominants chez le tremble), mais une seconde partie de cette variabilité demeure inconnue (telles que les pics de mortalité observés chez l'épinette blanche).

Les résultats obtenus nous aident à mieux comprendre une partie de la dynamique naturelle des peuplements de la région étudiée. Et ceci, entre autre, pour la théorie de dégénérescence des peuplements (Bergeron 2000, Cumming et al. 2000). Cette théorie amène l'idée que les peuplements de peupliers faux-tremble subissent une augmentation spontanée de mortalité due à la sénescence généralisée de la cohorte. Nos recherches indiquent qu'effectivement une importante hausse de mortalité est observable, mais que par contre, cette hausse ne s'effectue pas de façon spontanée et n'affecte pas tout le peuplement en même temps. Elle est plutôt étalée sur une vingtaine d'années et les arbres ne sont affectés que par petits groupes à la fois. Ce qui explique, la difficulté pour les chercheurs d'identifier des peuplements où l'entière cohorte serait sous l'effet d'une dégénérescence. Nos résultats valident aussi l'idée que la mortalité induite par cette dégénérescence serait suffisante pour produire une seconde cohorte (figure 7). Ainsi le peuplier faux-tremble, une espèce intolérante à l'ombre, peut induire la venue d'une seconde cohorte sous un couvert forestier.

De plus, nos résultats démontrent que cette espèce possède une espérance de vie comparable à celle de l'épinette blanche à l'intérieur des peuplements étudiés. Malheureusement, le jeune âge de ces peuplements ne permet pas d'évaluer la longévité maximale de l'épinette blanche. En fait, aucun individu de plus de 160 ans ne fut observé. Cependant, la faible quantité d'individus âgés, additionnée, à la faible capacité de l'épinette à se reproduire à l'intérieur de ces peuplements (Kneeshaw et Bergeron 1996), semble supporter l'hypothèse que cette espèce ne possède pas la faculté de dominer les peuplements de fin de succession comme elle le fait dans l'ouest du Canada.

Une importante application de nos résultats est la validation et la « paramétrisation » des modèles de simulation de la dynamique des peuplements. Par exemple, SORTIE (Pacala et al. 1994), est un modèle « spatialement » explicite largement dépendant de la mortalité individuelle induite par la disponibilité en lumière chez les arbres en sous canopée. Présentement, SORTIE utilise un taux de mortalité constant chez les arbres supérieurs à 10 cm (diamètre à hauteur de poitrine). Nos données indiquent clairement que cette méthode de calcul peut être correcte pour les arbres tolérants à l'ombre tel l'épinette, mais incorrecte pour les arbres intolérants tel le tremble. Ainsi, les données telles que présentées dans cette étude semblent tout indiqués pour raffiner les modèles basés sur la mortalité des arbres adultes.

Puisque la mortalité des arbres adultes est très peu documentée, cette recherche s'est concentrée à recueillir les informations de base sur deux importantes espèces de la forêt boréale. Ce projet achevé, plusieurs voies sont envisageables pour continuer la recherche. Ainsi, le patron de mortalité pourrait être comparé à celui d'autres régions de la forêt boréale, tel que l'Ouest canadien. Dans un contexte davantage forestier, des recherches pourraient viser à élaborer des coupes forestières ayant le but d'imiter la mortalité naturelle.

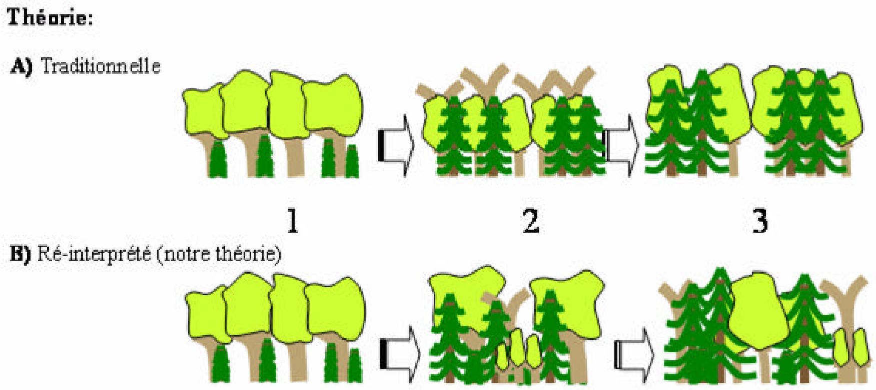
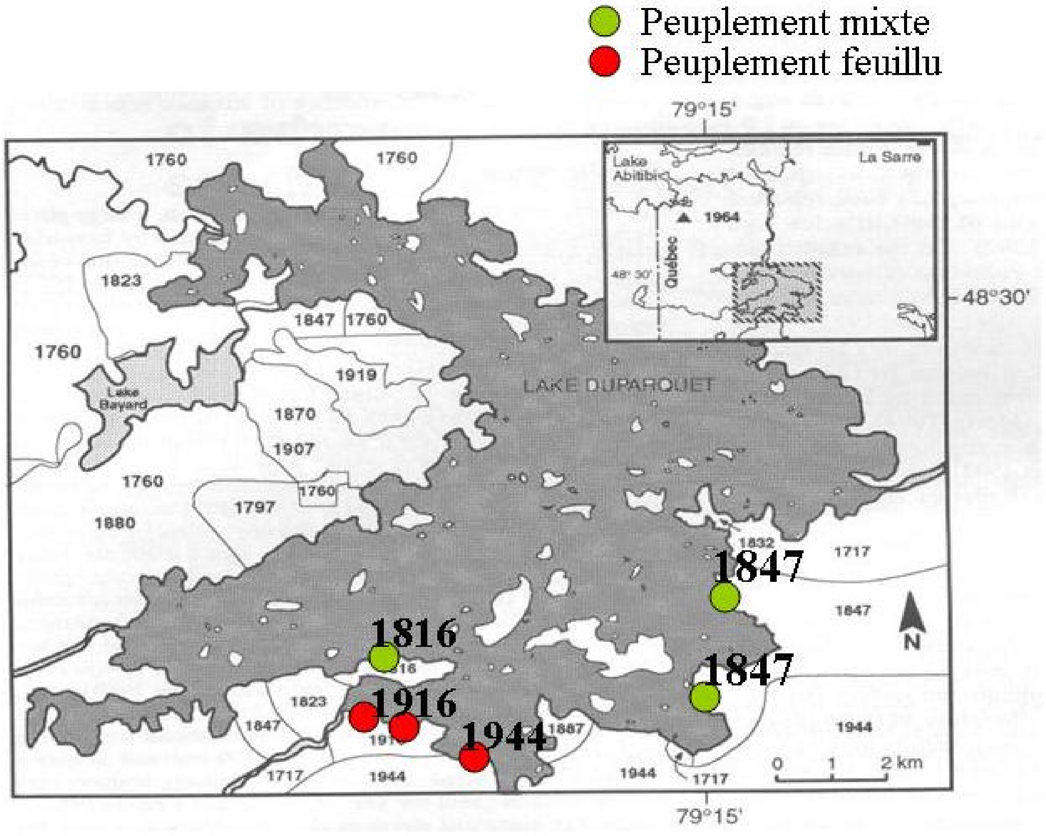


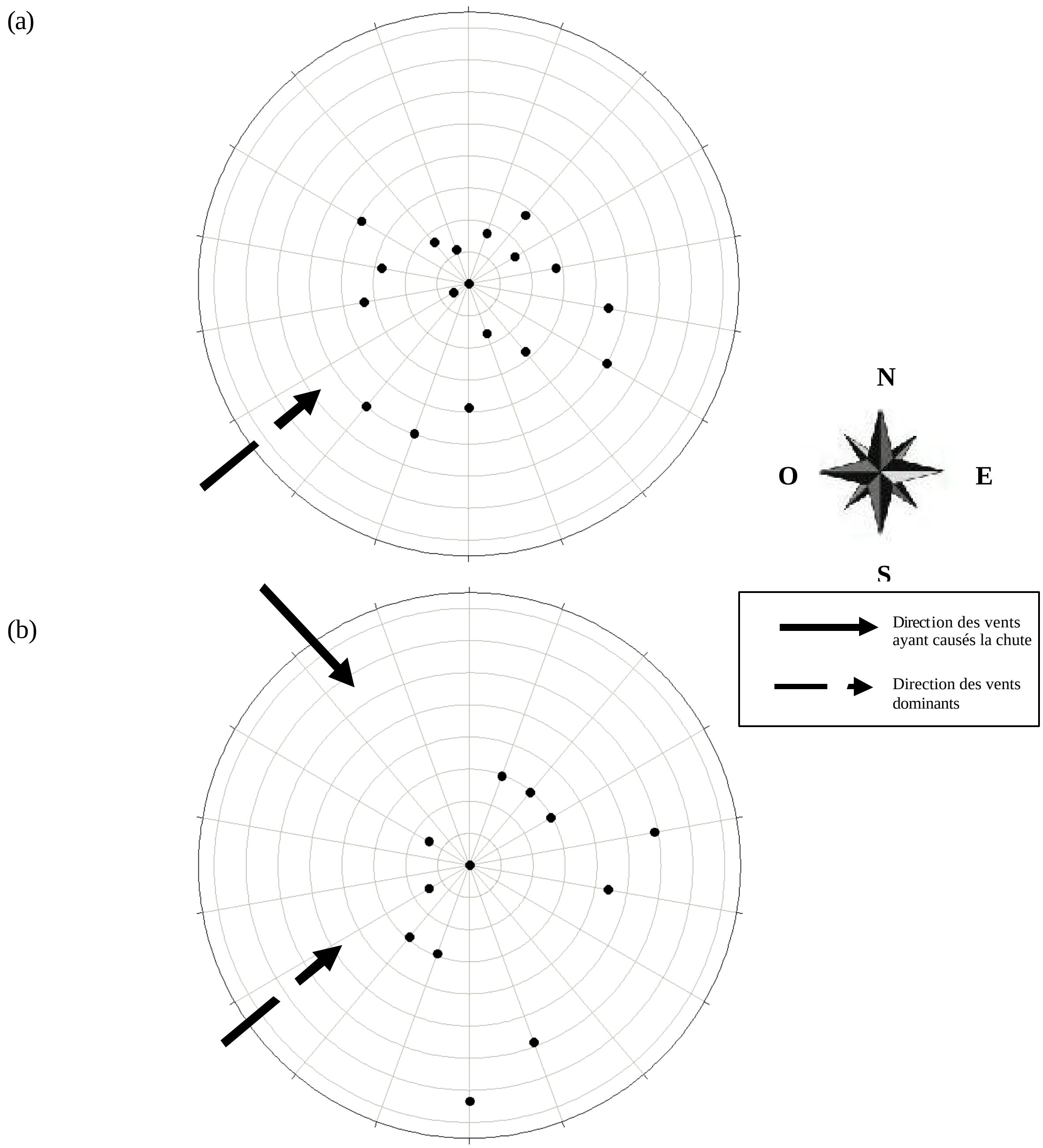
Figure 7 : Théorie traditionnelle a) et ré-interprétée b) du remplacement des peuplements feuillus par des peuplements mixtes en forêt boréale. Selon la théorie traditionnelle, les conifères établis en sous couvert atteignent la canopée suite à l'ouverture du couvert provoquée par la dégénérescence généralisée des individus dominants (Bergeron 2000). Tandis que notre théorie indique que les individus dominants ne meurent pas de façon généralisée, mais bien par petits groupes (« patch »). Ainsi le remplacement des espèces se produit de façon localisée et ceci sur un long intervalle de temps (environ 20 ans).

Ou encore, puisqu'il n'est pas exclu qu'un arbre subissant une perte de vigueur physiologique (provoquée par une source endogène), devienne plus susceptible et succombe à la suite d'un second événement (de source exogène), il serait intéressant de regrouper les sources de mortalité selon l'échelle à laquelle elles risquent de se manifester. De cette façon, il serait possible d'identifier les sources occasionnant une mortalité à l'échelle de l'arbre (sénescence), de celles qui agissent à l'échelle d'un groupe d'arbres (chablis), de celles qui agissent à l'échelle du peuplement ou encore à l'échelle régionale.

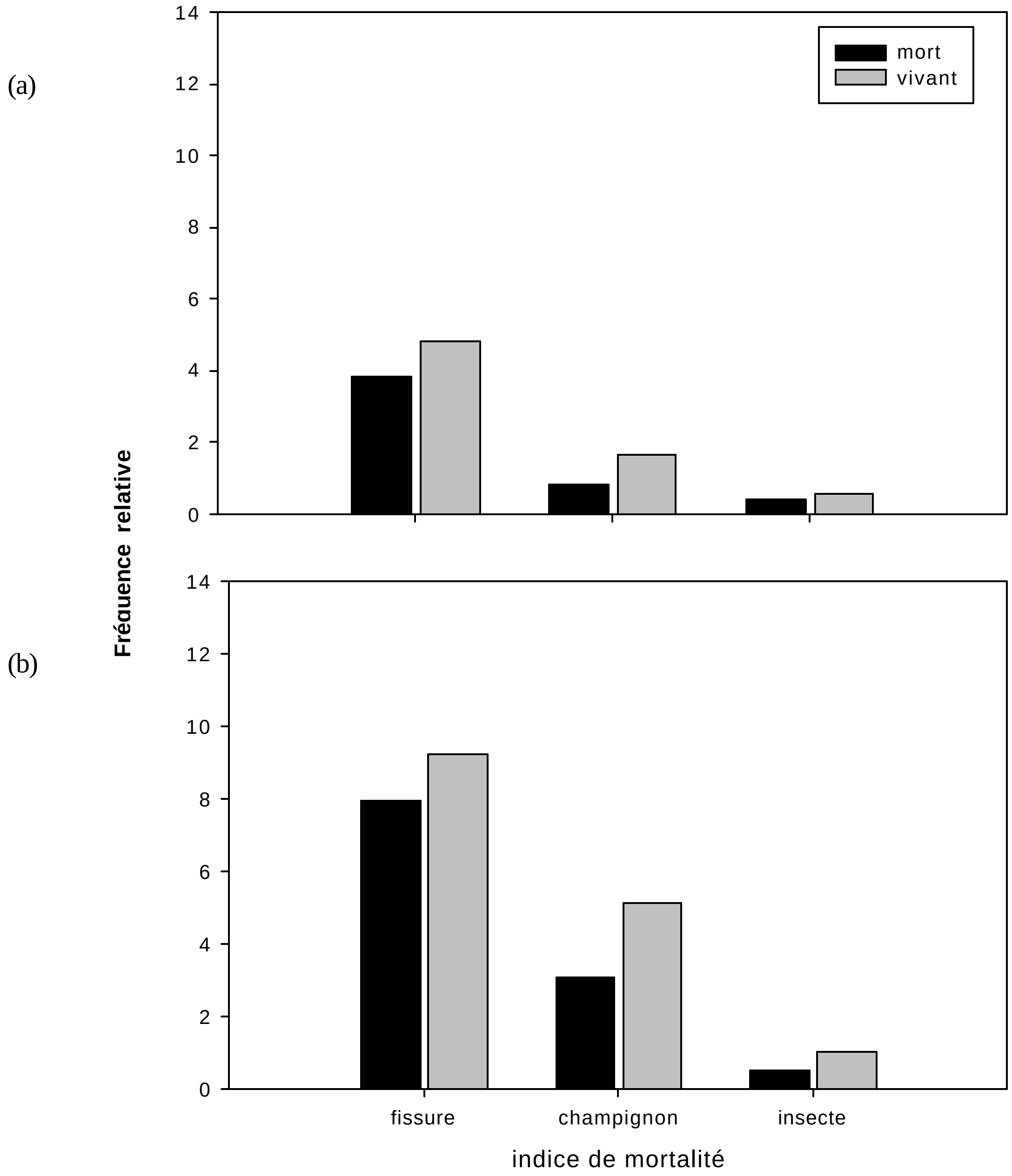
> > > > > > Les données qui suivent n'ont pas été insérées à l'article pour éviter d'alourdir le contenu et ainsi diminuer la fluidité. Par contre elles démontrent des résultats intéressants qui aide à la compréhension du patron de mortalité. De plus, elles pourraient être utile aux chercheurs visant l'étude des causes de mortalité à l'intérieur de la forêt boréale. Ainsi ces figures sont présentées en annexes pour favoriser la compréhension.



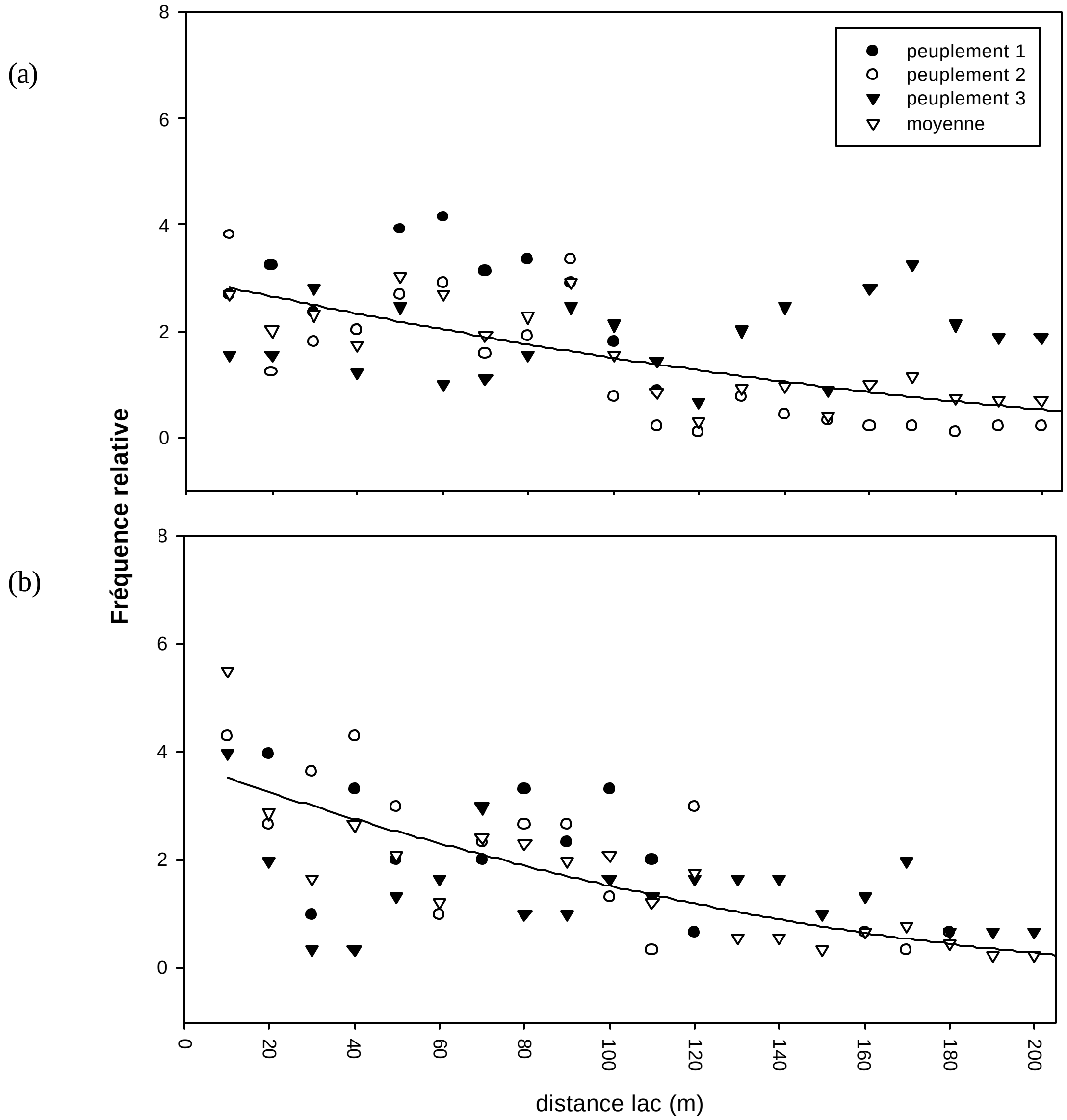
ANNEXE A : Localisation des sites d'échantillonnages au Lac Duparquet, en Abitibi, en fonction du type de peuplement et de l'année du dernier feu.



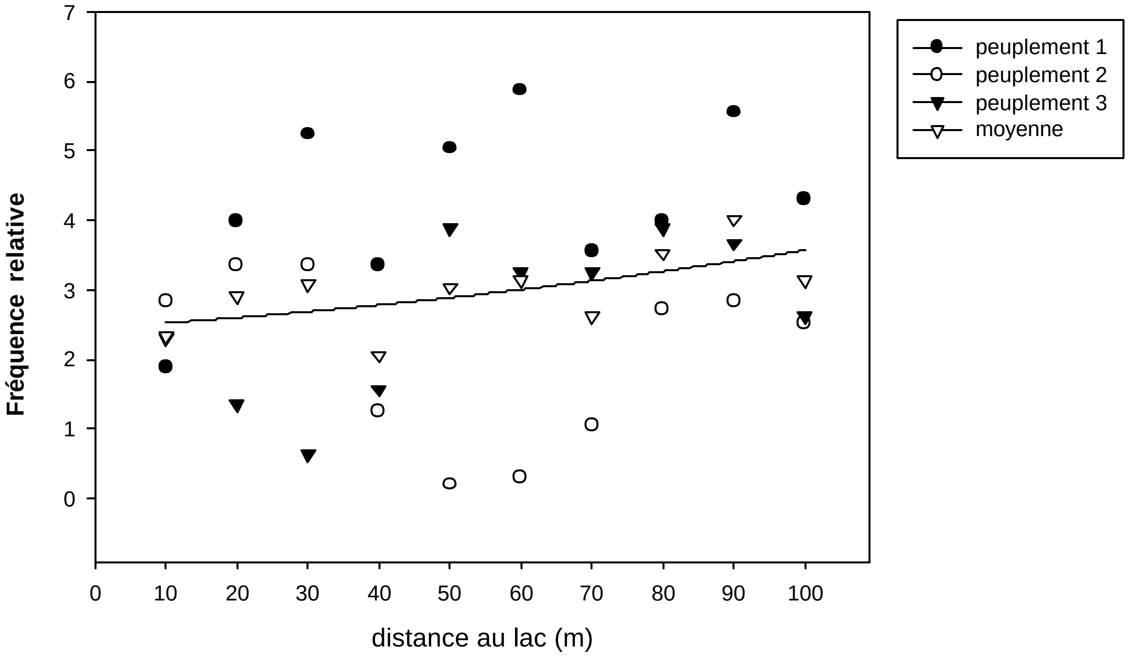
Annexe B : Orientation géographique des arbres morts et tombés sur le sol pour (a) le peuplier faux-tremble et (b) l'épinette blanche. Le sens de chute pour le tremble ne démontre aucune relation avec le vent, tandis que l'épinette semble être sensible aux vents provenant du nord-ouest.



Annexe C : Indice sur la cause de la mort des chicots (a) de peuplier faux-tremble et d'épinette blanche. Présence de fissures, de champignons et d'insectes notée sur les arbres morts et vivants. Chez les deux espèces étudiées les fissures sur le tronc semblent la plus importante cause de mortalité.



Annexe D : Disposition relative des arbres morts en fonction de la distance au lac (m) pour le (a) peupliers faux-tremble et (b) l'épinette blanche en peuplement mixte. Une importante diminution de la fréquence, des deux essences étudiées, peut être observée avec l'augmentation de la distance au lac.



Annexe E: Disposition relative des peupliers faux-tremble en peuplement feuillu en fonction de la distance au lac (m). Contrairement au peuplement mixte (annexe D) les peuplements feuillus ne démontrent aucune diminution de la mortalité avec l'augmentation de la distance au lac.

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