UNIVERSITE DU QUEBEC A MONTREAL

DYNAMIQUE DES ARBRES MORTS EN FORET BOREALE MIXTE ET CONIFERIENNE

THESE
PRESENTEE
COMME EXIGENCE PARTIELLE
DU DOCTORAT EN BIOLOGIE

PAR
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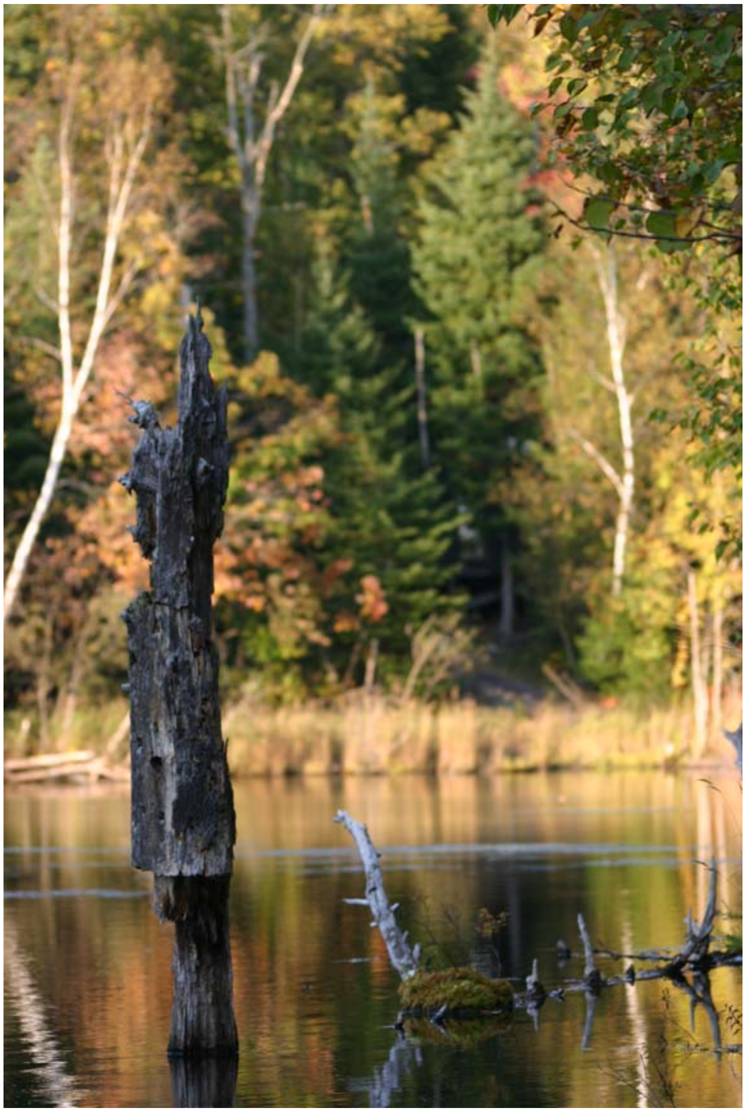
À mon père (1919-1999), écologiste des hommes,
qui m'a transmis son amour de la nature,
la Flore Laurentienne à la main,
lors de nos expéditions en forêt.



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Un peu comme le carpophore d'un champignon saproxylique ne représente que la partie visible d'une colonisation étendue mais inapparente de mycélium, cette thèse représente le concentré de cinq années de lectures, de récolte d'échantillons, de travail en laboratoire, de réflexion et de rédaction. Bien que seul mon nom figure au dos de ce volume, cette thèse constitue le résultat des nombreuses collaborations, rencontres et discussions qui ont marqué ces dernières années. Mes remerciements sont presque aussi nombreux que les organismes qui peuplent le bois mort.

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AVANT-PROPOS

Cette thèse est présentée sous la forme de quatre articles scientifiques. Dans presque tous les cas, j'ai été responsable du design d'expérimentation, de la récolte et de la compilation de données, de l'analyse des échantillons, des analyses statistiques et de la rédaction. Dans le cas du chapitre 3, le design d'expérimentation a été mis en place en 1997 et des données ont été récoltées par des membres de la Chaire AFD jusqu'à ce que je prenne la relève en 2004. Toutes les personnes physiques ou morales qui ont contribué aux articles, par leur aide sur le terrain, lors de l'analyse des données, lors de la rédaction ou par leur contribution financière sont identifiées à la fin des articles.

Le premier chapitre s'intitule « Snag degradation pathways of four North American boreal tree species ». Les co-auteurs sont Pierre Drapeau et Yves Bergeron. Cet article a été publié dans la revue *Forest Ecology and Management* en 2010 (259: 246-256).

Le second chapitre a pour titre «Mineralization rates and factors influencing snag decay in four North American boreal tree species». Les co-auteurs sont aussi Pierre Drapeau et Yves Bergeron. Il sera soumis sous peu à la *Revue canadienne de recherche forestière*.

Le troisième chapitre est le fruit d'une collaboration plus étendue et s'intitule «Tree mortality and snag dynamics in North American boreal tree species after a wildfire: a long-term study». Sylvie Gauthier, Pierre Drapeau, Karelle Jayen et Yves Bergeron en sont les co-auteurs. Sylvie Gauthier a effectué un travail de supervision des analyses statistiques et a participé à la rédaction du chapitre. J'ai réalisé les travaux de recherche bibliographique, d'échantillonnage sur le terrain en 2004 et en 2006, d'analyse des données, de rédaction et de création des figures. Pierre Drapeau et Yves Bergeron ont effectué un travail de supervision lors des étapes préliminaires du projet et ont participé à la rédaction du chapitre. Karelle Jayen a participé aux travaux d'échantillonnage sur le terrain, a effectué des travaux d'analyse relatifs à la mortalité lors de travaux antérieurs (Jayen 2004) et a participé à la rédaction du chapitre. Cet article a été accepté pour publication dans la revue *International Journal of Wildland Fire* en 2011.

Le dernier chapitre se veut intégrateur des chapitres précédents. Il a été co-écrit avec Yves Bergeron et Pierre Drapeau et s'intitule « Morphological attributes and snag classification of four North American boreal tree species: relationships with time since death and wood density». Il sera soumis sous peu à la *Revue canadienne de recherche forestière*.

Cette thèse a été défendue le 28 mars 2010 à l'Université du Québec à Montréal. Les membres du jury de thèse étaient :

- Pierre Drapeau, professeur, directeur de thèse, Département des sciences biologiques, Université du Québec à Montréal;
- Yves Bergeron, professeur, co-directeur de thèse, Département des sciences appliquées, Université du Québec en Abitibi-Témiscamingue;
- Daniel Gagnon, professeur, président du jury, Département des sciences biologiques, Université du Québec à Montréal;
- Daniel Kneeshaw, professeur, Département des sciences biologiques, Université du Québec à Montréal;
- Lori D. Daniels, professeure, évaluatrice externe, Département de géographie, Université de la Colombie-Britannique.

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RÉSUMÉ

Plusieurs études ont mis en lumière l'importance du bois mort dans la dynamique des écosystèmes forestiers boréaux, qu'il soit sur pied (chicot) ou au sol. Chez les espèces boréales de l'est de l'Amérique du nord, on dispose cependant de relativement peu d'informations sur la dynamique des arbres morts *per se*, en termes de recrutement, de taux de dégradation, de rapidité de décomposition, etc. Cette thèse vise à approfondir les connaissances sur la dynamique des arbres morts de quatre espèces très communes en forêt boréale de l'est: le peuplier faux-tremble (*Populus tremuloides* Michx.), le sapin baumier (*Abies balsamea* [L.] Mill.), le pin gris (*Pinus banksiana* Lamb.) et l'épinette noire (*Picea mariana* [Mill.] BSP). La thèse est divisée en quatre chapitres.

Le premier chapitre décrit les trajectoires de dégradation du bois mort en forêt mature ou surannée. Des courbes de persistance sur pied des chicots ont été construites pour chaque espèce, et les trajectoires de dégradation ont été documentées en se basant sur la forme de la relation, le délai dans l'initiation de la chute et la demi-vie (le temps requis pour que la moitié des tiges soient tombées). Chez la plupart des espèces, les courbes de survie ont pris la forme de fonctions sigmoïdes inversées. Le peuplier faux-tremble, le pin gris et dans une moindre mesure le sapin baumier présentaient des délais significatifs avant que les taux de chute ne deviennent importants. De plus forts taux de chute étaient observables chez l'épinette noire dans les premières années suivant la mort. Le pin gris était clairement l'espèce la plus persistante vu sa grande résistance à la chute et aux bris. Le diamètre des arbres n'a pas influencé significativement la probabilité de chute.

Au deuxième chapitre, je me suis intéressée aux taux de minéralisation du bois des chicots et aux facteurs qui les influencent. Les taux de minéralisation différaient significativement entre les espèces. Le peuplier faux-tremble présentait un taux de minéralisation plus rapide que ceux des conifères. Le pin gris occupait le deuxième rang, suivi par le sapin baumier. L'épinette noire s'est révélée particulièrement résistante à la minéralisation. Aucune différence n'a été observée entre les taux de minéralisation à la base et à hauteur de poitrine chez les conifères, tandis qu'à la base des chicots de peuplier faux-tremble, ce taux était significativement plus élevé qu'à hauteur de poitrine. Le temps écoulé depuis la mort de l'arbre (TDM) et l'activité des Cérambycidés étaient significativement associés à une minéralisation plus rapide chez le peuplier faux-tremble, le sapin baumier et le pin gris, alors qu'une croissance lente et un faible diamètre étaient associés à des taux de minéralisation plus lents chez l'épinette noire. Je suggère que les conditions environnementales dans lesquelles se trouvaient les pessières noires échantillonnées pourraient expliquer pourquoi le TDM influence moins la minéralisation du bois des chicots chez l'épinette noire.

Au chapitre 3, j'ai examiné les patrons temporels de mortalité et la dynamique des arbres morts après feu sur une période de dix ans chez le peuplier faux-tremble, le

pin gris et l'épinette noire. Les patrons temporels de mortalité des trois espèces ont révélé que la mortalité était décalée dans le temps. La majeure partie de la mortalité a eu cours dans les deux années suivant le feu, mais le processus de mortalité s'est poursuivi jusqu'à la fin de la période d'étude de dix ans. Le pin gris était l'espèce la

plus persistante comme chicot, suivi du peuplier faux-tremble et de l'épinette noire. Les facteurs influençant la persistance des chicots représentaient plusieurs échelles et étaient généralement spécifiques à chaque espèce. La sévérité du feu était le seul facteur commun à toutes les espèces influençant la persistance des chicots, ceux situés dans des peuplements sévèrement brûlés étant moins susceptibles de tomber. La persistance sur pied des chicots de peuplier faux-tremble augmentait avec la surface terrière et le diamètre des tiges. La présence de coupes de récupération dans le paysage n'a affecté que la persistance des chicots d'épinette noire. Les patrons de chute différaient aussi selon les espèces. Le court-circuitage du stade de chicot (i.e. quand un arbre vivant tombe directement au sol) ainsi que le déracinement de chicots étaient communs. La mortalité décalée dans le temps des arbres dans plusieurs peuplements, ainsi que la persistance relativement élevée des chicots dix ans après feu, ont assuré un recrutement continu de bois mort frais qui a permis la présence d'une importante quantité de chicots ainsi que l'abondance simultanée de bois mort de différents stades de dégradation.

Le dernier chapitre est intégrateur des chapitres précédents. J'y ai examiné quels traits morphologiques prévoient le mieux le TDM et la densité résiduelle du bois et j'y ai évalué dans quelle mesure un système de classification de la dégradation communément utilisé est représentatif de ces deux variables. Les résultats indiquent que les meilleures combinaisons de traits prédictifs du TDM et de la densité du bois diffèrent d'une espèce à l'autre. Le recouvrement d'écorce et la pénétrabilité du bois constituaient les seuls traits morphologiques prédictifs communs à toutes les espèces relativement au TDM et à la densité résiduelle du bois, respectivement. Le stade de dégradation constituait un indicateur grossier de l'âge des chicots (i.e. TDM). L'âge moyen des chicots croissait généralement avec les stades de dégradation, mais des chevauchements significatifs dans les TDM de stades de dégradation adjacents ont été observés chez toutes les espèces. Le même phénomène a été observé relativement à la densité du bois. Cette étude montre que le système de classification de la dégradation utilisé peut être utile lorsque des estimations grossières sont requises. Cependant, lorsque des estimations plus précises sont nécessaires, les modèles spécifiques à chaque espèce construits selon des traits morphologiques significatifs ne représentent pas des outils demandant plus de temps ou de ressources sur le terrain et procurent des estimations du TDM et de la densité plus précises.

Les résultats de cette thèse montrent que la dynamique de dégradation et de décomposition différentielle des quatre espèces à l'étude traduit des réponses individuelles des espèces qui sont liées à leur autécologie. Ces différences entre espèces sont observables dans tous les chapitres, que ce soit en regard des trajectoires de dégradation des tiges (chapitres 1 et 3), de la minéralisation du bois

(chapitre 2) ou des indicateurs morphologiques de l'état d'un chicot (chapitre 4). Cette conclusion est aussi valable pour les assemblages de facteurs qui influencent la dégradation (chapitre 3) et la minéralisation (chapitre 2). Le bois mort ne peut donc pas être considéré comme un substrat uniforme et la spécificité des espèces peut avoir d'importantes conséquences pour plusieurs fonctions écologiques liées au bois mort. Dans une perspective d'aménagement écosystémique, ces résultats devraient être considérés lors de l'élaboration de stratégies de rétention d'arbres à valeur de conservation.

Mots-clés: Bois mort, chicots, taux de chute, taux de minéralisation, mortalité, systèmes de classification de la dégradation, dendrochronologie, peuplier faux-tremble, *Populus tremuloides* Michx., sapin baumier, *Abies balsamea* (L.) Mill., pin gris, *Pinus banksiana* Lamb., épinette noire, *Picea mariana (*Mill.) BSP.

ABSTRACT

In boreal ecosystems dynamics, many studies have highlighted the importance of dead wood, whether standing (snag) or fallen. However, a dearth of literature exists regarding the dynamics of these structures (i.e. recruitment, degradation rates, mineralization rates, etc.) in northeastern American boreal species. The aim of this thesis is to increase current knowledge on the snag dynamics of four common tree species of the eastern boreal mixedwood and conifer forests of Canada: trembling aspen (*Populus tremuloides* Michx.), balsam fir (*Abies balsamea* [L.] Mill.), jack pine (*Pinus banksiana* Lamb.) and black spruce (*Picea mariana* [Mill.] BSP). The thesis is divided in four chapters.

Chapter 1 describes snag degradation pathways in mature to late-successional stands. Survival curves were constructed for each species and degradation pathways were documented based on the shape of the relationship, lag time if applicable (time period from death to fall onset) and half-life (time required for half of the stems to fall). Survival curves of most species exhibited a reverse sigmoid function. Trembling aspen, jack pine and to a lesser extent balsam fir presented significant lag times before initiation of a period with high fall rates. Black spruce experienced more snag losses during the first years following death. Jack pine was clearly the most persistent species due to the high resistance of snags to fall and stem breakage. Within the range of tree diameters in our study area, diameter *per se* did not significantly influence fall probability.

In Chapter 2, mineralization rates of snags (measured as wood density loss) and potentially influencing variables were assessed. Mineralization rates varied significantly among species. Trembling aspen exhibited a more rapid rate of loss than conifers. Jack pine was the second most rapid species to lose wood density, followed by balsam fir. Black spruce was particularly resistant to mineralization. No differences were detected in mineralization rates at the base and at breast height for conifers, whereas mineralization at the base of trembling aspen snags was significantly higher than at breast height. Time since death (TSD) coupled with Cerambycidae activity was associated with lower wood densities in trembling aspen, balsam fir and jack pine, whereas slower growth and smaller diameter were associated with a decreased mineralization rate in black spruce. We suggest that stand environmental conditions could explain why TSD is less influential in black spruce wood decay.

In Chapter 3, I investigated temporal patterns of post-fire mortality and snag dynamics after fire over ten years in jack pine, trembling aspen and black spruce. Temporal patterns of tree mortality for the three species revealed that mortality was delayed through time. Most post-fire tree mortality occurred within two years following fire but continued until the end of the 10-year observation period. Jack pine was the most persistent snag species, followed by trembling aspen and black spruce. Factors influencing the persistence of snags were multi-scaled and generally species-specific. Fire severity was the only common factor influencing snag persistence among all species, with snags located in severely-burned stands being less susceptible to falling. Trembling aspen snag persistence increased with basal area and diameter. Salvage logging in the vicinity affected black spruce. Fall patterns also differed among species. Bypasses of the snag stage (i.e. when a living tree falls directly to the forest floor) as well as uprooting of snags were common. The delayed tree mortality in many stands coupled with the relatively high persistence of snags 10 years after fire ensured a continuous input of fresh dead wood that led to the occurrence of a high density of snags and the simultaneous availability of dead wood at different stages of degradation.

Chapter 4 constitutes an integration of the preceding chapters. I examined which morphological attributes best predicted TSD and wood density in snags and I evaluated how a commonly used snag degradation classification system relates to these two variables. Results indicate that the best assemblage of predictors of TSD and wood density differed from one species to another. A first set of multiple linear regressions showed that bark cover was the only morphological attribute common to models of all species. A second set of multiple linear regressions showed that the combination of predictors for wood density was also species-specific and that wood penetrability was a common predictor in all species. Degradation stage appeared as a rough indicator of snag age (i.e. TSD). Average TSD generally increased with degradation stage, but significant overlap in TSD between adjacent stages occurred in all species. The same was true for the relationship between degradation stage and wood density. This study shows that the degradation classification system used can be helpful when rough estimates are needed. However, species-specific models built according to significant morphological attributes do not represent more time- and resource-consuming field assessments while providing more precise measurements of TSD and wood density.

The results of this thesis show that the differential dynamics in degradation and decomposition of the four studied species translate individualistic responses that are related to species autecology. These differences are observed in all chapters, regarding degradation pathways (chapters 1 and 3), wood mineralization (chapter 2), and morphological attributes indicating snag degradation stage (chapter 4). This conclusion also applies regarding factors influencing degradation (chapter 3) and decomposition (chapter 2). Therefore, dead wood can not be considered as a uniform substrate and individualistic responses of each species can have important implications for all ecological functions related to dead wood. In an ecosystem management perspective, these results should be considered when planning retention strategies of legacy trees.

Key words: Dead wood, snags, fall rates, mineralization rates, mortality, degradation classification systems, dendrochronology, trembling aspen, *Populus tremuloides*

Michx., balsam fir, *Abies balsamea* (L.) Mill., jack pine, *Pinus banksiana* Lamb., black spruce, *Picea mariana* (Mill.) BSP.

INTRODUCTION GÉNÉRALE

Historique de l'étude du bois mort

Historiquement, la présence de bois mort dans les forêts aménagées était considérée comme un gage de mauvaise gestion, comme un gaspillage de ressources. La démonstration de sa valeur écologique au sein des écosystèmes forestiers n'est maintenant plus à faire. Au cours des dernières décennies, des centaines d'études ont mis en lumière ses divers rôles au sein des écosystèmes forestiers.

Les premiers chercheurs à s'intéresser aux arbres morts ont été des forestiers de la côte ouest des États-Unis, au cours de la première moitié du XX^{e} siècle. Suite à une importante épidémie de scolytes qui avait engendré un fort taux de mortalité des arbres, on craignait qu'une grande disponibilité de bois mort n'entraîne des complications phytosanitaires et des risques élevés d'incendies forestiers, en plus des dangers pour la sécurité des travailleurs et des équipements (Keen 1929, Keen 1955, Harmon 2001). Afin de diminuer les risques, on récoltait les chicots. L'opération étant cependant très coûteuse, on a voulu connaître l'espérance de vie d'un arbre mort sur pied (Keen 1929, Dahms 1949, Keen 1955). L'étude de la dynamique des arbres morts était née et encore aujourd'hui, ces articles sont couramment cités.

Toujours sur la côte ouest, on a commencé au tournant des années 1980 à s'intéresser aux arbres morts en tant qu'habitats (Thomas *et al.* 1979) et comme éléments structuraux caractéristiques des forêts anciennes (Franklin *et al.* 1981, Cline *et al.* 1980). Cette période a aussi marqué le début d'une lancée de publications sur les rôles physico-chimiques du bois mort (Grier 1978, Harmon 1982, Foster et Lang 1982, Lambert *et al.* 1980). En 1986, la littérature concernant l'écologie des débris ligneux dans les écosystèmes tempérés était suffisamment importante pour qu'Harmon *et al.* (1986) y consacrent une revue exhaustive.

Un peu plus tard, en Fennoscandinavie, on commença à percevoir les impacts de l'aménagement intensif sur la biodiversité. La raréfaction des vieilles forêts (Östlund *et al.* 1997) et la disparition des attributs structuraux de ces dernières en forêts aménagées (Linder et Östlund 1998) ont résulté en une perte importante d'espèces, autant aux échelles locales, régionales que nationales (Berg *et al.* 1994). En 1994, on estimait que le quart des espèces menacées en Suède était associé au bois mort (Berg *et al.* 1994).

Les principales connaissances sur la dynamique des arbres morts en forêts boréale et tempérée proviennent donc de ces deux grandes régions, en raison des crises qui y ont sévi et des efforts de recherche qui ont suivi.

Rôles et importance du bois mort

Le bois mort, qu'il soit sur pied (chicot) ou au sol, représente un élément essentiel au bon fonctionnement des écosystèmes forestiers. D'une part, il constitue un habitat nécessaire à la survie d'une multitude d'organismes. Dans les forêts de la Nouvelle-Angleterre, on estime que 25% des vertébrés sont associés, à un moment ou à un autre de leur cycle de vie, au bois mort (DeGraaf *et al.* 1992). Au Québec, on compte plus de soixante espèces de vertébrés qui sont utilisatrices de bois mort (Darveau et Desrochers 2001). La guilde la plus étudiée est sans conteste celle des oiseaux, particulièrement les nicheurs de cavités (Evans et Conner 1979, Roberge et Desrochers 2004, Doyon *et al.* 1999, 2005, Nappi 2000, Drapeau *et al.* 2002, 2009), mais on compte de nombreux autres groupes d'espèces animales utilisatrices de bois mort comme les mammifères (Thomas *et al.* 1979, Darveau et Desrochers 2001), les amphibiens (Darveau et Desrochers 2001, Petranka *et al.* 1994) et les invertébrés (Saint-Germain *et al.* 2004, Siitonen et Martikainen 1994, Bouchard 2001). Il est particulièrement important de noter que chaque utilisateur de bois mort

est associé à des caractéristiques de bois mort (espèce, statut, stade de dégradation, taille) qui lui sont spécifiques (Harmon *et al.* 1986, Berg *et al.* 1994, Jonsson *et al.* 2005, Saint-Germain *et al.* 2007). Dans bien des cas, différentes étapes du cycle de vie de ces utilisateurs (ex.: alimentation, reproduction) correspondent à différentes combinaisons de ces caractéristiques (McComb et Muller 1983, Nappi 2009).

Les débris ligneux en état de décomposition avancé jouent un rôle important dans le processus de régénération de certaines forêts, offrant un substrat d'établissement et de croissance dont les conditions de température et d'humidité sont plus stables que l'humus ou le sol minéral (Harmon *et al.* 1986). Dans l'ouest américain, on a même conféré aux débris ligneux bien décomposés l'appellation de « nurse logs ». Les semis de plusieurs espèces, comme la pruche de l'ouest (*Tsuga heterophylla* [Raf.] Sarg.; Harmon *et al.* 1986), le bouleau jaune (*Betula alleghaniensis* Britt.; McGee et Birmingham 1997), l'épinette blanche (*Picea glauca* [Moench] Voss; Simard *et al.* 1998) et le thuya occidental (*Thuja occidentalis* L.; Scott et Murphy 1987, Simard *et al.* 1998) y sont particulièrement associés. De nombreuses espèces d'herbacées (Miller *et al.* 2002), de bryophytes, de lichens (Söderström 1988, Desponts *et al.* 2002) et de champignons saprophytes (Ståhl *et al.* 1999, Renvall 1995, Boddy 2001) y sont aussi intimement liées.

Finalement, le bois mort est largement impliqué dans de multiples processus biogéochimiques comme la séquestration du carbone et le cyclage des éléments nutritifs (Lambert *et al.* 1980, Bond-Lamberty *et al.* 2002, Laiho et Prescott 2004, Brais *et al.* 2006). Les débris ligneux représentent aussi un substrat qui permet la fixation de l'azote et le stockage de grandes quantités d'eau.

Région d’étude et choix des espèces

Dans l’est de l’Amérique du nord, on s’est jusqu’à récemment peu intéressé aux questions relatives au bois mort. Historiquement, l’abondance de forêts, la faible intensité d’aménagement et le caractère naturel des écosystèmes forestiers ont fait en sorte que le capital de bois mort a été peu amputé. Depuis la fin des années 1990, on perçoit cependant une préoccupation croissante pour la question, tant auprès de la communauté scientifique que des décideurs (Tyrrell et Crow 1994, Watt et Caceres 1999, Drapeau *et al.* 2002, Darveau et Desrochers 2001, Crête *et al.* 2004, Nappi *et al.* 2004, MRNFP 2005, Angers 2009).

Cet intérêt vient en partie du fait que la majeure partie du territoire forestier, qu’il soit feuillu, mixte ou résineux, est sous aménagement. Cette situation implique une raréfaction des quantités de bois mort qu’on y trouve en comparaison avec les forêts non-aménagées. D’une part, la récolte hâtive des peuplements élimine la mortalité liée à la sénescence, induit un rajeunissement de la matrice forestière et conduit à une perte des attributs liés aux vieilles forêts (Hunter 1990). D’autre part, en forêt boréale, les superficies affectées par des perturbations naturelles telles que les feux ou les épidémies d’insectes font l’objet de récupération de la matière ligneuse morte, ce qui réduit d’autant la disponibilité naturelle de cette ressource (Nappi *et al.* 2004, Lindenmayer *et al.* 2004, Schmiegelow *et al.* 2006). Finalement, au Québec, l’industrie se doit de récolter les arbres déjà morts si leur bois présente un potentiel de transformation (appellation de bois secs et sains).

Les connaissances sur les arbres morts en forêt boréale mixte et coniférienne de l’est de l’Amérique du Nord sont pour la plupart dérivées d’études ayant trait à la disponibilité de bois mort en fonction de l’âge, du stade successionnel ou de l’historique de perturbation des forêts (Sturtevant *et al.* 1997, Drapeau *et al.* 2002, Hély *et al.* 2000, Roberge et Desrochers 2004). Plusieurs s’y sont intéressés indirectement, en tant qu'habitat (Courteau *et al.* 1997, Bergeron *et al.* 1997, Drapeau *et al.* 2001, 2003, Potvin et Bertrand 2004, Doyon *et al.* 2005), qu'élément structural (Desponts *et al.* 2001, 2002, Harper *et al.* 2004, Mascarúa López *et al.* 2006, Angers *et al.* 2005) ou comme outil de reconstruction de la dynamique forestière (Bergeron et Charron 1994, Pham *et al.* 2004). On dispose donc de données ponctuelles sur la disponibilité de la ressource arbres morts, mais les études portant sur la dynamique des arbres morts *per se*, en termes de recrutement, de taux de chute, de rapidité de décomposition, etc. sont relativement récentes (Lee 1998, Garber *et al.* 2005, Boulanger et Sirois 2006, Saint-Germain *et al.* 2007, Taylor et MacLean 2007, Aakala *et al.* 2008) et une grande partie des connaissances restent encore à acquérir. Ce constat est particulièrement frappant pour le pin gris (*Pinus banksiana* Lamb.) pour lequel aucune donnée relative aux taux de dégradation ou de décomposition n'existe à notre connaissance, et ce, malgré qu'on ait rapporté sa longévité exceptionnelle comme chicot (Dansereau et Bergeron 1993).

Facteurs qui influencent la dynamique des arbres morts

Dans cette thèse, on réfèrera à la dynamique des arbres morts en termes de dégradation et de décomposition. La dégradation correspond aux taux de chute des arbres morts, aux trajectoires qu'ils empruntent pour tomber au sol (ex.: bris successifs, bris à la souche, déracinement) et à l'apparence extérieure des arbres (présence de branches, de ramilles, d'écorce, etc.). Il s'agit donc des caractéristiques externes de l'arbre. La décomposition réfère quant à elle aux caractéristiques internes du bois des arbres morts sur pied et s'exprime principalement par la perte de densité du bois engendrée par la respiration et le lessivage. La dégradation externe et la décomposition interne sont deux paramètres intrinsèquement liés.

Plusieurs études ont mis en évidence comment certaines caractéristiques propres aux tiges mortes ou à l'environnement dans lequel elles évoluent influencent leur dynamique:

L'espèce

Dans la littérature sur les taux de dégradation et de décomposition, les travaux ne se sont souvent concentrés que sur une seule espèce (Lambert *et al.* 1980, Means *et al.* 1985, Naesset 1999, Storaunet et Rolstad 2002). Comme les systèmes de classification de la dégradation, les méthodes de mesure de la densité du bois, la localisation géographique et les conditions environnementales changent d'une étude à l'autre, les résultats sont difficilement comparables (Creed *et al.* 2004). Néanmoins, quelques études se sont penchées sur plusieurs espèces à la fois, ce qui permet de faire quelques généralisations, bien que les résultats soient parfois contradictoires d'une étude à l'autre.

En ce qui concerne les taux de dégradation, deux études ont documenté la longévité de chicots de conifères et de feuillus de forêts mixtes de l'est de l'Amérique du Nord. Garber *et al.* (2005) ont observé que la persistance sur pied des chicots de feuillus (bouleau à papier [*B. papyrifera* Marsh.] et érable rouge [*Acer rubrum* L.]) était similaire ou légèrement plus élevée que celle des conifères (sapin baumier [*Abies balsamea* (L.) Mill.] et épinettes blanche et rouge [*P. rubens* Sarg.]) et Lee (1998) a observé une persistance des chicots de peupliers faux-tremble (*Populus tremuloides* Michx.) et baumiers (*P. balsamifera* L.) légèrement plus élevée que ceux d'épinette blanche. Par ailleurs, les résultats concernant les sapins et les épinettes sont contradictoires: Garber *et al.* (2005) ont documenté des longévités plus élevées chez le sapin baumier que chez les épinettes alors qu'Aakala *et al.* (2008) ont observé l'inverse chez le sapin et l'épinette noire (*P. mariana* Mill.). Les résultats disponibles concernant les genres *Abies* et *Pinus* proviennent quant à eux de la côte ouest où Raphael et Morrison (1987) et Morrison et Raphael (1993) ont montré que les sapins

(*A. concolor* et *A. magnifica*) se dégradent moins rapidement que les pins (*P. jeffrey* et *P. contorta*).

Les taux de décomposition du bois des arbres morts sont mieux documentés que les taux de dégradation, mais ont toutefois le plus souvent été rapportés pour les arbres morts au sol. Les taux de décomposition sont généralement plus rapides chez les feuillus boréaux que chez les conifères (Harmon 1982, Alban et Pastor 1993, Krankina et Harmon 1995, Harmon *et al.* 2000, Tarasov et Birdsey 2001, Yatskov *et al.* 2003, Brais *et al.* 2006, Mäkinen *et al.* 2006, Saint-Germain *et al.* 2007). Ces taux de décomposition différentiels sont vraisemblablement liés aux différences dans l'anatomie et la composition chimique du bois (Harmon *et al.* 1986). Par exemple, par rapport aux conifères, le peuplier faux-tremble présente une forte concentration d'hydrates de carbone et relativement peu de lignine (Peterson et Peterson 1992), ce qui en fait une espèce plus vulnérable aux agents décomposeurs et donc plus susceptible à la décomposition. Chez les conifères, le bois de certaines épinettes (épinette blanche, épinette de Norvège [*P. abies* (L.) Karst.]) se décompose plus rapidement que celui de pins (pin gris [*P. banksiana* Lamb.], pin sylvestre [*P. sylvestris* L.] ; Alban et Pastor 1993, Tarasov et Birdsey 2001, Yatskov *et al.* 2003) et les taux de décomposition du sapin baumier et de l'épinette rouge ne diffèrent pas significativement (Foster et Lang 1982).

La taille

Dans l'ouest américain, plusieurs chercheurs ont observé des taux de chute et de décomposition plus rapides chez les arbres de faible diamètre (Keen 1929, 1955, Cline *et al.* 1980, Means *et al.* 1985, Harmon *et al.* 1986, Raphael et Morrison 1987, Morrison et Raphael 1993, Everett *et al.* 1999, Tarasov et Birdsey 2001). Le diamètre d'un arbre influence entre autres les variations d'humidité, de température et de temps de colonisation des champignons saproxyliques (Boddy et Watkinson

1995). Cette résistance des gros arbres, qui contiennent une proportion d'aubier plus faible que les petits, serait entre autres expliquée par la plus grande susceptibilité de l'aubier à la décomposition (Keen 1955, Harmon *et al.* 1986) et par un faible rapport surface/volume qui retarderait la colonisation des organismes décomposeurs (Harmon *et al.* 1986).

L'influence du diamètre ne fait cependant pas l'unanimité. D'autres études n'ont observé aucune relation significative entre le diamètre et les probabilités de chute (Johnson et Greene 1991, Lee 1998, Kruys *et al.* 2002, Storaunet et Rolstad 2002) ou les taux de décomposition (Foster et Lang 1982, Mattson *et al.* 1987, Johnson et Greene 1991, Tarasov et Birdsey 2001).

Ces différences de résultats sont probablement associées au fait que l'étendue des diamètres échantillonnée est très variable d'une étude à l'autre. Ainsi, il est plus probable que des différences soient observées dans les écosystèmes de la côte ouest où la fourchette de diamètres est très étendue que dans les écosystèmes de la forêt boréale de l'est de l'Amérique ou de la Scandinavie, où le spectre de diamètres est plus faible (Foster et Lang 1982, Mattson *et al.* 1987, Johnson et Greene 1991).

Les causes de mortalité

La littérature fait souvent mention de l'influence que peuvent avoir les facteurs ayant conduit à la mort de l'arbre sur les trajectoires de dégradation et de décomposition des arbres (Everett *et al.* 1999), mais relativement peu d'études ont directement abordé le sujet. En ce qui concerne le feu, Morrison et Raphael (1993) ont observé des taux de chute plus élevés chez les arbres tués par le feu que chez les autres, un phénomène qui pourrait être expliqué par un affaiblissement à la souche et une plus grande exposition au vent qu'en forêt fermée (Harmon *et al.* 1986). Toutefois, selon Keen (1955) et Dahms (1949), les taux de chute des arbres brûlés et tués par les scolytes seraient similaires. Storaunet (2004) a aussi noté que les arbres qui présentent un déclin de la croissance avant la mort restent sur pied plus longtemps

que ceux dont la croissance est normale. Finalement, les tiges mortes suite à la défoliation par des insectes connaîtraient un décalage dans l'initiation de leur dégradation et seraient par conséquent plus persistantes que celles ayant connu d'autres causes de mortalité (Huggard 1999, Storaunet et Rolstad 2004, Garber *et al.* 2005). En effet, les tiges défoliées sont laissées intactes, ce qui limite la colonisation des champignons saproxyliques par rapport aux tiges brisées, et leur bois n'est pas nécessairement déjà colonisé par des champignons de carie qui affaiblissent leur résistance mécanique et les rendent plus susceptibles au bris.

Les agents biologiques

Les événements qui surviennent pendant la vie d'un arbre peuvent être déterminants dans sa trajectoire de dégradation une fois l'arbre mort. Avant même de mourir, l'arbre peut avoir localement été envahi par des champignons saproxyliques qui contribuent à la décomposition de son bois. Parmi les cas classiques chez les espèces boréales, on compte celui de la carie du cœur du sapin baumier, le plus souvent causée par *Stereum sanguinolentum* (Alb. et Schw. ex Fr.), ou celle du peuplier faux-tremble, le plus souvent causée par le polypore du tremble *(Phellinus tremulae* [Bond.]), qui forment des colonnes de pourriture à l'intérieur d'une coquille de bois sain bien avant la mort de l'arbre (Boulet 2003). Les blessures constituent également des portes d'entrées pour divers pathogènes, qui initient le processus de décomposition d'une partie de l'arbre avant sa mort. Même s'ils ne sont pas la cause de mortalité de l'arbre, ces agents ont pour effet d'induire une hétérogénéité dans la densité et la résistance du bois avant même que l'arbre ne meure. Ils influenceront la composition et la succession des communautés d'agents décomposeurs une fois l'arbre mort, et par conséquent les trajectoires de décomposition de l'arbre (Storaunet et Rolstad 2004, Renvall 1995, Boddy 2001).

D’autre part, plusieurs organismes utilisateurs de bois mort constituent des vecteurs

de propagation des agents décomposeurs. Ainsi, les insectes xylophages et les pics, créant des portes d’entrée et étant porteurs de spores, pourraient contribuer à l’introduction de champignons saprophytes et accéléreraient par conséquent le processus de décomposition (Farris *et al.* 2004, Cline *et al.* 1980).

Les conditions environnementales

Le taux d'humidité du sol et la température sont probablement les facteurs environnementaux dont on fait le plus mention comme ayant une influence sur la décomposition des débris ligneux qui sont en contact avec le sol (Harmon *et al.* 1986). Plus l'humidité du sol est grande, plus les taux de décomposition sont rapides (Naesset 1999, Boddy 2001). Toutefois, lorsque le milieu atteint des taux d'humidité excessifs associés à une raréfaction de l'oxygène disponible, on observe un ralentissement de la décomposition, tout comme dans le cas d'une sécheresse excessive (Laiho et Prescott 2004). La température joue aussi pour beaucoup, les taux de décomposition étant beaucoup plus élevés en région tropicale que dans les écosystèmes boréaux. L'altitude (Foster et Lang 1982) et l'exposition (Naesset 1999, Everett *et al.* 1999), ont aussi été mis en cause comme facteurs explicatifs dans la dynamique du bois mort.

Enfin, l'effet des conditions environnementales associées au peuplement et au paysage a très peu été documenté chez les chicots. Notons l'étude de Chambers et Mast (2005) qui ont observé que des chicots situés dans des peuplements brûlés de pin ponderosa (*P. ponderosa* Dougl.) en Arizona étaient plus susceptibles de tomber lorsque la surface terrière était faible. Toujours après feu, Russel *et al.* (2006) ont noté que pour un diamètre donné, les chicots de pin ponderosa et de sapin Douglas (*Pseudotsuga menziesii* Mirb.) situés dans des coupes de récupération partielles avaient les mêmes probabilités de chute que dans des peuplements non récupérés.

Représentation de la dynamique du bois mort par les systèmes de classification

Avec les débuts de l'étude du bois mort sont apparus les premiers systèmes de classification de la dégradation, qui sont maintenant utilisés dans une panoplie d'études en écologie forestière liées de près ou de loin au bois mort. Ces systèmes sont basés sur un ensemble de critères morphologiques pouvant généralement être évalués visuellement ou à tout le moins très rapidement (ex.: présence de branches, ramilles, feuilles, écorce, intégrité de la tige, pourcentage de hauteur résiduelle, pénétrabilité du bois). De nombreux systèmes de classification ont été élaborés au cours des ans. Dans la plupart des cas, ces classifications ne sont pas spécifiques à une espèce et sont d'ailleurs utilisées dans plusieurs écosystèmes. À titre d'exemple, le système de Thomas *et al.* (1979) a été développé pour les espèces conifériennes du nord-ouest des États-Unis mais a depuis été utilisé pour des espèces boréales de l'est de l'Amérique du Nord (ex.: Harper *et al.* 2005, Taylor et MacLean 2007). Cette utilisation à grande échelle suggère que toutes les espèces suivent grossièrement le même patron de dégradation, ce qui n'a toutefois pas été vérifié.

Dans bien des cas, les systèmes de classification de la dégradation sont utilisés comme indicateurs du temps écoulé depuis la mort (TDM) ou des caractéristiques internes du bois, inférant une forte corrélation entre ces paramètres. Plusieurs études ont évalué la relation entre les stades de dégradation des chicots de différents systèmes de classification et le TDM, et ont obtenu des corrélations allant de très faibles (Mast et Veblen 1994, Daniels *et al.* 1997) à relativement bonnes (Huggard 1999, Campbell et Laroque 2007, DeLong *et al.* 2008). Les mêmes conclusions ont été trouvées pour la densité du bois (Yatskov *et al.* 2003, Creed *et al.* 2004, Saint-Germain *et al.* 2007). Ces forts degrés de variabilité sont entre autres explicables par le fait que les chicots ne suivent pas toujours le patron de succession de la dégradation typique et que le choix d'une classe de dégradation pour décrire un chicot constitue souvent un compromis entre plusieurs critères. Cette situation suggère que certains critères morphologiques constituent peut-être de meilleurs indicateurs que d'autres. Peu d'études se sont toutefois penchées sur cette question, mais celles qui l’ont fait ont montré que c’était effectivement le cas (Yatskov *et al.* 2003, Newberry *et al.* 2004, Storaunet 2004, Waskiewicz *et al.* 2007).

Aperçu des approches utilisées dans la littérature et dans cette thèse

Les études sur la dynamique du bois mort sont essentiellement basées sur deux types de dispositifs d’échantillonnage: les suivis à long terme et les reconstitutions rétrospectives. Les suivis à long terme, surtout lorsque les échantillonnages sont rapprochés dans le temps, permettent les analyses les plus fines et sont par conséquent les plus performants. Ils requièrent cependant d’importants investissements dans l’implantation du dispositif, dans son entretien et dans le suivi. Les processus de dégradation et de décomposition du bois étant lents, on doit également attendre plusieurs années avant de pouvoir utiliser les données générées. Les données peuvent par la suite être analysées par régression logistique (Vanderwel *et al.* 2006) ou avec l’analyse de survie (Lee 1998, Garber *et al.* 2005, Russell *et al.* 2006). Dans cette thèse, cette dernière approche a été utilisée au chapitre 3. En effet, un dispositif visant à étudier la dynamique forestière après feu a été mis en place en 1997 et a ensuite été suivi annuellement ou aux deux ans sur une période de dix ans.

Les reconstitutions rétrospectives requièrent quant à elles généralement moins d’investissements et génèrent des résultats plus rapidement. Elles se déclinent sous plusieurs formes selon les écosystèmes à l’étude et le choix des auteurs. Elles peuvent être menées sur la base de chronoséquences, où une série de sites représentant différents stades évolutifs sont échantillonnés (ex.: Foster et Lang 1982, Yatskov *et al.* 2003, Boulanger et Sirois 2006, Brais *et al.* 2006). Cette approche se prête bien à l’analyse d’arbres morts issus de perturbations sévères dont on connaît l’année d’origine (ex.: feux, coupes) mais n’est pas applicable à l’analyse de la dynamique d’arbres morts au cours de l’évolution d’un peuplement.

Plusieurs études ont eu recours à des reconstitutions dendrochronologiques.

L'année de la mort de l'arbre est déterminée par l'analyse des cernes de croissance et l'année de la chute par divers indices observables lors de l'échantillonnage. Très souvent, notamment sur la côte pacifique nord-américaine, on a daté les cicatrices infligées au cambium des arbres vivants situés en périphérie lors de la chute de l'arbre mort (Means *et al.* 1985, Sollins *et al.* 1987, Dynesius et Jonsson 1991, DeLong *et al.* 2005, Daniels *et al.* 1997, Storaunet et Rolstad 2002, Yatskov *et al.* 2003). Un temps minimum depuis la chute peut aussi être établi en estimant le temps requis pour qu'un débris soit suffisamment décomposé pour être colonisé par la végétation. On peut aussi déterminer l'âge au collet des semis établis sur les débris ligneux couchés ou dans le sol minéral mis à nu suite à un chablis (Means *et al.* 1985, Sollins *et al.* 1987, Dynesius et Jonsson 1991, Daniels *et al.* 1997). D'autres méthodes moins répandues, telles que la datation du bois de réaction des arbres pliés par la chute de la tige (voir Dynesius et Jonsson 1991 pour une revue) et la datation au C^{14} ont aussi été utilisées (Daniels *et al.* 1997).

Contrairement aux écosystèmes de la côte ouest où l'on retrouve de très grosses tiges dont la dégradation et la décomposition se font sur des décennies et des centaines d'années, les arbres de la forêt boréale de l'est de l'Amérique du Nord sont habituellement de trop petit diamètre pour pouvoir infliger des blessures significatives qui peuvent être retracées après plusieurs années. Les forêts sont aussi parfois très ouvertes, ce qui réduit les possibilités de contact avec les arbres environnants lors de la chute. De plus, on dispose de trop peu d'information sur les taux de décomposition des débris ligneux au sol et sur les exigences de décomposition du substrat d'établissement des espèces végétales pour utiliser ces indices.

Dans ces conditions, les données générées par l'analyse dendrochronologique permettent de connaître le TDM mais ne renseignent pas sur le moment de la chute, dans le cas des arbres au sol, ou sur le moment où l'arbre tombera, dans le cas des chicots. Les données sont donc toutes censurées, soit vers la droite ou vers la gauche (Gore *et al.* 1985), ce qui ne permet pas l'utilisation d'analyses telles que la régression logistique ou l'analyse de survie (Allison 1995). Afin de contourner cette limite, plusieurs auteurs ont eu recours à la modélisation pour estimer les taux de chute ou de décomposition du bois des chicots. Cette approche repose cependant sur certaines prémisses. Kruys *et al.* (2002) ont proposé une approche où l'on présume que le recrutement de bois mort est constant dans la population. Gore *et al.* (1985), Johnson et Greene (1991), et plus récemment Richards et Johnson (2007) ont proposé une approche basée sur des estimations du maximum de vraisemblance qui contourne cette prémisse de recrutement constant mais qui présume que le taux de chute est exponentiel, i.e. qu'une proportion constante de chicots tombe à chaque intervalle de temps et que les taux de décomposition des chicots sont très faibles.

Dans cette thèse, la date de mort des arbres a été déterminée par analyse dendrochronologique aux chapitres 1, 2 et 4. Au chapitre 1, comme on s'intéressait aux taux de chute, les approches de modélisation ont été évaluées mais n'ont pas été retenues puisque les prémisses n'étaient pas respectées. En effet, les patrons de mortalité témoignaient dans plusieurs cas d'un recrutement non constant dans le temps (chapitre 1), nous limitant dans l'application du modèle proposé par Kruys *et al.* (2002), et les taux de décomposition du bois des chicots étaient trop élevés (chapitre 2) pour utiliser l'approche de Richards et Johnson (2007). On a donc dû documenter les taux de chute à l'aide d'une approche descriptive basée sur le rapport entre le nombre d'arbres morts toujours debout et le nombre total d'arbres morts (voir le chapitre 1 pour plus de détails).

Étude de la dynamique des arbres morts en forêt boréale – Structure de la thèse et liens entre les chapitres

Cette thèse propose d'enrichir les connaissances relatives à la dynamique des arbres morts sur pied en milieu naturel de quatre espèces communes en forêt boréale mixte et coniférienne de l'est du Canada: le peuplier faux-tremble, le sapin baumier, le pin gris et l'épinette noire. Les sites à l'étude sont présentés à la figure 0.1. Dans chaque chapitre, j'ai voulu comparer les espèces entre elles en posant l'hypothèse que les différences qui leur sont intrinsèques pendant leur vie (e.g. autécologie, caractéristiques anatomiques) devraient se traduire dans les patrons de dégradation et de décomposition observés après leur mort.

Le premier chapitre de la thèse vise à documenter les patrons de dégradation des quatre espèces en forêt « verte » (i.e. peuplements matures ou surannés qui n'ont pas subi de perturbation sévère récente). Ce chapitre constitue la référence méthodologique des chapitres 2 et 4 (aire d'étude, historique des sites à l'étude, caractérisation des patrons de mortalité de chaque espèce au cours des dernières décennies). La dégradation des arbres y est analysée en regard de la probabilité de persistance des tiges sur pied, de la forme que prend la courbe de persistance, des trajectoires de chute suggérées par différents indices, de la taille des tiges, de la dynamique du peuplement et de l'autécologie de chacune des espèces. Ce chapitre met en lumière les différences qui existent dans les trajectoires de dégradation des arbres morts et lie ces différences aux caractéristiques intrinsèques des espèces à l'étude.

Le deuxième chapitre est consacré à l'analyse des propriétés du bois mort à l'intérieur du tronc. Pour les mêmes espèces d'arbres qu'au chapitre 1 et en grande partie avec les mêmes échantillons, les taux de minéralisation du bois des chicots sont mesurés. Par minéralisation, je réfère ici à la perte de densité du bois, qui est principalement due à la respiration et au lessivage, le processus de fragmentation des sections échantillonnées n'ayant pas encore débuté. Intuitivement, je m'attendais à ce que la densité du bois diminue avec le TDM. Des facteurs écologiques évoqués dans la littérature qui influencent cette minéralisation sont aussi analysés, notamment l’activité des insectes saproxyliques, un facteur souvent soupçonné d’accélérer le processus de minéralisation, mais qui a très peu été testé.

Au troisième chapitre, on passe de la dynamique des chicots morts dans les vieilles forêts à celle qui a cours suite à une perturbation importante, soit un feu. Ce chapitre vise à documenter deux aspects très peu documentés dans la littérature, soit les patrons temporels de mortalité des arbres et de dégradation des arbres morts après feu. Les facteurs qui influencent ces patrons sont également examinés. Trois espèces sont à l’étude: le peuplier faux-tremble, le pin gris et l’épinette noire. Le dispositif de recherche utilisé est unique pour ce genre d’étude car plus de 2000 arbres répartis dans des parcelles permanentes ont été suivis annuellement ou bisanuellement sur dix ans, et le dispositif permet de tester à la fois l’effet de la composition du peuplement et de la sévérité du feu. En ce qui a trait à la mortalité, je me suis intéressée aux arbres qui survivent à des feux de sévérité variable, afin de voir s’ils se maintiennent en vie à court et moyen terme ou si le processus de mortalité est décalé dans le temps. Pour ce qui est des arbres morts, j’ai analysé des facteurs qui influencent la chute des arbres morts en intégrant des variables explicatives mesurées à plusieurs échelles (arbre, peuplement, contexte du paysage adjacent aux parcelles permanentes).

Le quatrième chapitre est intégrateur des chapitres précédents. Comme la littérature ainsi que les trois premiers chapitres de cette thèse suggèrent que chaque espèce présente des patrons de dégradation qui lui sont propres, j’ai posé l’hypothèse qu’un système de classification universel de la dégradation ne pouvait permettre des évaluations précises de l’état d’un arbre mort. J’ai donc évalué un système de classification de la dégradation couramment utilisé pour les espèces à l’étude aux chapitres 1 et 2 en quantifiant dans quelle mesure chacun des stades de dégradation est représentatif 1- du TDM, et 2- du degré de décomposition du bois. Dans le même ordre d’idée, je m’attendais à ce que les attributs morphologiques qui sont les meilleurs indicateurs du TDM et du degré de décomposition soient différents d’une espèce à l’autre. J’ai donc vérifié cette hypothèse puis proposé un raffinement du système de classification qui est spécifique à chaque espèce tout en étant novateur et fonctionnel sur le terrain.

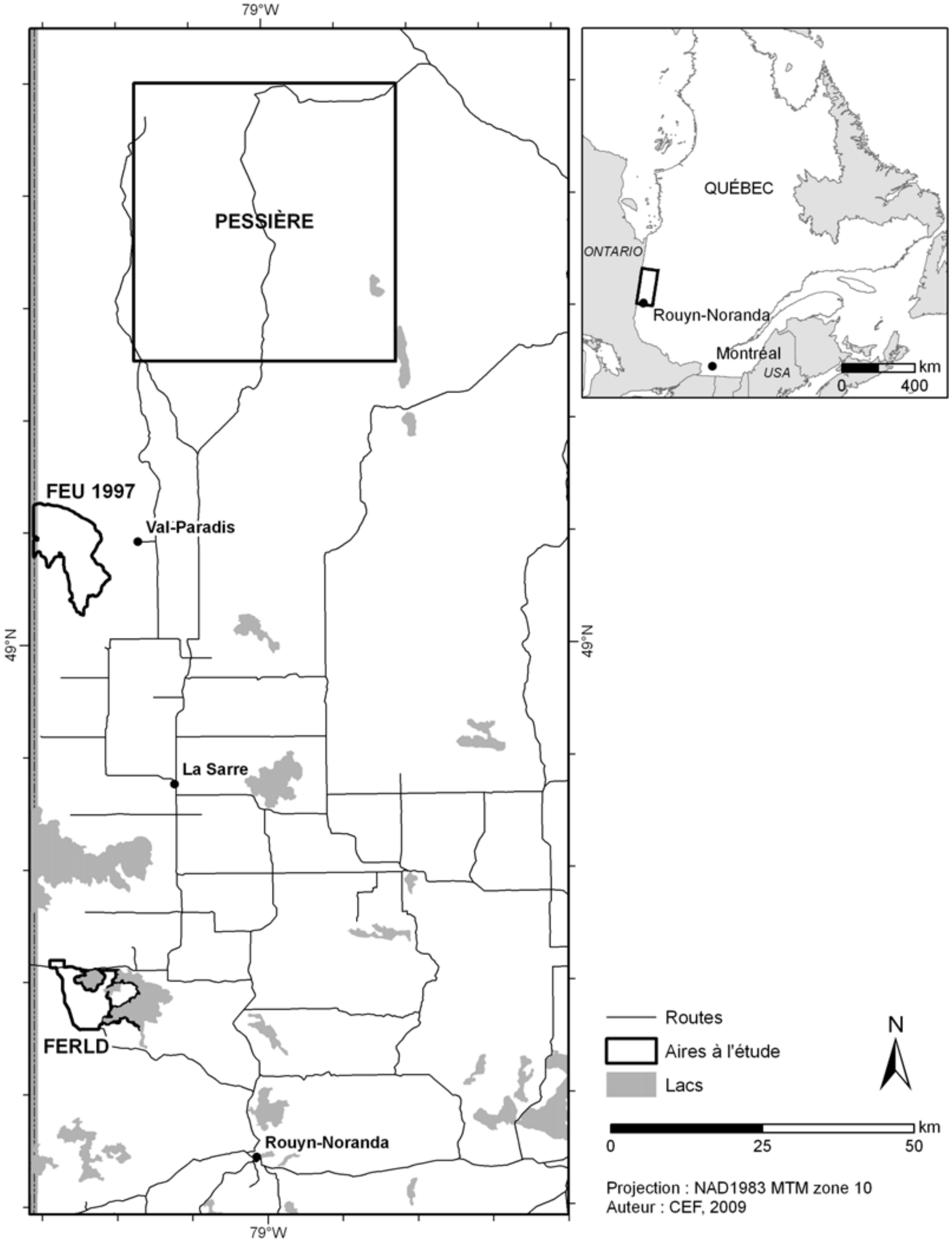

Figure 0.1. Localisation des sites à l'étude. L'échantillonnage des chapitres 1, 2 et 4 a eu lieu à la Forêt d'enseignement et de recherche du lac Duparquet (FERLD) ainsi que dans la pessière, au nord. L'échantillonnage du chapitre 3 a eu lieu dans le feu de 1997, à l'ouest de Val-Paradis.

CHAPITRE 1

SNAG DEGRADATION PATHWAYS OF FOUR NORTH AMERICAN BOREAL TREE SPECIES

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1.1 Résumé

Plusieurs études ont mis en lumière l'importance du bois mort dans la dynamique des écosystèmes forestiers boréaux, qu'il soit sur pied (chicot) ou au sol. Les taux de persistance des chicots et leurs trajectoires de chute sont cependant peu documentés chez les espèces boréales américaines. Dans cette étude, nous avons documenté les trajectoires de chute de quatre espèces d'arbres des forêts boréales mixte et coniférienne de l'est de l'Amérique: le peuplier faux-tremble (*Populus tremuloides* Michx.), le sapin baumier (*Abies balsamea* [L.] Mill.), le pin gris (*Pinus banksiana* Lamb.) et l'épinette noire (*Picea mariana* [Mill.] BSP). L'échantillonnage a été réalisé dans des forêts non aménagées du nord-ouest du Québec. Des disque-échantillons ont été prélevés sur 363 chicots et débris ligneux, et l'année de mort a été déterminée par interdatation dendrochronologique.

Des courbes de survie ont été construites pour chaque espèce, et les trajectoires de dégradation ont été documentées en se basant sur la forme de la relation, le délai dans l'initiation de la chute et la demi-vie (le temps requis pour que la moitié des tiges soient tombées). Chez la plupart des espèces, les courbes de survie ont pris la forme de fonctions sigmoïdes inversées. Le peuplier faux-tremble, le pin gris et dans une moindre mesure le sapin baumier présentaient des délais significatifs avant que les taux de chute ne deviennent importants. De plus forts taux de chute étaient observables chez l'épinette noire dans les premières années suivant la mort. Le pin gris était clairement l'espèce la plus persistante vu sa grande résistance à la chute et aux bris. Le diamètre des arbres n'a pas influencé significativement la probabilité de chute, probablement parce que la fourchette de diamètres disponibles dans l'aire d'étude était trop restreinte.

Les trajectoires de dégradation différentielles des quatre espèces à l'étude traduisent des réponses individuelles des espèces qui sont liées à leur autécologie. Cette conclusion a d'importantes conséquences pour toutes les fonctions écologiques liées au bois mort et devrait être considérée lors de l'élaboration de stratégies de rétention d'arbres à valeur de conservation dans une perspective d'aménagement écosystémique.

Mots-clés: Bois mort, chicots, taux de chute, dendrochronologie, peuplier faux-tremble, *Populus tremuloides* Michx., sapin baumier, *Abies balsamea* (L.) Mill., pin gris, *Pinus banksiana* Lamb., épinette noire, *Picea mariana (*Mill.) BSP.

1.2 Abstract

Many studies have highlighted the importance of dead wood, whether standing (snags) or fallen, in boreal ecosystem dynamics. However, a dearth of literature exists regarding the persistence and degradation pathways of these structures in northeastern American boreal species. Degradation pathways were examined in four tree species of the eastern boreal mixedwood and conifer forests of Canada: trembling aspen (*Populus tremuloides* Michx.), balsam fir (*Abies balsamea* [L.] Mill.), jack pine (*Pinus banksiana* Lamb.) and black spruce (*Picea mariana* [Mill.] BSP). Sampling was conducted in unharvested forests of northwestern Quebec. Discs were collected from 363 snags and logs and dendrochronological analyses conducted to determine year of death by crossdating.

Survival curves were constructed for each species and degradation pathways were documented based on the shape of the relationship, lag time if applicable (time period from death to fall onset) and half-life (time required for half the stems to fall). Most species survival curves exhibited a reverse sigmoid function. Trembling aspen, jack pine and to a lesser extent balsam fir presented significant lag times before initiation of a period with high fall rates. Black spruce experienced more snag losses during the first years following death. Jack pine was clearly the most persistent species due to snags high resistance to fall and stem breakage. Within the range of tree diameters in our study area, diameter *per se* did not significantly influence fall probability.

Differential degradation pathways of the four species are the result of individualistic responses related to species autecology. This has important implications for all ecological functions related to dead wood and should be considered when planning retention strategies of legacy trees within an ecosystem management perspective.

Key words: Dead wood, snag fall, dendrochronology, trembling aspen, *Populus tremuloides* Michx., balsam fir, *Abies balsamea* (L.) Mill., jack pine, *Pinus banksiana* Lamb., black spruce, *Picea mariana* (Mill.) BSP.

1.3 Introduction

Dead wood is a key component in many functions and processes of forest ecosystems (Harmon et al. 1986, Jonsson and Kruys 2001). Whether standing (snag) or fallen (log), it provides nesting, denning, perching, sheltering, breeding and foraging sites for many vertebrates and invertebrates (Thomas et al. 1979, Harmon et al. 1986), as well as germination and growth substrates for many fungi, bryophytes and vascular plants (Harmon et al. 1986, Söderström 1988, Renvall 1995, Simard et al. 1998). Furthermore, dead wood plays an important role in physical and chemical processes such as carbon sequestration and nutrient cycling (Krankina and Harmon 1995, Brais et al. 2006, but see Laiho and Prescott 2004).

Dead wood dynamics, i.e. the rate at which dead trees degrade, decompose and fall, and the factors that influence how these processes occur (e.g. tree mortality patterns, tree-, stand- and landscape-level variables), has been studied extensively in coniferous forests of the North American West Coast (e.g. Harmon et al. 1986, Raphael and Morrison 1987, Daniels et al. 1997) and Fennoscandia (e.g. Kruys et al. 2002, Storaunet and Rolstad 2002, 2004). In the boreal forest of eastern North America, the amount of dead wood in different forest types relative to their age, successional status or disturbance history has been quantified in several studies (e.g. Sturtevant et al. 1997, Hély et al. 2000, Harper et al. 2003). Studies on dead wood dynamics of boreal tree species in this part of the boreal ecosystem, particularly the transition from standing dead trees to logs, are, however, more recent (Lee 1998, Garber et al. 2005, Boulanger and Sirois 2006, Taylor and MacLean 2007, Aakala et al. 2008) and the dynamics of individual tree species remains largely unknown. This is particularly true in the case of jack pine (*Pinus banksiana* Lamb.). Indeed, despite its reported longevity as a snag (Dansereau and Bergeron 1993), no information exists on its snag to log dynamics to our knowledge.

Snag survival, i.e. the probability of a standing dead tree to remain standing after a given time, in opposition to the fall rate, i.e. the rate at which snags fall to the forest floor, is a major component in understanding dead wood dynamics. From a population dynamics' perspective, the fall rate represents both loss in the snag population and recruitment in the log population. Since functions and roles of dead wood change with its status and degradation stage, quantifying patterns of degradation, particularly the fall process of standing dead wood, is a primary step in the understanding of shifts in dead wood ecological functions. Probability of survival has been described with negative exponential (e.g. Storaunet and Rolstad 2002, 2004) or reverse sigmoid functions (e.g. Keen 1929, Garber et al. 2005). The former is observed when the survival is constant, whereas the latter results from an initial slow fall rate period expressed by a lag time, followed by a period where fall rate is more rapid and finally levels off.

Trees may take different degradation pathways and be the result of uprooting or of single or multiple bole breakages. Many factors are implied, including species, diameter, height, cause of death, bole condition at time of death, exposure to wind, climate, surficial deposit type, stand history and disturbance regime (Harmon et al. 1986, Raphael and Morrison 1987, Garber et al. 2005).

In this study we document the degradation pathways of snags of four of the main boreal species in eastern North America: trembling aspen (*Populus tremuloides* Michx.), balsam fir (*Abies balsamea* [L.] Mill.), jack pine and black spruce (*Picea mariana* [Mill.] BSP). Using empirical data from unharvested forests in both boreal mixedwood and conifer stands we develop and compare snag survival curves of each species and assess their degradation pathways. We discuss these findings with regards to stand dynamics and the autecology of each species.

1.4 Methods

1.4.1 Study area

The study was conducted in northwestern Quebec, at the transition between the mixedwood and coniferous boreal forest. For balsam fir, trembling aspen and jack pine, sampling was conducted in the Lake Duparquet Research and Teaching Forest (LDRTF; 48^{o}26’-48^{o}29’N, 79^{o}26’-79^{o}18’W), which is located 45 km northwest of Rouyn-Noranda. Elevation ranges from 274 to 411 m above sea level. The area is located in the Rouyn-Noranda ecological region, within the balsam fir-white birch (*Betula papyrifera* Marsh.) bioclimatic domain (Robitaille and Saucier 1998), where associations of balsam fir, black spruce, white spruce, paper birch and trembling aspen dominate. Disturbance history includes recurrent fires (Dansereau and Bergeron 1993), with spruce budworm (*Choristoneura fumiferana* Clem.) outbreaks when the fire cycle is long enough (Morin et al. 1993).

For black spruce, sampling was conducted in the coniferous boreal forest, 120 km further north (49^{o}25’-49^{o}50’N, 79^{o}18’-78^{o}41’W), in the Lake Matagami Lowland ecological region, within the black spruce–feathermoss (*Pleurozium schreberi* [Brid.] Mitt.) bioclimatic domain (Robitaille and Saucier 1998). Elevation ranges from 239 to 400 m above sea level. The disturbance regime is characterized by large stand-replacing fires (Bergeron et al. 2004) with return intervals long enough for successional paludification processes to take place, organic deposits to accumulate and low productive, open forests to develop (Simard et al. 2007).

Both areas are part of a broad physiographic unit known as the Northern Clay Belt, an area characterized by fairly flat topography and clay deposits originating from the proglacial lakes Barlow and Ojibway (Vincent and Hardy 1977). Climate is cold and continental, with a mean annual temperature of 0.7^{o}C and mean annual total precipitation of 889.8 mm (weather station of La Sarre, Environment Canada 2010).

1.4.2 Data collection

Data collection was conducted during the summers of 2004 and 2005. Seventeen stands were selected, based on species composition, surficial material type, drainage and age. Site selection was further constrained by accessibility and absence or very few harvesting activities based on historical reconstructions (Bescond 2002, Lecomte et al. 2006). In cases where more sites fulfilled all requirements than what was necessary, sites were randomly selected. Sites were mesic and surficial material composed of glaciolacustrine clay in LDRTF, whereas black spruce sites were subhydric and composed of glacio lacustrine clay overlain by a thick organic layer. All stands were mature to late-successional. Stand origins and harvesting history are presented in Table 1.1.

In each stand, a 20 m x 20 m plot was randomly established, at least 50 m from any edge (road, cut, different stand). Every snag (tree without green foliage, at least 1.3 m tall and with diameter at breast height [DBH] ≥ 5 cm) and every log from which the stump was located within the plot (DBH ≥ 5 cm) was recorded. Leaning dead trees were considered as logs if their angle from the ground was below 45^o (Harmon and Sexton 1996). Buried logs that were still judged datable, particularly those covered by mosses or sphagnum in black spruce stands, were also located. Direction of fall of logs was measured to the nearest degree using a compass. Characterization of snags and logs included species, DBH (± 0.1 cm), height (in snags, ± 0.1 m) and stem integrity (whether entire, broken or uprooted). Uprooted trees were considered as such when at least the bases of some coarse roots were still visible. A total of 363 dead trees were characterized.

Snags were felled and cross-sections were taken from all dead trees that were sound enough to suggest potential use for dendrochronological analyses. Fragile samples were taped with thread-enforced tape and cut using a fine-toothed bow saw to lessen fragmentation. To optimize chances of successful crossdating, three cross-sections were taken from each bole when possible: at base height, breast height and near the top (around 3 m from the top for intact trees and near breakage height for broken trees). This sampling procedure 1) reduced the risk of crossdating failure due to advanced decay, 2) validated year of death with multiple crossdated sections and 3) increased capture of the last ring produced in stressed trees (Mast and Veblen 1994, V.A. Angers *unpublished data*). For broken trees, if the fallen tree top was reliably identifiable, a cross-section was also taken. In boles with advanced decay, height at which cross-sections were taken varied depending on bole periphery preservation to maximize crossdating success.

1.4.3 Tree ring analysis

All cross-sections were dried and sanded until xylem cells were clearly visible. When necessary, hot glue was used to consolidate fragmented samples prior to sanding. Ring width was measured for each cross-section along two radii (one when decay impeded ring visibility elsewhere on the cross-section) using a Velmex micrometer (precision of 0.001 mm, Velmex incorporated, Bloomfield, New York, USA).

To establish year of death, each individual ring width series generated by all 756 cross-sections was crossdated against a master series built for balsam fir, jack pine and trembling aspen from nearby living trees at LDRTF (V.A. Angers, *unpublished data*) and from a master chronology built for black spruce by Simard et al. (2007). Crossdating was performed using marker years, and with COFECHA (Holmes 1983) and TSAP (Rinn 1996) programs, the latter being used for visually comparing the pattern generated by each series and the average of the master series. When discrepancies in years of death were obtained for cross-sections belonging to the same dead tree, the most recent year was retained.

Of the 363 stems detected in the field, only 12 were not successfully crossdated. These trees either had cross-sections that were too decayed to perform measurements or were too young (not enough rings) for reliable crossdating. Seventeen (17) stems had their periphery eroded and thus their outmost rings were possibly missing, impeding an accurate assessment of year of death (one stem of trembling aspen, seven of balsam fir, nine of black spruce). Given that this represented a small proportion of the sampled trees, those minimum death years were considered as the actual ones. Time since death was calculated as the difference between year of sampling and year of death.

1.4.4 Analysis of tree mortality data

To assess to what extent mortality was constant through time, we conducted survival analysis using the Kaplan-Meier estimator on uncensored data for each species. The survival curves generated were then compared with constant survival models using the Mantel-Haenszel and the Tarone-Ware tests. The Mantel-Haenszel test (also known as the Mantel-Cox or log-rank test) applies equal weighting to the whole time-series whereas the Tarone-Ware test gives less emphasis on the later part of the time-series (SYSTAT 2004). In order to avoid bias potentially caused by undetected dead trees, we selected time frames where we assume that most trees that died during those periods were detected (1980-2004 for trembling aspen and balsam fir, 1970-2004 for jack pine and black spruce).

Uprooting occurrence was estimated as the ratio between uprooted logs to total fallen logs. Also, to assess if a massive fall event related to wind disturbance occurred, we used polar plots showing directions of fallen stems coupled with time of death for every site.

1.4.5 Analysis of snag survival data

Since sampling was conducted at one point in time, time since death and dead tree status (standing vs. fallen) are known. However, the time when fall occurred in logs or when it will occur in snags remains unknown. All data is therefore either right- or left-censored (Gore et al. 1985), which impedes the use of classical analyses such as logistic regression or survival analysis to build snag survival relationships.

To overcome this problem and in order to approximate event of fall, many authors have successfully used alternative methods such as dating fell scars on neighboring trees and age of seedlings growing on logs (Daniels et al. 1997, Storaunet and Rolstad 2002, Yatskov et al. 2003, DeLong et al. 2008) or dating release growth on surrounding stems and reaction wood in stems bent over by a falling tree (Daniels et al. 1997), but these proxies were not transferable to the studied ecosystem given the small size, relatively rapid decay rates of trees and low reliability of these estimates.

Modelling approaches have also been suggested to estimate longevity of standing snags with right- and left-censored data. Kruys et al. (2002) proposed an approach which assumes that all snags are halfway through their total standing time and that there is a constant input of dead wood in the population. In most cases, this latter assumption was not met (see results). Gore et al. (1985), Johnson and Greene (1991), and more recently Richards and Johnson (2007) proposed snag survival modelling approaches based on maximum likelihood estimates that circumvent to some extent the assumption of constant mortality and that only require time since death of dead trees and their status at time of observation (standing vs. fallen). However, these methods assume an exponential distribution of snag fall, i.e. a constant proportion of snags falling at each time interval and very little decomposition occurring within the standing dead boles. These two assumptions do not hold in the ecosystems under study (see results, Chapter 2).

Given the limitations of both our data set and the statistical methods in use, we decided to document the degradation pathways of tree species with a descriptive approach that depicts survival curves of snags. First, for each species, survival relationships were constructed using the ratio between the cumulative number of trees still standing after at least a given number of years since death and the number of trees dead since at least that given time. Curves were then fitted to determine which function among linear, negative exponential and reverse sigmoid best described the relationship. Because standing time may be underestimated in all snags and time since fall overestimated in all logs, these relationships can at best be considered approximations of real survival probabilities. Although our descriptive curves cannot determine statistically the critical time period of snag fall, differences between standing and fallen dead trees can, however, be assessed statistically using one-way analysis of variance with dead wood status (standing and fallen) as a fixed factor. Analyses of variance on each tree species were thus conducted to assess if time since death differed in standing versus fallen dead trees.

As with other studies on snag dynamics' (e.g. Boulanger and Sirois 2006, Aakala et al. 2008), uprooted trees were not included in the analyses since it is not possible to assess retrospectively whether an uprooted tree was living or dead prior to the event. However, uprooting can occur in dead standing trees of the species under study (Taylor and MacLean 2007, V. Angers pers. obs.). By excluding these trees we may overestimate snag survival rates given that some uprooted trees were snags. On the other hand, trees that break off near the base are included in our analyses. Some of these trees may have been alive prior to the event. Thus, inclusion of these trees may underestimate snag survival rates. Consequently, our snag survival rates may be viewed as a coarse index of snag survival that incorporates these biases.

Survival probability curves can be described with regards to lag time, maximal longevity observed and half-life (Fig. 1.2a). Lag time corresponds to the delay from death to fall onset, maximal longevity observed designates the longest survival time observed, and half-life refers to the time required for half the stems dead at a given time to fall to the forest floor.

1.4.6 Analysis of degradation pathways

Linear regressions were used to assess the effect of time since death on snag height and DBH. Using 10 year periods in each species, analysis of variance was used to assess if DBH influenced the standing/fallen status. Prior to all analyses requiring it, assumptions of normality and homoscedasticity were verified and data were transformed when necessary.

1.5 Results

1.5.1 Tree mortality

Graphical examination and survival analysis of temporal mortality patterns showed major differences between species (Fig. 1.1). Despite year to year variations in mortality, observed annual mortality and constant mortality did not significantly differ in jack pine and black spruce (jack pine: $p = 0.156$ [log-rank], $p = 0.152$ [Tarone-Ware]; black spruce: $p = 0.554$ [Mantel-Haenszel], $p = 0.734$ [Tarone-Ware]). In trembling aspen, increased mortality in the last decade induced a significant departure from constant mortality ($p = 0.012$ [Mantel-Haenszel], $p = 0.028$ [Tarone-Ware]). Balsam fir mortality also differed significantly from constant mortality ($p \leq 0.001$ [Mantel-Haenszel and Tarone-Ware]): 68% of trees died between 1980 and 1984 and tree deaths were sporadic between 1990 and 2005, a pattern typical of mortality caused by a severe spruce budworm outbreak.

Uprooting occurred in all species. Balsam fir appeared to be the least susceptible, with only 10.4% of logs uprooted. Trembling aspen showed a slightly higher proportion of uprooting (12.5%) whereas black spruce and jack pine had similar values, with 17.9% and 20.8%, respectively. Although wind certainly plays a major role in live tree and snag fall by breaking or uprooting already weakened stems, polar plots showing directions of fallen stems (not shown) coupled with time of death for every site did not indicate any massive mortality or fall occurrence that would be related to a particular windstorm.

1.5.2 Snag survival

For all species, average time since death was significantly shorter in snags than in logs (Table 1.2). Survival probability curves clearly showed different patterns among tree species (Fig. 1.2). Trembling aspen followed two distinct stages that are best described by two linear functions representing these two stages. First, the species exhibited a short but distinct lag time, followed by a very rapid and linear fall rate that suggests that once snags start falling, the time window within which all snags are on the ground is relatively short compared with the other species studied. Jack pine survival exhibited a reverse sigmoid relationship with high retention of snags in the first years after death (no log observed among the 8 trees that died in the first 13 years), suggesting that there is an important delay from death to fall of first snags. Balsam fir also showed this reverse sigmoid relationship but lost a significant amount of snags in the first years after death, followed by a relatively constant survival for the next few years. Black spruce survival was also best expressed as a reverse sigmoid function, but the fall rate was too rapid in the first years to observe a lag time.

Trembling aspen had a 15.1 year half-life, the shortest of all species, meaning there is a 50% chance that a snag will have fallen within the first 15 years after death (Fig. 1.2). Jack pine showed the greatest persistence as a snag, with a 25.8 year half-life.

Balsam fir and black spruce were in an intermediate position with similar half-lives of 19.5 and 18.1 years, respectively.

1.5.3 Degradation pathway

Stem integrity of snags (broken vs. unbroken) was highly variable among species but, as one would expect, broken snag's relative abundance generally increased with time since death (Fig. 1.3). This was particularly evident for trembling aspen and black spruce, although black spruce snags seemed to stay intact longer: in trembling aspen, the oldest unbroken snags died 10 years before sampling whereas in black spruce, the oldest unbroken snag died 21 years before sampling.

Also, snag height rapidly decreased to less than 5 m in both trembling aspen and black spruce, the two species for which the relationship between snag height and time since death was curvilinear (Fig. 1.3). Jack pine and balsam fir exhibited opposite patterns relative to each other. As in survival probability, jack pine showed the greatest resistance to breakage, with the youngest broken snag dead 17 years before sampling and only 5 out of 31 snags broken (Fig. 1.3b). Although balsam fir seemed to be the most breakage-prone species, with only one out of 28 snags unbroken, snags remained quite tall with most taller than 5 m 20 years after death (Fig. 1.3c).

Height was used as a proxy to assess the degradation pathway of trees following their death. Prior to this analysis, the possibility that height was biased by stand age was investigated. Many stands were relatively young (time since fire was 81 years in the youngest stands) and mortality due to stem exclusion in the first cohort after fire might introduce a bias towards snags being taller with time since disturbance. To explore this, height of unbroken stems was related to time since death. When few stems were unbroken, DBH was also used as an indicator. In jack pine, and to a lesser extent in trembling aspen, this analysis revealed a bias induced by the cohort effect (data not shown), making assessments of degradation pathways based on snag height hazardous. However, there was no such cohort effect in black spruce and balsam fir. In black spruce, snags were significantly shorter as time since death increased (Fig. 1.3d) whereas in balsam fir, no transformation allowed both a significant relationship and respect of the normality of residuals assumption (Fig. 1.3c).

In all species, looking at successive periods of 10 years since death where sample size was sufficient, DBH had no influence on the probability of a dead tree to be standing or fallen (Table 1.2).

1.6 Discussion

1.6.1 Tree mortality, snag recruitment and influence of stand dynamics

Along with fall and decomposition rates, dead wood recruitment is a major component in the study of dead wood dynamics. Therefore, mortality patterns that model dead wood input have to be considered when studying snag dynamics. In this regard, mortality generated by a factor such as uprooting is important to consider in snag dynamics since it bypasses the snag stage when occurring in living trees and because uprooted trees create different habitats than other logs (Schaetzl et al. 1989). Episodic and relatively severe disturbance events provide pulses of snags whereas mortality induced by succession processes is usually less severe and more continuous in time (Everett et al. 1999, Harper et al. 2003). Moreover, cause of death may have an effect on the temporal pattern in fall rates of trees after death (Harmon et al. 1986, Raphael and Morrison 1987, Renvall 1995).

1.6.1.1 Trembling aspen

In aspen our results indicate that mortality was induced by a set of different causes. Based on harvesting history, stand age (Table 1.1) and results of Harvey and Brais (2007), the aspen stands studied are in a transitional stage between stem exclusion and decline. Self-thinning and senescence were thus presumably two important sources of mortality. In addition, the Abitibi region experienced a forest tent caterpillar (*Malacosoma disstria* Hbn.) outbreak that lasted from the late 1990’s to the early 2000’s (Cooke and Lorenzetti 2006, Fig. 1.1). Although less lethal than other defoliators, the forest tent caterpillar can trigger decline and eventually death in trembling aspen (Churchill et al. 1964, Candau et al. 2002), especially in suppressed trees that are more susceptible (Churchill et al. 1964). High mortality in 1995 is essentially due to synchronized mortality in one stand (ANI, Table 1.1) that might be attributed to competition (all stems were suppressed), drought at the end of summer 1995 and successive years of low intensity defoliation by the forest tent caterpillar (F. Lorenzetti pers. comm.).

The low uprooting occurrence found in our study (12.5%) was a little less than that reported by Hill et al. (2005) in northeastern Ontario (18%). Trembling aspen is a likely wind firm species given that stands of clonal origin are characterized by suckers issued from a developed lateral network of roots that are anchored to the soil by vertically penetrating roots (Peterson and Peterson 1992).

1.6.1.2 Jack pine

For jack pine snags, height (most <15 m), as well as DBH (most <15 cm) and stand age, suggests that most snags were recruited via self-thinning mortality. This mortality process was fairly constant (Fig. 1.1). We found a high rate of uprooting among jack pine logs (20.8%). This was unexpected since jack pine usually features a tap root or at least a vertical root system (Rudolph and Laidly 1990), root rot is not prevalent in this species (Basham 1991), and sampling was conducted on finetextured deposits that do not restrict root development (Béland et al. 1999). Part of these stems might be old snags that fell many years after death, when rotten roots broke as suggested by coarse and very short root fragments still connected to the stumps.

1.6.1.3 Balsam fir

Balsam fir stands experienced the 1970-1987 spruce budworm outbreak (Morin et al. 1993), which was likely responsible for a large part of our sample set of dead trees (Fig. 1.1) as supported by suppressed or missing rings indicative of severe defoliation in the early 1980's (data not shown). Thus most dead stems came from stands where balsam fir dominated the forest cover before the outbreak and experienced high mortality (Bergeron et al. 1995). Spruce budworm-related mortality in balsam fir usually begins 3 to 4 years after the first severe defoliation (MacLean and Ostaff 1989) and is mostly completed with a similar time delay after defoliation ceases (Blais 1981), which corresponds well with the mortality distribution observed in our study and in Bergeron et al. (1995).

Because of its shallow root system, balsam fir is generally considered an uprooting-prone species (Frank 1990) and commonly uproots after death (Taylor and MacLean 2007). We found, however, a relatively low level of uprooting (12.5%) in comparison with Taylor and MacLean (2007) who observed a 20% mortality rate caused by uprooting in living balsam fir. This is likely explained by the spruce budworm being the predominant cause of mortality.

1.6.1.4 Black spruce

Most black spruce deaths were presumably due to senescence. Indeed, all black spruce stands were initiated by fires 169 years ago or more (Table 1.1), average tree age at death was 165 years, and stands were relatively open, thus reducing stem competition. The observed mortality peak in the late 1980's (Fig. 1.1) may however be partly related to the spruce budworm outbreak. Growth reduction and tree mortality in black spruce that are linked with spruce budworm outbreaks (based on dendrochronological reconstructions) have been observed elsewhere (Simard and Payette 2001, Lussier et al. 2002, Morin et al. 2008) as well as in the study area (M. Simard, *unpublished data*). Although not as severe as in balsam fir-dominated stands, mortality due to the spruce budworm in black spruce can significantly contribute to dead wood recruitment.

Uprooting has been documented to be a major cause of death of black spruce in the Clay Belt region, especially in old stands (Smith et al. 1987, Harper et al. 2003), which is supported by our results (17.9% of fallen trees uprooted). This is explained in part by the lateral and very shallow root system of the species, combined with poorly drained organic and gleysolic soils with high water table that limit rooting depth (Smith et al. 1987), as well as infection by root decay (Basham 1991, Whitney 1989).

1.6.2 Snag survival

For the four species under study, snags died significantly more recently than logs, on average, indicating that snag fall is not a random process and that time since death influences snag survival. All species had a different temporal pattern in fall rates, but trembling aspen, jack pine and to a lesser degree balsam fir exhibited a reverse sigmoid curve with a lag time before onset of snag fall indicating high snag retention in the first years after death. Such functions have also been reported in other studies (e.g. Keen 1929, 1955, Cline et al. 1980, Lee 1998, Garber et al. 2005, Mäkinen et al. 2006). Lag times following death vary from 1 to 5 years in other studies conducted on boreal species with similar DBH (Lee 1998, Garber et al. 2005, Taylor and MacLean 2007), which is a little less than what was found in this study. In Alberta's midboreal ecoregion, Lee (1998) found very similar results in the sequence of fall of trembling aspen: most snags remained standing during the first 5 years after death and the fall rate increased strikingly 10-20 years after death.

Other authors found negative exponential survival functions, implying a constant fall rate through time (Everett et al. 1999, Storaunet and Rolstad 2004). In these studies, the absence of lag time may simply be explained by the studied species' pattern of degradation or because lag time was too short to be detectable given the interval between observations (no observations in the first years following death).

Half-life patterns in our study were generally similar to what was found in other studies. Trembling aspen snags half-life values were between results reported by Vanderwel et al. (2006) in southern Ontario, who modelled a 9 year half-life at 25 cm DBH, and those from Lee (1998) in Alberta, who observed a half-life of 22 years. For balsam fir, the half-life found in this study was slightly higher than the 16 years found by Taylor and MacLean (2007) but was much greater than the 6-10 year reported by Garber et al. (2005). In black spruce stands located about 500 km north of our study area, Boulanger and Sirois (2006) observed a comparable half-life for post-fire black spruce snags (16.2 years). In eastern Quebec, Aakala et al. (2008) modelled considerably higher half-lives in balsam fir and black spruce (30-35 years and 35-40 years, respectively), but these high values are likely due to the fact that their models were based on a more limited range of dead trees than was the case in our study (e.g. DBH > 19cm, rejection of very decayed samples, transition model based on decay classes with highly variable times since death).

The absence of a significant influence of DBH on snag survival is generally consistent with what has been reported in other studies that documented snag survival within the DBH range we analysed. Higher survival probabilities in large snags have mostly been observed in ecosystems where trees were much larger than those sampled in this study (Keen 1929, 1955, Dahms 1949, Raphael and Morrison 1987, Everett et al. 1999, Morrison and Raphael 1993), except for Garber et al. (2005) in Maine, who had slightly larger but still similar DBH values. In our study, the size effect might have been undetectable given the relatively narrow DBH range observed (Table 2, Johnson and Greene 1991, Lee 1998, Kruys et al. 2002, Storaunet and Rolstad 2002).

Snapshot sampling, or retrospective reconstruction based on observations made in a given year, when compared with continuous sampling over time, might introduce biases (Harmon and Sexton 1996, Kruys et al. 2002, Storaunet and Rolstad 2002, 2004). First, as dead wood pieces age, they decompose and collapse as a result of decay, thus becoming harder to detect or date retrospectively and hence impossible to include in the reconstruction. Because slow-decaying individuals are more likely to be detected than individuals that died during the same period but decayed more rapidly, the reliability of the reconstruction period diminishes as one goes back in time and is a function of decay rates. Since snags generally decay more slowly than logs, this could lead to an overestimation of survival probability in old snags (right end of survival curves, Fig. 1.2) and thus overestimated half-lives. This possible overestimation is likely in rapidly decaying species, such as trembling aspen in our case (Alban and Pastor 1993, Chapter 2). Second, causes of death were roughly estimated. However, these causes varied between stands and through the observation period and introduced spatial and temporal variability, both in the mode of death (died standing, snapped, broken at the base) and in the degradation pathways that is difficult to assess retrospectively. Survival curves might thus have been different if other causes of mortality were involved, if sampling had been conducted in other stands or if sampling had been conducted in the same stands but at a different time.

1.6.3 Specific degradation pathway

As opposed to uprooting, breakage decreases the height of snags but does not necessarily bypass the snag stage. Factors that influence breakage susceptibility include wood density, wood mechanical properties, cause of death, stem integrity and condition at time of death, and exposure to wind and snow (Putz et al. 1983, Morrison and Raphael 1993, Storaunet and Rolstad 2002, Taylor and MacLean 2007). Although many studies found that wood density loss is low as long as dead trees remain standing (Johnson and Greene 1991, Krankina and Harmon 1995, Boulanger and Sirois 2006), others found that wood density effectively decreases in snags over time (Yatskov et al. 2003, Saint-Germain et al. 2007). Breakage can induce feedback effects on future snag degradation, either positive, through opening passages for decay agents that increase decay rates for the rest of the bole and thus hasten breakage likelihood (Everett et al. 1999), or negative, by partially or completely removing crown, making snags less susceptible to wind breakage (Dahms 1949, Huggard 1999, Lee 1998). Degradation pathways are related to species autecology and, hence, are treated separately for each species.

1.6.3.1 Trembling aspen

Most trembling aspen seem to die standing (Senecal et al. 2004) and the degradation pathway of *Populus* snags is generally considered to pass by bole breakage at various heights along the bole rather than uprooting (Peterson and Peterson 1992). The aspen root system being well anchored, wind stress is concentrated along the bole. Stems are commonly colonized and weakened by wood-decaying fungi prior to death, especially in the upper part of the bole, reducing competitive abilities and making stems very prone to breakage, whether living or dead (Basham 1991, Harvey and Brais 2007). In our study, more than 61% of snags were broken and no snag older than 10 years remained unbroken (Fig. 1.3a). Susceptibility to breakage has also been reported for *Populus tremula*, for which Hytteborn et al. (1991) found that 75% of gap makers died by snapping off at some point along the bole. Once the crown is decimated, snags offer less resistance to wind and likely reduce risk of breakage (Lee 1998). However, as decay migrates downwards, successive breakages may occur before the snag finally collapses, resulting in snag shortening instead of snag fall. Multiple breakages were not directly observed in our study, but the presence of many bole segments on the forest floor is consistent with this interpretation.

The last forest tent caterpillar outbreak has probably been a decisive factor in the recent death of aspen trees in our study area. Compared with pathogen-killed snags for which mechanical properties of the wood are already altered prior to death or broken trees that offer an entry to decay fungi, forest tent caterpillar mortality leaves an intact stem with fresh and solid wood. These snags might therefore follow a delayed degradation process (Huggard 1999, Storaunet and Rolstad 2004, Garber et al. 2005), as suggested by the fact that all snags that died during the seven years prior to sampling were still standing.

1.6.3.2 Jack pine

Jack pine was the most persistent snag species in our study. Many boreal *Pinus* species also display high resistance to degradation and decomposition relative to *Abies* and *Picea* genus (Alban and Pastor 1993, Yatskov et al. 2003). When compared with other coniferous species, the relatively high wood density (Chapter 2), vertical root system (Rudolph and Laidly 1990) and the low susceptibility to stem and butt decay of jack pine in trees < 100 years (Basham 1991) all contribute to its longevity, whether as snags or logs.

Jack pine was also the most breakage-resistant species. Indeed, breakage lagged by about 30 years after tree death and is likely to be more pronounced beyond the time scale considered in this study. Its intertangled branches and the relatively high stem density of the sampled stands might contribute to postpone fall and breakage by enhancing resistance to wind penetration in the stand. Furthermore, the scarcity of breakage might have delayed further breakage and fall due to the lack of entry for decay fungi. The very low amount of broken snags observed in our study (Fig. 1.3b) suggests that jack pine snags fall directly to the forest floor by breaking below 1.3 m or uprooting. As examined in Chapter 2 on the same samples, this is apparently not related to a higher decay rate of the wood at the base of snags than at breast height.

Even though jack pine snags are clearly the most persistent of the four studied species, their persistence time is likely to be underestimated given the relatively young age of our sampled stands (≈ 80 years). In older stands, the reconstruction period would have been extended, leading to longer persistence at the snag stage. In the same study area, Dansereau and Bergeron (1993) noted that fire-killed jack pine snags can remain standing for over 100 years. Older jack pine stands were not available in the region but dendrological reconstruction of pre-fire mortality and snag dynamics over 70 years in three 120 year-old stands burned in 1996 located 350 km northeast of LDRTF showed a similar lag time, though a half-life of 38.5 years (V.A. Angers, data not shown). Even though fire might have influenced snag dynamics during an eight year period between fire and sampling, the half-life is considerably longer.

1.6.3.3 Balsam fir

Even though the survival curve of balsam fir snags did not exhibit a lag time as obvious as trembling aspen or jack pine, there was a clear high initial retention period (more than 90% of snags were still standing 12 years after death, Fig. 1.2c). This represents a higher survival rate than reported by Bergeron et al. (1995) in the same study area, who noted that 25% of spruce budworm-killed balsam firs had fallen within 7 to 8 years after the mortality peak occurred. This difference may be related to a temporal issue as sampling in our study was conducted almost 20 years after the mortality peak occurred. Recent mortality causes may not be directly related to the spruce budworm outbreak and probably induced a different degradation pathway.

Data from our study corroborate results from other studies that balsam fir is prone to breakage. Of all snags observed, only one remained intact (Fig. 1.3c). In Ontario, 5 years after the mortality peak induced by the spruce budworm, Stocks (1987) observed top breakage in 70% of dead trees. In New-Brunswick, Taylor and MacLean (2007) observed successive breakage over time in balsam fir snags. Of the three coniferous species studied, balsam fir had the least dense wood (Chapter 2, same samples as in this study), which likely contributed to its reduced mechanical resistance.

Balsam fir is moreover the most susceptible eastern boreal species to stem decay (Basham 1991) which, combined with butt rot, enhances its susceptibility to breakage. The environmental context of our study sites probably also contributed to breakage vulnerability: the strong and synchronized opening of the canopy caused by the severe mortality of balsam fir resulted in higher exposure of snags to wind and this might have hastened snag breakage and fall when compared with snags that would have been surrounded by live trees.

1.6.3.4 Black spruce

The temporal pattern in the fall rate of black spruce may seem contradictory. Considering its half-life, this species is the least persistent of the three coniferous species studied due to the absence of a lag time following death. On the other hand, the slope of its survival curve is the least pronounced, with snags falling more constantly than in other species (Fig. 1.2d) and the oldest snags observed in this study (> 40 years since death).

This contrasting pattern may be reconciled by a twofold explanation. Some snags fall quite rapidly following their death. Infection by rot and butt decay, especially by *Armillaria* sp, is common in the region (Basham 1991) and given that the average minimal age at death is 165 years and that extensive decay becomes more common as trees age, snags were likely to be highly susceptible to stump breakage (Basham 1991, Whitney 1989). On the other hand, snags that remained standing for decades may be particularly decay resistant. Black spruce stands were paludified and had low levels of productivity (Simard et al. 2007). Trees therefore experienced a very slow growth which in turn generated high density wood with physiological and chemical properties that limit the decay capacity of fungi (Chapter 2, see Edman et al. 2006 for a review).

1.7 Conclusion

This study provides original baseline information on patterns of degradation of individual tree species following death in mature and late-succesional stands under natural disturbances in North America's eastern boreal forest. Even though our approach was based on a single sample in time combined with dendrochronological reconstruction, it appears to be robust and comparable with results from approaches based on chronosequence (Boulanger and Sirois 2006) as well as modelling and/or repeated measures designs (Lee 1998, Garber et al. 2005, Vanderwel et al. 2006, Taylor and MacLean 2007). Our approach is not limited by assumptions that are difficult to verify or meet, as is often the case in modelling studies, or by the shortcomings of chronosequence approaches, such as differences in dead wood dynamics due to site characteristics and small sample sizes. Compared with repeated measures designs, it does not require waiting for years before data is available and time since death is estimated to the annual level rather than approximated based on the midpoint between two inventories when the tree was last observed alive and was first found dead (e.g. Garber et al. 2005, Taylor and MacLean 2007). Nevertheless, the study of dead wood dynamics would benefit from a regularly measured permanent sampling design coupled with a monitoring of abiotic factors and decomposer organisms that would provide a more comprehensive understanding of dead wood degradation patterns, especially regarding fall, and underlying mechanisms (see Morrison and Raphael 1993, Lee 1998, Garber et al. 2005, Vanderwel et al. 2006, Mäkinen et al. 2006, Taylor and MacLean 2007).

Similar to the paradigm that species exhibit individualistic responses to their environment during their lifetime (Gleason 1926, Whittaker 1957), this individualistic way of responding continues after death and is expressed through differential degradation pathways between species. The propensity for trees to remain standing after death, the differential steepness of survival curves of snags, and the differences in susceptibility to uprooting or stem breakage all represent individualistic responses that have important implications for different ecological functions of dead wood, ranging from habitat and species conservation to resource allocation (e.g. light transmission in gaps) to nutrient and carbon cycling.

Three species, trembling aspen, jack pine and to a lesser extent balsam fir, exhibited a high retention of snags in the first years after death. This delay is of great biological importance for organisms that use fresh standing dead wood, meaning that this resource is largely available during a limited time period. In systems where mortality patterns generate a relatively constant recruitment of dead trees, continuity in habitat availability though time would be ensured for long periods of time. Since black spruce snags have low persistence, companion species, even low in density, are particularly important in providing snag availability in systems dominated by black spruce. This is especially true for species that can attain larger diameters than black spruce (jack pine and trembling aspen, for instance).

From an ecosystem management perspective, maintenance of biological legacies (*sensu* Franklin et al. 2002) through key structural attributes such as snags is often presented as an approach to mitigate habitat alteration by conventional forest management. Development of natural-based silviculture approaches that incorporate dead wood management will necessarily require baseline data on fall rates of snags for long-term planning of dead wood recruitment in managed forest landscapes (DeLong et al. 2008). The fact that snags of tree species respond in an individualistic manner will require flexibility in live and dead wood retention strategies with regards to the dominant tree species or forest cover types under management. Moreover, differential degradation status and decay stages are used by different species

(Harmon et al. 1986, Saint-Germain et al. 2007, Drapeau et al. 2009). Wildlife managers will need to consider habitat dynamics and therefore snag demography in order to propose recommendations and guidelines related to dead wood-dwelling species conservation (e.g. Bull et al. 1997). Finally, this study was conducted in unharvested stands. To effectively include dead wood legacies in forest management strategies, dead wood dynamics also needs to be studied more thoroughly in managed systems.

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1.9 References

Aakala, T., Kuuluvainen, T., Gauthier, S., De Grandpré, L. 2008. Standing dead trees and their decay-class dynamics in the northeastern boreal old-growth forests of Quebec. Forest Ecology and Management 255, 410-420.

Alban, D.H., Pastor, J. 1993. Decomposition of aspen, spruce, and pine boles on two sites in Minnesota. Canadian Journal of Forest Research 23, 1744-1749.

Basham, J.T. 1991. Stem decay in living trees in Ontario's forests: a user's compendium and guide. Forestry Canada, Ontario region, Great Lakes Forestry Centre, Information report O-X-408.

Béland, M., Bergeron, Y., Zarnicovan, R. 1999. Natural regeneration of jack pine following harvesting and site preparation in the Clay Belt of northwestern Quebec. Forestry Chronicle 75, 821-831.

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

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

Bescond, H. 2002. Reconstitution de l'historique de l'exploitation forestière sur le territoire de la forêt d'enseignement et de recherche du lac Duparquet au cours du 20ème siècle et influence sur l'évolution des peuplements forestiers. Master thesis, Université du Québec à Montréal.

Blais, J.R. 1981. Mortality of balsam fir and white spruce following a spruce budworm outbreak in the Ottawa River watershed in Quebec. Canadian Journal of Forest Research 11, 620-629.

Boulanger, Y., Sirois, L. 2006. Postfire dynamics of black spruce coarse woody debris in northern boreal forest of Quebec. Canadian Journal of Forest Research 36, 1770-1780.

Brais, S., Paré, D., Lierman, C. 2006. Tree bole mineralization rates of four species of the Canadian eastern boreal forest: implications for nutrient dynamics following stand-replacing disturbances. Canadian Journal of Forest Research 36, 2331-2340.

Bull, E.L., Parks, C.G., Torgersen, T.R., 1997. Trees and Logs Important to Wildlife in the Interior Columbia River Basin. USDA Forest Service General Technical Report no 391.

Candau, J.N., Abt, V., Keatley, L. 2002. Bioclimatic analysis of declining aspen stands on northeastern Ontario. Ontario forest research institute Forest Research Report 154.

Churchill, G.B., John, H.H., Duncan, D.P., Hodson, A.C. 1964. Long-term effects of defoliation of aspen by the forest tent caterpillar. Ecology 45, 630-633.

Cline, S.P., Berg, A.B., Wight, H.M. 1980. Snag characteristics and dynamics in douglas-fir forests, western Oregon. Journal of Wildlife Management 44, 773-786.

Cooke, B.J., Lorenzetti, F. 2006. The dynamics of forest tent caterpillar outbreaks in Québec, Canada. Forest Ecology and Management 226, 110-121.

Dahms, W.G. 1949. How long do ponderosa pine snags stand? USDA Forest Service Research Note 57.

Daniels, L.D., Dobry, J., Klinka, K., Feller, M.C. 1997. Determining year of death of logs and snags of *Thuja plicata* in southwestern coastal British Colombia. Canadian Journal of Forest Research 27, 1132-1141.

Dansereau, P.-R., Bergeron, Y. 1993. Fire history in the southern boreal forest of northwestern Quebec. Canadian Journal of Forest Research 23, 25-32.

DeLong, S.C., Sutherland, G.D., Daniels, L.D., Heemskerk, B.H., Storaunet, K.O. 2008. Temporal dynamics of snags and development of snag habitats in wet spruce-fir stands in east-central British Columbia. Forest Ecology and Management 255, 3613-3620.

Drapeau, P., Nappi, A., Imbeau, L., Saint-Germain, M. 2009. Standing dead wood for keystone bird species in the eastern boreal forest: managing for snag dynamics. Forestry Chronicle 85: 227-234.

Edman, M., Möller, R., Ericson, L., 2006. Effects of enhanced tree growth rate on the decay capacities of three saprotrophic wood-fungi. Forest Ecology and Management 232, 12-18.

Environment Canada 2010. National Climate Data and Information Archive. Available at www.climate.weatheroffice.gc.ca/climate_normals/results_e.html, accessed 8 November 2010 [Verified 8 November 2010].

Everett, R., Lehmkuhl, J., Schellhaas, R., Ohlson, P., Keenum, D., Riesterer, H., Spurbeck, D. 1999. Snag dynamics in a chronosequence of 26 wildfires on the east slope of the Cascade Range in Washington states, USA. International Journal of Wildland Fire 9, 223-234.

Fenton, N., Lecomte, N., Légaré, S., Bergeron, Y. 2005. Paludification in black spruce (*Picea mariana*) forests of eastern Canada: Potential factors and management implications. Forest Ecology and Management 213, 151-159.

Frank, R.M. 1990. Balsam fir. In: Burns, R.M., Honkala, B.H. (Eds.), Silvics of North America. USDA Agric. Handb. 654.

Franklin, J.F., Spies, T.A., Van Pelt, R., Carey, A.B., Thornburgh, D.A., Berg, D.R., Lindenmayer, D.B., Harmon, M.E., Keeton, W.S., Shaw, D.C., Bible, K., Chen, J. 2002. Disturbances and structural development of natural forest ecosystems with silvicultural implications, using Douglas-fir forests as an example. Forest Ecology and Management 155, 399-423.

Garber, S.M., Brown, J.P., Wilson, D.S., Maguire, D.A., Heath, L.S. 2005. Snag longevity under alternative silvicultural regimes in mixed-species forests of central Maine. Canadian Journal of Forest Research 35, 787-796.

Gleason, H.A. 1926. The individualistic concept of the plant association. Bulletin of the Torrey Botanical Club 53, 1-20.

Gore, A.P., Johnson, E.A., Lo, H.P. 1985. Estimating the time a dead tree has been on the ground. Ecology 66, 1981-1983.

Harmon, M.E., Franklin, J.F., Swanson, F.J., Sollins, P., Gregory, S.V., Lattin, J.D., Anderson, N.H., Cline, S.P., Aumen, N.G., Sedell, J.R., Lienkaemper, G.W., Cromack, K.Jr., Cummins, K.W. 1986. Ecology of coarse woody debris in temperate ecosystems. Advances in Ecological Research 15, 133-302.

Harmon, M.E., Sexton, J. 1996. Guidelines for measurements of woody detritus in forest ecosystems. U.S. Long Term Ecological Research Network Office, University of Washington, LTER Publ. No. 20.

Harper, K., Boudreault, C., De Grandpré, L., Drapeau, P., Gauthier, S., Bergeron, Y. 2003. Structure, composition and diversity of old-growth black spruce boreal forest of the Clay Belt region in Quebec and Ontario. Environmental Review 11, S79-S98.

Harvey B. D., Brais, S. 2007. Partial cutting as an analogue to stem exclusion and dieback in trembling aspen (*Populus tremuloides*) dominated boreal mixedwoods: implications for dead wood dynamics. Canadian Journal of Forest Research 37, 1525-1533.

Hély, C., Bergeron, Y., Flannigan, M.D. 2000. Coarse woody debris in the southeastern Canadian boreal forest: composition and load variations in relation to stand replacement. Canadian Journal of Forest Research 30, 674-687.

Hill, S.B., Mallik, A.U., Chen, H.Y.H. 2005. Canopy gap disturbance and succession in trembling aspen dominated boreal forests in northeastern Ontario. Canadian Journal of Forest Research 35, 1942-1951.

Holmes, R.L. 1983. Computer-assisted quality control in tree-ring dating and measurement. Tree-Ring Bulletin 43, 69-78.

Huggard, D.J. 1999. Static life-table analysis of fall rates of subalpine fir snags. Ecological Applications 9, 1009-1016.

Hytteborn, H., Liu, Q., Verwijst, T. 1991. Natural disturbance and gap dynamics in a Swedish boreal spruce forest. *In:* Nakagoshi, N., Golley, F.B. (Eds.), Coniferous forest ecology, from an international perspective. SPB Academic Publishing, The Hague, pp. 93-108.

Johnson, E.A., Greene, D.F. 1991. A method for studying dead bole dynamics in *Pinus contorta* var. *latifolia - Picea engelmannii* forests. Journal of Vegetation Science 2, 523-530.

Jonsson. B.G. and Kruys, N. (Eds) 2001. Ecology of woody debris in boreal forests. Ecological bulletins 49.

Keen, F.P. 1929. How soon do yellow pine snags fall? Journal of Forestry 27, 735-737.

Keen, F.P. 1955. The rate of natural falling of beetle-killed ponderosa pine snags. Journal of Forestry 53, 720-723.

Krankina, O.N., Harmon, M.E. 1995. Dynamics of the dead wood carbon pool in northwestern Russian boreal forests. Water Air Soil Pollution 82, 227-238.

Kruys, N., Jonsson, B.G., Ståhl, G. 2002. A stage-based matrix model for decay-class dynamics of woody debris. Ecological Applications 12, 773-781.

Laiho, R., Prescott, C.E. 2004. Decay and nutrient dynamics of coarse woody debris in northern coniferous forests: A synthesis. Canadian Journal of Forest Research 34, 763-777.

Lecomte, N., Simard, M., Bergeron, Y. 2006. Effects of fire severity and initial tree composition on stand structural development in the coniferous boreal forest of northwestern Québec, Canada. Ecoscience 13, 152-163.

Lee, P. 1998. Dynamics of snags in aspen-dominated midboreal forests. Forest Ecology and Management 105, 263-272.

Lussier, J.-M., Morin, H., Gagnon, R. 2002. Mortality in black spruce stands of fire or clear-cut origin. Canadian Journal of Forest Research 32, 539-547.

MacLean, D.A., Ostaff, D.P. 1989. Patterns of balsam fir mortality caused by an uncontrolled spruce budworm outbreak. Canadian Journal of Forest Research 19, 1087-1095.

Mäkinen, H., Hynynen, J.S.J., Sievänen, R. 2006. Predicting the decomposition of Scots pine, Norway spruce, and birch stems in Finland. Ecological Applications 16, 1865-1879.

Mast, J.N., Veblen, T.T. 1994. A dendrochronological method of studying tree mortality patterns. Physical Geography 15, 529-542.

Morin, H., Laprise, D., Bergeron, Y. 1993. Chronology of spruce budworm outbreaks near Lake Duparquet, Abitibi region, Quebec. Canadian Journal of Forest Research 23, 1497-1506.

Morin, H., Laprise, D., Simard, A.-A., Amouch, S. 2008. Régime des épidémies de la tordeuse des bourgeons de l'épinette dans l'Est de l'Amérique du Nord. *In*: Gauthier, S., Vaillancourt, M.-A., Leduc, A., De Grandpré, L., Kneeshaw, D., Morin, H., Drapeau, P., Bergeron, Y. (Eds). Aménagement écosystémique en forêt boréale. Presses de l'Université du Québec, Montréal, pp. 165-192.

Morrison, M.L., Raphael, M.G. 1993. Modeling the dynamics of snags. Ecological Applications 3, 322-330.

Peterson, E.B., Peterson N.M. 1992. Ecology, management, and use of aspen and balsam poplar in the prairie provinces. Forestry Canada, Northern Forestry Centre, Special report 1.

Putz, F.E., Coley, P.D., Lu, K., Montalvo, A., Aiello, A. 1983. Uprooting and snapping of trees: structural determinants and ecological consequences. Canadian Journal of Forest Research 13, 1011-1020.

Raphael, M.G., Morrison, M.L. 1987. Decay and dynamics of snags in the Sierra Nevada, California. Forest Science 33, 774-783.

Renvall, P. 1995. Community structure and dynamics of wood-rotting Basidiomycetes on decomposing conifer trunks in northern Finland. Karstenia 35, 1-51.

Richards, S.A., Johnson, E.A. 2007. Using decomposition rates to infer how far back tree populations can be reconstructed. Ecology 88, 1582-1586.

Rinn, F. 1996. TSAP (Time series Analysis and Presentation) Version 3.0. Rinntech, Heidelberg, Germany.

Robitaille, A., Saucier, J.-P. 1998. Paysages régionaux du Québec méridional. Les publications du Québec, Ste-Foy.

Rudolph, T.D., Laidly, P.R. 1990. Jack pine. In: Burns, R.M., Honkala, B.H. (Eds.), Silvics of North America. USDA Agric. Handb. 654.

Saint-Germain, M., Drapeau, P., Buddle, C.M. 2007. Host-use patterns of saproxylic phloeophagous and xylophagous Coleoptera adults and larvae along the decay gradient in standing dead black spruce and aspen. Ecography 30, 737-748.

Schaetlz, R.J., Burns, S.F., Johnson, D.L., Small, T.W., 1989. Tree uprooting: review of impacts on forest ecology. Vegetatio 79, 165-176.

Senecal, D., Kneeshaw, D., Messier, C. 2004. Temporal, spatial and structural patterns of adult trembling aspen and white spruce mortality in Quebec's boreal forest. Canadian Journal of Forest Research 34, 396-404.

Simard, M., Lecomte, N., Bergeron, Y., Bernier, P.-Y., Paré, D. 2007. Forest productivity decline caused by successional paludification of Boreal soils. Ecological Applications 17, 1619-1637.

Simard, M., Payette, S. 2001. Black spruce decline triggered by spruce budworm at the southern limit of lichen woodland in eastern Canada. Canadian Journal of Forest Research 31, 2160-2172.

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

SYSTAT 2004. SYSTAT 12. SYSTAT Software Inc., Richmond, CA.

Smith, V.G., Watts, M., James, D.F. 1987. Mechanical stability of black spruce in the clay belt region of northern Ontario. Canadian Journal of Forest Research 17, 1080-1091.

Söderström, L. 1988. Sequence of bryophytes and lichens in relation to substrate variables of decaying coniferous wood in Northern Sweden. Nordic Journal of Botany 8, 89-97.

Stocks, B.J. 1987. Fire potential in the spruce budworm-damaged forests of Ontario. Forestry Chronicle 63, 8-14.

Storaunet, K.O., Rolstad, J. 2004. How long do Norway spruce snags stand? Evaluating four estimation methods. Canadian Journal of Forest Research 34, 376-383.

Storaunet, K.O., Rolstad, J. 2002. Time since death and fall of Norway spruce logs on old-growth and selectively cut boreal forest. Canadian Journal of Forest Research 32, 1801-1812.

Sturtevant, B.R., Bissonette, J.A., Long, J.N., Roberts, D.W., 1997. Coarse woody debris as a function of age, stand structure, and disturbance in boreal Newfoundland. Ecological Applications 7, 702-712.

Taylor, S.L., MacLean, D.A. 2007. Dead wood dynamics in declining balsam fir and spruce stands in New Brunswick, Canada. Canadian Journal of Forest Research 37, 750-762.

Thomas, J.W., Anderson, R.G., Maser, C., Bull, E.L. 1979. Snags. *In*: Thomas, J.W. (Ed.)., Wildlife habitats in managed forests: the Blue Mountains of Oregon and Washington. USDA Forest Service Agriculture Handbook no. 553, pp. 60-77.

Vanderwel, M.C., Caspersen, J.P., Woods, M.E. 2006. Snag dynamics in partially harvested and unmanaged northern hardwood forests. Canadian Journal of Forest Research 36, 2769-2779.

Vincent, J.S., Hardy, L. 1977. L'évolution et l'extinction des lacs glaciaires Barlow et Ojibway en territoire québécois. Géographie physique et Quaternaire 31, 357-372.

Whitney, R.D. 1989. Root rot damage in naturally regenerated stands of spruce and balsam fir in Ontario. Canadian Journal of Forest Research 19, 295-308.

Whittaker, R.H., 1957. Recent evolution of ecological concepts in relation to the eastern forests of North America. American Journal of Botany 44, 197-206.

Yatskov, M., Harmon, M.E., Krankina, O.N. 2003. A chronosequence of wood decomposition in the boreal forests of Russia. Canadian Journal of Forest Research 33, 1211-1226.

Table 1.1 Stand composition, disturbance history and snag availability.

Species	Stand	Composition*	Time since fire (years)[†]	Past harvesting activity[‡]	Snag density (nb/ha)[§]	Snag basal area (m^2/ha) [§]	Nb of dead trees sampled
Trembling aspen							
	ANI	Trembling aspen - white spruce	134	Potentially partially cut between 1926-1945	550	4.7	28
	KAN	Trembling aspen	88	None	275	6.4	14
	ORA	Trembling aspen	82	None	275	4.7	7
	PET	Trembling aspen	81	None	275	9.9	10
	STI	Trembling aspen - eastern white cedar	189	Potentially partially cut between 1916-1926	225	11.1	6
Balsam fir[¤]							
	LAG	White birch - trembling aspen	82	None	250	7.2	5
	PET	Trembling aspen	81	None	275	9.9	6
	PHI	White birch - white spruce	245	Potentially partially cut between 1926-1945	250	6.8	23
	STI	Trembling aspen - eastern white cedar	189	Potentially partially cut between 1916-1926	225	11.1	20
	TBK	White spruce - white birch - eastern white cedar	208	Potentially partially cut between 1926-1945	175	5.2	20
	TIM	White birch - white spruce	82	None	325	5.4	31
Jack pine							
	GUM	Jack pine	82	None	275	4.9	16
	MAC	Jack pine	82	None	525	7.9	33
	PLU	Jack pine	82	None	425	6.1	6

Species	Stand	Composition*	Time since fire (years)[†]	Past harvesting activity[‡]	Snag density (nb/ha)[§]	Snag basal area (m^2/ha) [§]	Nb of dead trees sampled
Black spruce							
	H1	Black spruce	350	None	300	3.2	23
	N5	Black spruce	169	None	375	4.3	30
	N6	Black spruce	710 [җ]	None	325	5.4	30
	N16	Black spruce	1585[җ]	None	375	4.0	25
	N50	Black spruce	365 [җ]	None	150	2.6	18

*Composition of living tree species based on prism sampling from the plot centre.

[†] At time of sampling. Based on fire reconstructions by Dansereau (1993, Lake Duparquet Research and Teaching Forest) and Lecomte et al. (2006) and Fenton et al. (2005) in black spruce stands.

[‡] Based on historical reconstitutions by Bescond (2002, Lake Duparquet Research and Teaching Forest) and Lecomte et al. (2006, black spruce stands).

[¤] Composition of stands where balsam fir snags were collected was mainly balsam fir prior to the 1980's spruce budworm outbreak.

[§] All species included.

[җ] Based on calibrated ^{14}C charcoal age (Lecomte et al. 2006).

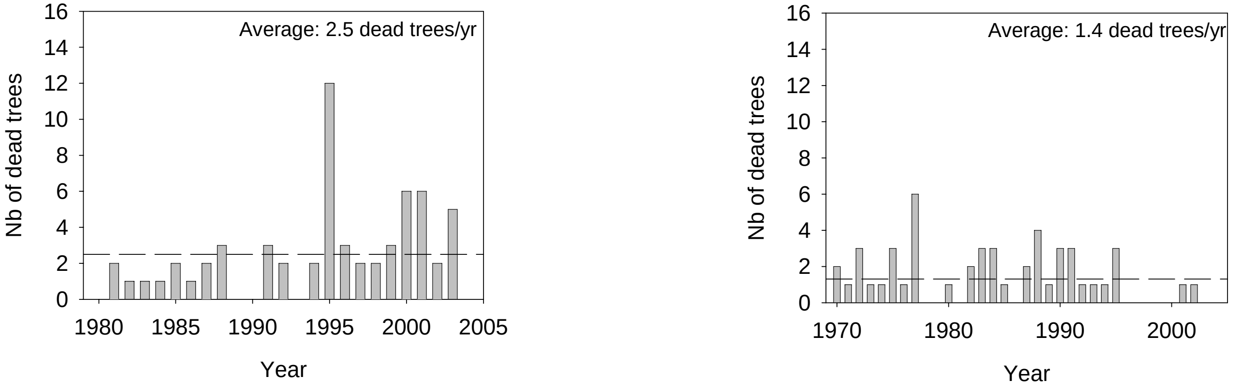
Table 1.2 Time since death, diameter at breast height (DBH) and comparison between DBH of snags and logs sampled. *p* values shown are for comparison between average time since death among snags and logs belonging to the same species and for comparison between DBH of snags and logs by 10 year periods.

Species*		TRA		JAP		BAF		BLS	
		Snags	Logs	Snags	Logs	Snags	Logs	Snags	Logs
Time since death									
	Average (yrs)	8.0	18.0	18.8	29.1	18.2	22.3	16.5	24.0
	SE (yrs)	0.8	2.2	1.6	1.7	1.3	0.5	1.5	1.8
	n	49	14	31	19	28	69	59	55
	p	< 0.0001		< 0.0001		0.0004		0.0018	
DBH									
	Average (cm)	14.8		11.9		14.5		12.4	
	SE (cm)	0.8		0.5		0.4		0.4	
DBH 0-9 ysd[‡]	*p*	-[†]		-[†]		-[†]		0.6016	
DBH 10-19 ysd[‡]	*p*	-[†]		-[†]		0. 8244		0. 7413	
DBH 20-29 ysd[‡]	*p*	-[†]		0. 9672		0. 4020		0. 2935	
DBH 30-39 ysd[‡]	*p*	-[†]		0. 2039		-[†]		-[†]	

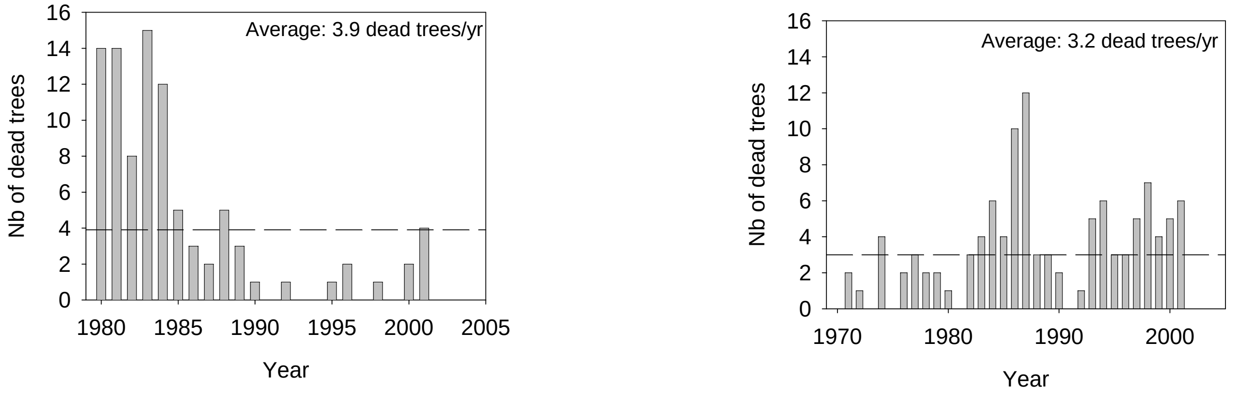
*TRA: trembling aspen, JAP: jack pine, BAF: balsam fir, BLS: black spruce.

[†] Sampling size was insufficient to proceed with comparison of means (less than 5 individuals per group).

[‡] ysd: years since death

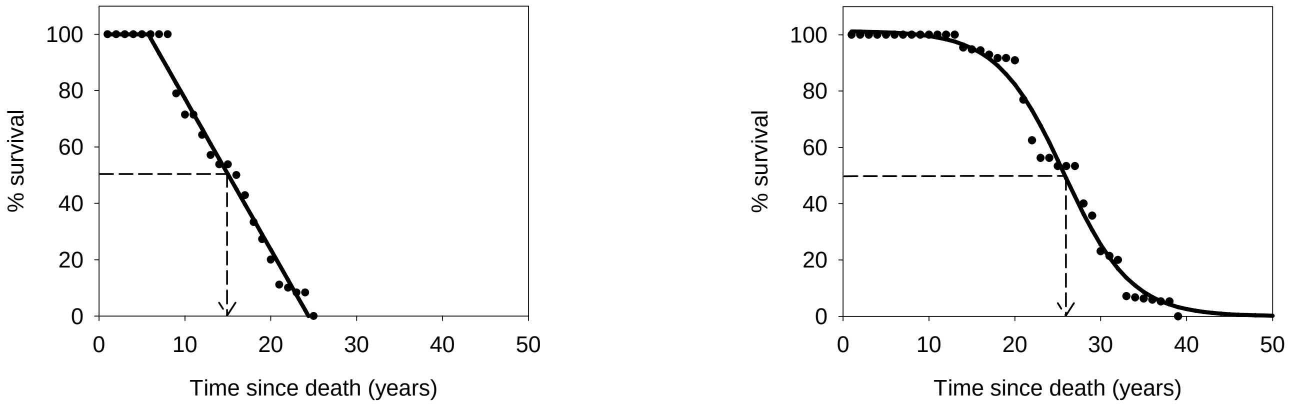

a) Trembling aspen (*n* = 61)

b) Jack pine (*n* = 49)

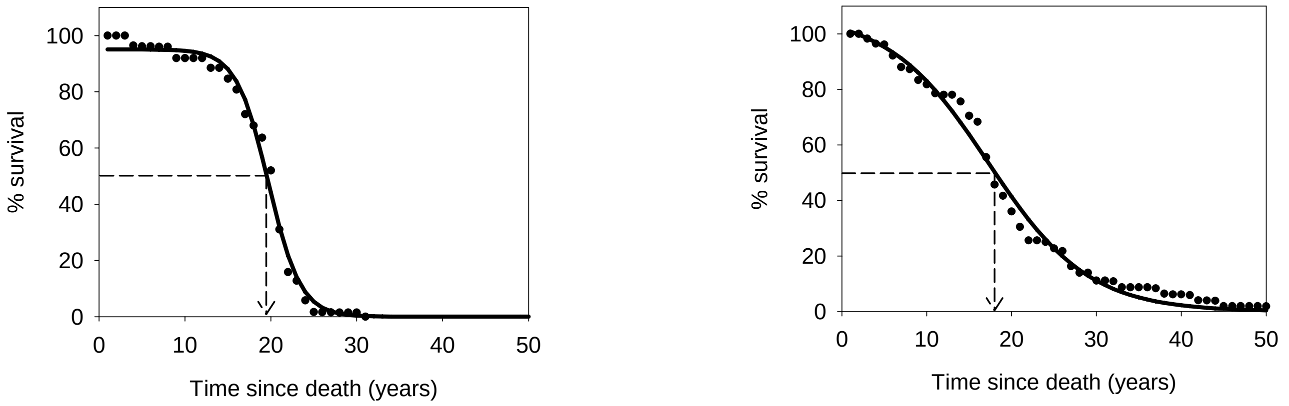

c) Balsam fir (*n* = 93)

d) Black spruce (*n* = 109)

Figure 1.1. Individual and average mortality (dotted lines) of sampled dead trees (standing and fallen) during specified periods.


a) Trembling aspen (*n* = 63)

b) Jack pine (*n* = 50)

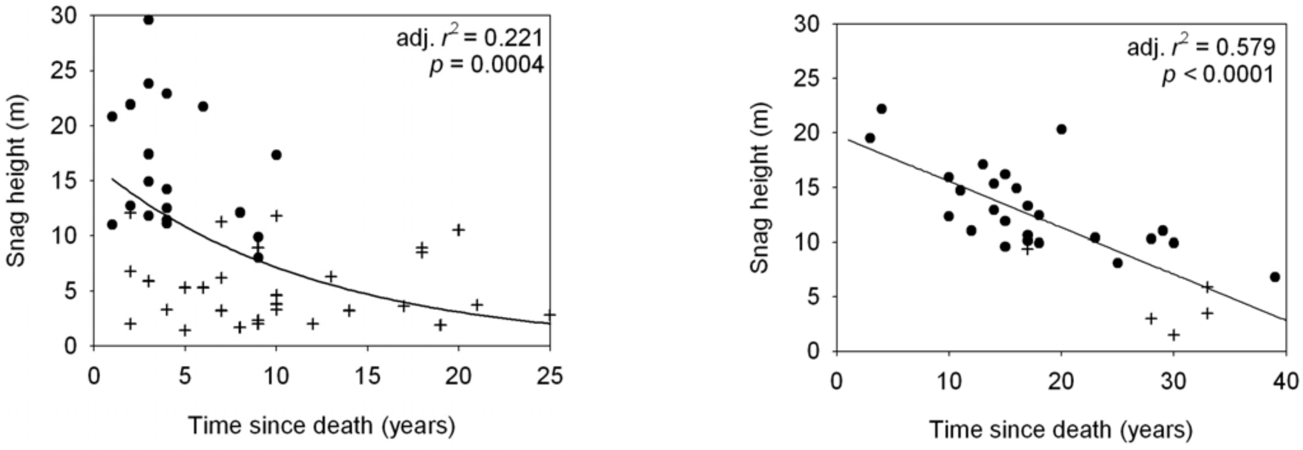

c) Balsam fir (*n* = 97)

d) Black spruce (*n* = 114)

Figure 1.2. Cumulative percentage of snag survival over time. Dots represent the annual standing/fallen cumulative ratio observed (see Methods) whereas curves represent the general trend. Half-life, the time required for half the stems dead at a given time to fall to the ground, is represented by the dashed arrows.

a) Trembling aspen (*n* = 49)

b) Jack pine (*n* = 31)



c) Balsam fir (*n* = 28)

d) Black spruce (*n* = 59)

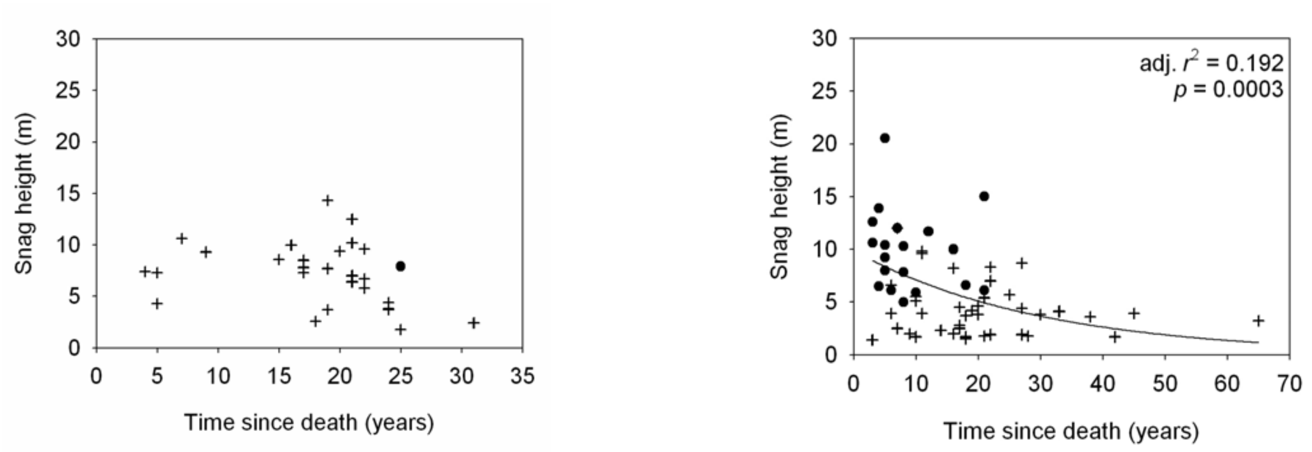


Figure 1.3. Relationships between snag height and time since death. Dots represent unbroken stems and crosses, broken stems.

CHAPITRE 2

MINERALIZATION RATES AND FACTORS INFLUENCING SNAG DECAY IN FOUR NORTH AMERICAN BOREAL TREE SPECIES

Virginie-Arielle Angers, Pierre Drapeau et Yves Bergeron

2.1 Résumé

Nous avons mesuré les taux de minéralisation (i.e. la perte de densité du bois) de chicots de quatre espèces boréales: le peuplier faux-tremble (*Populus tremuloides* Michx.), le sapin baumier (*Abies balsamea* (L.) Mill.), le pin gris (*Pinus banksiana* Lamb.) et l'épinette noire (*Picea mariana (*Mill.) BSP). Les facteurs influençant ces taux ont aussi été examinés. L'échantillonnage a eu lieu dans le nord-ouest du Québec, au Canada. La densité du bois et les variables pouvant potentiellement influencer les taux de minéralisation (temps écoulé depuis la mort, âge, croissance radiale moyenne, diamètre à hauteur de poitrine, activité des Cérambycidés et activité des Scolytinés) ont été mesurées sur des disques prélevés sur 207 chicots.

Les taux de minéralisation différaient significativement entre espèces. Le peuplier faux-tremble présentait un taux de minéralisation plus rapide que ceux des conifères (k = 0.0351). Le pin gris occupait le deuxième rang (k = 0.0152), suivi par le sapin baumier (k = 0.0094). L'épinette noire s'est révélée particulièrement résistante à la minéralisation (k = 0.0065). Aucune différence n'a été observée entre les taux de minéralisation à la base et à hauteur de poitrine chez les conifères, tandis qu'à la base des chicots de peuplier faux-tremble, ce taux était significativement plus élevé qu'à hauteur de poitrine. Le temps écoulé depuis la mort jumelé à l'activité des Cérambycidés était associé à une densité du bois plus faible chez le peuplier faux-tremble, le sapin baumier et le pin gris, alors que la croissance plus lente et le diamètre plus faible de l'épinette noire étaient associés à des taux de minéralisation plus lents. Nous suggérons que les conditions environnementales dans lesquelles se trouvaient les pessières noires pourraient expliquer pourquoi le temps écoulé depuis la mort influence moins la minéralisation du bois des chicots chez l'épinette noire.

Mots-clés: Bois mort, chicots, taux de minéralisation, densité du bois, dendrochronologie, peuplier faux-tremble, *Populus tremuloides* Michx., sapin baumier, *Abies balsamea* (L.) Mill., pin gris, *Pinus banksiana* Lamb., épinette noire, *Picea mariana (*Mill.) BSP.

2.2 Abstract

Mineralization rates (measured as wood density loss) were assessed in snags of four boreal species: trembling aspen (*Populus tremuloides* Michx.), balsam fir (*Abies balsamea* (L.) Mill.), jack pine (*Pinus banksiana* Lamb.) and black spruce (*Picea mariana* (Mill.) BSP). Wood density and variables potential influencing decay rates (time since death; age; average radial growth; diameter at breast height; Cerambycidae activity, and Scolytinae activity) were measured on discs of 207 snags in northwestern Québec, Canada.

Mineralization rates varied significantly among species. Trembling aspen exhibited a more rapid rate of loss than conifers (k = 0.0351). Jack pine was the second most rapid species to lose wood density (k = 0.0152), followed by balsam fir (k = 0.0094). Black spruce was particularly resistant to mineralization (k = 0.0065). No differences were detected in mineralization rates at the base and at breast height for conifers, whereas mineralization at the base of trembling aspen snags was significantly higher than at breast height. Time since death coupled with Cerambycidae activity was associated with lower wood densities in trembling aspen, balsam fir and jack pine, whereas slower growth and smaller diameter were associated with a decreased mineralization rate in black spruce. We suggest that stand environmental conditions could explain why time since death is less influential in black spruce wood decay.

Key words: Dead wood, snags, mineralization rates, wood density, dendrochronology, trembling aspen, *Populus tremuloides* Michx., balsam fir, *Abies balsamea* (L.) Mill., jack pine, *Pinus banksiana* Lamb., black spruce, *Picea mariana* (Mill.) BSP.

2.3 Introduction

In boreal ecosystems, the estimation of decay rates in fallen tree boles has received extensive attention, particularly in northern Europe (Krankina and Harmon 1995; Naesset 1999; Tarasov and Birdsey 2001; Yatskov et al. 2003; Mäkinen et al. 2006). The decay of snags (i.e., standing dead trees), in contrast, has been less frequently studied, especially for species occurring in the eastern boreal forest of North America (Boulanger and Sirois 2006; Saint-Germain et al. 2007). This apparent lack of interest may be, in part, because standing dead trees are in a transitory state and generally decay far more slowly than boles in contact with the forest floor (Krankina and Harmon 1995; Yatskov et al. 2003; Boulanger and Sirois 2006). Decay rates of snags represent, however, an important parameter of forest ecosystem dynamics because dead trees provide habitat for many organisms (Harmon et al. 1986; Farris et al. 2004; Saint-Germain et al. 2007; Drapeau et al. 2009). Furthermore, wood density influences breakage susceptibility and, therefore, plays an important role in snag dynamics (Basham 1991). Finally, because of their slow decay rates, snags also represent important slow-released or stored carbon and nutrient pools (Kasischke 2000; Bond-Lamberty et al. 2002; Boulanger and Sirois 2006).

Decay rates of dead wood are often examined as a function of time since death (Lambert 1980; Miller 1983; Means et al. 1985; Krankina and Harmon 1995; Boulanger and Sirois 2006; Brais et al. 2006), but several interacting parameters have been found to influence decay rates and can be roughly divided into three categories: the substrate itself, environmental conditions, and decomposer organisms. Tree species, time since death, size, age, decay status at time of death, wood nutrients, concentrations of organic compounds, together with paths of entry for fungi such as wounds or branch stubs, have all been identified as substrate parameters affecting decay rates to some extent (Foster and Lang 1982; Harmon et al. 1986; Mattson et al. 1987; Alban and Pastor 1993; Blanchette 1995; Naesset 1999; Boddy 2001; Mäkinen et al. 2006). Growth may also be influential, as chemical properties and wood anatomy can delay or slow down mineralization rates in slowly growing trees (Blanchette 1995; Rayner and Boddy 1998; Boddy 2001). Environmental conditions that influence wood decay include temperature, humidity, slope, elevation, and contact with the forest floor (Foster and Lang 1982; Erickson et al. 1985; Harmon et al. 1986; Mattson et al. 1987; Naesset 1999; Boddy 2001). The composition of the decomposer community and interactions between species, which consist mainly of fungi in boreal ecosystems, also can affect decay rates (Harmon et al. 1986; Edmonds and Eglitis 1989; Boddy 2001).

The variables that influence decay in snags are likely to be different from those that influence downed woody debris, particularly in regard to the environmental context and the community of decomposer organisms. For instance, moisture content is more limiting in standing dead trees than in boles in contact with the forest floor, which in turn may influence the composition and activity of the decomposer community (Erickson et al. 1985; Harmon et al. 1986; Johnson and Greene 1991). The same argument applies when considering different parts of the bole: as temperature and humidity conditions close to the soil might favour biological activity responsible for wood decay while ground proximity might favour fungi colonization, one could expect higher decay rates at the base than in more distal parts of the bole (Tarasov and Birdsey 2001; Shorohova et al. 2008). Other agents such as saproxylic insects may also play an important role in wood decomposition of snags. Wood borers are particularly active in recently dead trees in boreal forest ecosystems (Saint-Germain et al. 2007). These agents have been suggested as decay accelerators because of the galleries they excavate in the wood (Rayner and Boddy 1988; Edmonds and Eglitis 1989; Zhong and Schowalter 1989).

In this paper, we document mineralization rates of snags of four commonly occurring species in northeastern North American boreal forest, i.e. trembling aspen (*Populus tremuloides* Michx.), balsam fir (*Abies balsamea* (L.) Mill.), jack pine (*Pinus banksiana* Lamb.), and black spruce (*Picea mariana* (Mill.) BSP). More specifically, for each tree species, our objectives were to: 1- assess mineralization rates based on loss of wood density with time, 2- compare mineralization rates at the snag base and at breast height (1.3 m), and 3- assess the influence of factors related to the tree itself (time since death, size, growth, age) and to the activity of two wood-boring insect groups (Cerambycidae and Scolytinae).

2.4 Methods

2.4.1 Study area

The study was conducted in northwestern Quebec (Canada), in the transition zone between mixedwood and coniferous boreal forest. The region is part of a broad physiographic unit known as the Northern Clay Belt, which is characterised by flat topography and clay deposits originating from the proglacial lakes Barlow and Ojibway (Vincent and Hardy 1977). Climate is cold and continental, with a mean annual temperature of 0.7^{o}C and mean annual total precipitation of 889.8 mm (weather station of La Sarre, Environment Canada 2010). Two distinct areas were sampled.

For balsam fir, trembling aspen and jack pine, sampling was conducted in the Lake Duparquet Research and Teaching Forest (LDRTF; 48^{o}26'-48^{o}29'N, 79^{o}26'-79^{o}18'W), which is located 45 km northwest of Rouyn-Noranda. The research forest is located in the Rouyn-Noranda ecological region, within the balsam fir-white birch (*Betula papyrifera* Marsh.) bioclimatic domain (Robitaille and Saucier 1998), where associations of balsam fir, black spruce, white spruce, paper birch and trembling aspen dominate. The disturbance regime includes recurrent wildfires (Dansereau and Bergeron 1993) and periodic spruce budworm (*Choristoneura fumiferana* [Clem.]) outbreaks (Morin et al. 1993).

For black spruce, sampling was conducted in coniferous forest 120 km further north (49^{o}25'-49^{o}50'N, 79^{o}18'-78^{o}41'W), in the Lake Matagami Lowland ecological region. This area is within the black spruce–feathermoss (*Pleurozium schreberi* [Brid.] Mitt.)

bioclimatic domain (Robitaille and Saucier 1998). The disturbance regime is characterized by large stand-replacing fires (Bergeron et al. 2004) with return intervals long enough for successional paludification processes to take place, organic deposits to accumulate, and low productivity open forests to develop (Simard et al. 2007).

Detailed stand characteristics including tree composition, stand age, past harvesting activities, snag density, species-specific annual mortality, and snag fall rates are provided in Chapter 1.

2.4.2 Field methods

Data collection was conducted during the summers of 2004 and 2005. Seventeen stands were selected, based on species composition, surficial material type (glaciolacustrine clay in LDRTF, glaciolacustrine clay overlain by a thick organic layer in black spruce stands), drainage class (mesic sites in LDRTF, subhydric sites in black spruce stands), and age (mature to overmature stands).

In each stand, a 20 m x 20 m plot was established in which every snag was identified. These were trees without green foliage that were at least 1.3 m tall, and which had a diameter at breast height (DBH) ≥ 5 cm. Additional snags were sampled in the surroundings of the plots to increase the number of samples of large-diameter stems and likely old snags based on their visual aspect (short broken bole, little bark remaining, soft wood). A total of 207 snags were sampled (see Table 2.1 for distribution among species). Characterization of snags included species, DBH (± 0.1 cm), and activity of Cerambycidae (Coleoptera) and Scolytinae (Coleoptera: Curculionidae). These two groups of wood-boring beetles were selected because they are common xylophagous insects of boreal forests (Saint-Germain et al. 2007) and because their activity is easily identifiable based on the size, shape and angle of the entry holes that they create (Vallentgoed 1991, Saint-Germain et al. 2004).

Cerambycidae activity (CER) was measured as the number of entry and exit holes between 1 and 1.3 m in height divided by the area covered, while Scolytinae activity (SCOL) was measured as the number of exit holes between 1 and 1.3 m in height divided by the area covered.

Cross-sections that were ≈ 5 cm thick were taken from all snags. Fragile samples were taped with thread-enforced tape and cut using a fine-toothed bow saw to minimize fragmentation. To optimize the chances of successful crossdating, three cross-sections were taken from each bole when possible: at the base, breast height, and near the top (around 3 m from top for intact trees and near the point of breakage for broken trees). This sampling procedure 1- reduced the risk of crossdating failure due to advanced decay, 2- validated year of death with multiple crossdated sections, and 3- increased capture of the last ring produced in stressed trees (Mast and Veblen 1994; V.A. Angers, *unpublished data*). For broken trees, if the fallen tree top was reliably identifiable, a cross-section was also taken to maximize crossdating success.

2.4.3 Sample manipulations

In this study, mineralization rates are expressed as wood density loss and were mostly due to respiration and leaching (Harmon et al. 1986). Fragmentation was likely of minor importance as no external bole fragmentation occurred in bole sections where samples were taken, while fragmentation by invertebrates (Harmon et al. 1986, mainly Cerambycidae) represented a negligible proportion of the sample volumes.

Following death, wood moisture often decreases in snags and fluctuates with environmental conditions (Johnson and Greene 1991; Boulanger and Sirois 2006). To avoid any bias related to influence of wood moisture on volume, we calculated sample volume on a dry-mass basis. In living trees, basic specific gravity (green volume, dry mass) is 7-12% lower than dry specific gravity (dry volume, dry mass, Jessome 1977) for the studied species. As moisture content is usually lower in snags than in trees, density values presented in this study are likely to be somewhat higher than those from other studies presented on a green volume basis, but not as much when compared with live wood density.

All cross-sections were oven-dried at 60°C and weighed to the nearest 0.01 g until mass was stable for at least 24 hours. Bark was stripped and dry volume was calculated assuming a cylindrical shape:

$$V = \pi \times \left(\frac{d_{\min} + d_{\max}}{4} \right)^2 \times \left(\frac{t_{\min} + t_{\max}}{2} \right)$$

where V (cm^3) is the calculated volume, $d_{\min}$ and $d_{\max}$ (cm) are the minimum and maximum cross-sectional diameters, and $t_{\min}$ and $t_{\max}$ (cm) are the minimum and maximum cross-sectional thicknesses, with d and t being measured to the nearest 1 mm. Wood density (g.cm^{-3}) was calculated as the ratio of dry mass to dry volume.

2.4.4 Tree ring analysis

All cross-sections were sanded until xylem cells were clearly visible. When necessary, hot glue was used to consolidate fragmented samples prior to sanding. Ring width was measured for each cross-section along two radii (one when decay impeded ring visibility elsewhere on the cross-section) using a Velmex micrometer (0.001 mm precision; Velmex Incorporated, Bloomfield, New York, USA).

Year of death was considered as the year of the last ring produced. To establish year of death, each individual tree ring series that was generated by all sampled cross-sections was crossdated against master series constructed for balsam fir, jack pine and trembling aspen from nearby living trees in LDRTF (Chapter 1) and from a master chronology developed for black spruce (Simard et al. 2007). Crossdating was performed using marker years, and verified with COFECHA (Holmes 1983) and TSAP (Rinn 1996) programs, with the latter being used for visually comparing the pattern generated by each tree ring series and the average of the master series. When discrepancies in years of death were obtained for cross-sections belonging to the same dead tree, the most recent year was retained. Cross-sections from only one snag (trembling aspen) could not be successfully crossdated. Time since death (TSD, y) was calculated as the difference between the year of sampling and the year of death. Tree age (AGE, y) was usually assessed as the difference between year of death and year of production of the innermost ring at base height. When the inner part of the bole was decayed at base height, we estimated the number of missing rings based on averages made on discs taken at the base where all rings were visible. Average annual growth (GROWTH, cm y^{-1}) was measured as DBH/AGE.

2.4.5 Data analysis

The negative exponential model has been the most widely used in the literature to describe changes in dead wood density over time since tree death (e.g. Foster and Lang 1982; Yatskov et al. 2003; Brais et al. 2006):

$$Y_t = Y_0 e^{-kt}$$

where Y_t is wood density ($g.cm^{-3}$) t years after death, Y_0 is initial wood density, and k is the mineralization rate constant (y^{-1}) (Olson 1963). Despite some concerns about its ability to adequately represent mineralization in some cases (Harmon et al. 2000; Laiho and Prescott 2004), this model provides the k constant that refers to the rate of mass loss each year, which is the typical benchmark used in most studies that compare mineralization rates.

The simple linear model has also been employed to describe decay, although to a lesser extent (e.g. Graham and Cromack 1982) :

$$Y_t = Y_0 + mt$$

Where Yt, Yo, and t are as previously defined, and m represents the fraction of initial mass that is lost each year.

As wood density loss was well-represented by the simple linear model in all species (see results), further analyses were based on that model. To assess if mineralization rates were different between breast height and base of snags, analysis of covariance (ANCOVA) was used on the linear regression of wood density at breast height and at the base vs. time since death.

Given verified or suggested relationships published in the literature, we assessed the influence of six variables on wood mineralization (TSD, DBH, AGE, GROWTH, SCOL, and CER, see Table 2.1) using the following procedure:

We first built a series of models using multiple linear regressions. The rationale of model construction was based on the potential biological influence of variables on wood mineralization (see Appendix A for the list of models). For all modelling analyses, we used wood density at DBH. Since TSD happened to be a significant factor influencing mineralization according to simple linear models (see results), we considered it alone and included it in all models. DBH, AGE and GROWTH are tree-level characteristics that are determined by tree life history. Models including these individual variables were tested, as well as models including several of them. Since GROWTH is derived from DBH and AGE and is therefore strongly correlated to those variables, we did not include GROWTH in the same models as AGE and DBH. Wood-boring insect effects (SCOL and CER) were considered separately. Finally, we ensured that models generated from standard least-square and stepwise (forward and backward) regressions were already included and were added if not, as well as the null and full models. Two full models were tested in order to assess the effect of GROWTH as well as DBH and AGE. In jack pine, TSD and AGE were highly related to one another because all trees originated from the same post-fire cohort. For this reason, models including those two variables were excluded. Prior to all regression models, assumptions of normality and homoscedasticity were verified and the data were transformed where necessary. A variance inflation factor (VIF) was also computed for each predictor to ensure that there was no collinearity between explanatory variables that were entered together in the models.

Akaike's information criterion (AIC) was then used to select the best model, i.e., the most simple and parsimonious among the candidate models (Burnham and Anderson 2002). Given that the sample size (*n*) for each species was rather small relative to the number of parameters K (i.e. $n/K < 40$), the second-order Akaike information criterion (AIC_c) was used, as expressed by:

$$AIC_c = -2(\text{log-likelihood}) + 2K + [2K(K+1)/(n-K-1)]$$

where K is the number of parameters in the model, including the intercept and variance.

When several models competed for the topmost rank among the candidates ($\Delta\ AIC_c < 2$), indicating uncertainty regarding the best model, we used multi-model inference (Burnham and Anderson 2002). To assess the magnitude of a given variable's effect, we computed a weighted average of the regression coefficients of that variable for all models that included it. Model-averaged estimates and unconditional standard errors were generated and used to build a 95% confidence interval.

2.5 Results

The range and distribution of snag ages changed from species to species and were related to stand dynamics, disturbance history, and snag fall rates (Chapter 1).

Trembling aspen snag recruitment was mainly caused by self-thinning and senescence. As that species was the least persistent as a snag, the time frame for recruitment was limited to 25 years (Fig. 2.1). Jack pine mortality was relatively constant through time and the time frame covered almost 40 years. In balsam fir, the 1970-1987 spruce budworm outbreak (Morin et al. 1993) was responsible for a large fraction of balsam fir mortality, as suggested by the high number of trees that had died c. 20 years ago. Black spruce mortality was relatively constant over the last 30 years with some old snags (≥ 30 years old) still standing.

2.5.1 Mineralization rates

Regardless of model type (linear or negative exponential), wood density decreased significantly with time since death for all tree species ($p < 0.05$, Table 2.2, Fig. 2.1), although more stronger in trembling aspen and jack pine ($r^2 > 0.40$, linear models) than in balsam fir (r^2 of 0.12). In black spruce, the relationship was weak (r^2 of 0.07) and did not significantly differed from 0 when the oldest snag (65 years old, 20 years older than the second oldest snag) was removed. Differences between linear and negative exponential models were so slight for all species (the difference in r^2 was always < 0.02) that they can be considered equivalent. This similarity indicates that, for the time periods sampled in this study, snags experienced a relatively constant loss of wood density for each time interval.

Mineralization rates, whether represented by a negative slope in linear models (absolute value of m) or a mineralization rate constant in the negative exponential model (k) were fastest in trembling aspen, followed by jack pine, balsam fir and black spruce (Table 2.2). ANCOVA on linear models indicated that the slope of trembling aspen was significantly steeper compared with that of the conifers. The jack pine mineralization rate was higher than that of balsam fir. As site conditions in black spruce stands differed from those of the other species (see discussion), direct comparisons of mineralization rates can be misleading.

Loss in wood density also progressed with time since death at the base of the snag in every species (Fig. 2.1), but mineralization rates were not significantly different from those recorded at breast height in all coniferous species. In aspen, however, mineralization rates were significantly greater at the tree base than at breast height.

2.5.2 Factors associated with mineralization rates

Trembling aspen, jack pine and balsam fir models all included TSD and CER as the most influential factors affecting wood mineralization, with increased Cerambycidae activity coupled with TSD at lower wood densities (Table 2.3). The three species presented at least three competitive models that included other variables but multi-model inference revealed that these additional variables did not add significant additional information regarding changes in wood density (Appendix A).

In black spruce, results from Akaike model selection revealed that, of the five variables included in competing models, only DBH and GROWTH influenced wood mineralization. Snags with small DBH and slow growth (Table 2.1 and 2.3) tended to decompose more slowly. As suggested by the very weak relationship between TSD and wood density, TSD did not emerge as a variable of influence in black spruce when compared with models that included other explanatory variables.

2.6 Discussion

2.6.1 Mineralization rates of snags

Mineralization occurred in all snag species that we studied. We found little comparable information on snag mineralization rates for the studied species. The only mineralization rates that have been reported for snags were for trembling aspen and black spruce. In the same region, Saint-Germain et al. (2007) found results similar to those obtained in our study. Both tree species showed a significant negative linear relationship between wood density and time since death, and snags in trembling aspen decreased in density at a significantly faster rate (m = -0.00746) compared to black spruce (m = -0.00319; M. Saint-Germain, *personal communication*). In fire-killed black spruce snags, Boulanger and Sirois (2006) estimated a mineralization rate (k) of 0.00063, but this value did not significantly differed from 0 along a 29-year-long chronosequence. Their results were likely influenced, however, by differing disturbance, environmental, and geographical contexts that would impede direct comparison with our study.

Whether or not mineralization occurs in snags seems to vary with both tree species and location. In boreal species, snag mineralization can be minimal, since wood density does not significantly change as a function of time (Johnson and Greene 1991; Krankina and Harmon 1995; Yatskov et al. 2003; Boulanger and Sirois 2006). Other studies have shown that mineralization does indeed occur, but that it is slow (Yatskov et al. 2003; Saint-Germain et al. 2007).

As all snags were detected in the field and that only one snag could not be crossdated, changes in wood density presented in this study represent the best possible estimation of the mineralization process occurring in standing dead trees. However, as wood density influences breakage susceptibility (Putz et al. 1983; Basham 1991), more rapidly decaying snags might have fallen before we had a chance to sample them. This likely introduces an underestimation bias in mineralization rates, particularly for old snags (Harmon and Sexton 1996; Kruys et al. 2002; Storaunet and Rolstad 2002, 2004).

It is generally acknowledged that downed logs decompose faster than snags (Fahey 1983; Johnson and Greene 1991; Krankina and Harmon 1995; Shorohova and Shorohov 2001; Yatskov et al. 2003; Boulanger and Sirois 2006; but see birch in Yatskov et al. 2003) as a result of more favourable environmental conditions such as wood moisture for decay organisms and better connections to the forest floor for microorganisms to access logs. When compared with mineralization rates of dead wood (logs, occasionally snags and logs) reported in other studies, our data indicate that snag mineralization rates are consistently slower for trembling aspen (k = 0.0351, this study; k = 0.080, Alban and Pastor 1993; k = 0.060, Brais et al. 2006; m = -0.0103, this study; m = -0.022, Miller 1983), balsam fir (k = 0.0094, this study; k = 0.0299, Lambert et al. 1980; k = 0.029, Foster and Lang 1982), and jack pine (k = 0.0152, this study; k = 0.042, Alban and Pastor 1993; k = 0.020, Brais et al. 2006) logs, and black spruce (k = 0.0065, this study; $k \approx 0.025$, Bond-Lamberty et al. 2002, Bond-Lamberty and Gower 2008).

Among our study species, mineralization rates were two to four times slower for conifers than for trembling aspen. Mineralization rates are known to be higher in deciduous than coniferous species, as has been demonstrated in species of *Betula* and *Populus* (Alban and Pastor 1993; Krankina and Harmon 1995; Harmon et al. 2000; Tarasov and Birdsey 2001; Yatskov et al. 2003; Brais et al. 2006; Mäkinen et al. 2006; Saint-Germain et al. 2007; Shorohova et al. 2008). Differences in anatomical structures and chemical composition are often cited to explain this trend (Harmon et al. 1986). When compared with conifers, the high carbohydrate and low lignin contents of aspen (Peterson and Peterson 1992) make this species more susceptible to decay.

The loss of wood density in black spruce exhibited an ambiguous response to TSD. The linear regression was significant, but weak. In the Akaike model selection approach, TSD was not identified as a significant factor influencing mineralization rates, suggesting that influence of TSD is minimal or, at best, secondary when other parameters are considered for black spruce (see below).

2.6.2 Modelling mineralization rates of dead wood

When modelling dead wood density loss over time (logs and/or snags), most authors have used the exponential decomposition model, i.e. a relationship that assumes that mineralization rate is constant though time (Foster and Lang 1982; Erickson et al. 1985; Mattson et al. 1987; Alban and Pastor 1993; Krankina and Harmon 1995; Naesset 1999; Tarasov and Birdsey 2001; Yatskov et al. 2003; Brais et al. 2006). To a lesser extent, linear models have also been used (Lambert et al. 1980; Graham and Cromack 1982; Yatskov et al. 2003; Saint-Germain et al. 2007), suggesting that snags experienced a constant loss of wood density at each time interval. Some studies have reported differential mineralization rates during the process of decay: sigmoid relationship (Tarasov and Birdsey 2001; Mäkinen et al. 2006) or multi-phase decay process representing periods with distinct mineralization rates along the decay process (Yatskov et al. 2003; Harmon et al. 2000). Those fits suggest that there is a lag time of slow wood density loss before mineralization becomes effective. This can be due to the time required for the decomposer community to colonize and establish in the substrate (Grier 1978; Means et al. 1985; Harmon et al. 2000). In studies where standing and fallen woody debris have been pooled, the lag phase could roughly correspond to the period where dead trees are still standing and experience slow mineralization (Mäkinen et al. 2006).

In our study, for the time frames sampled, linear and negative exponential relationships described density loss equally well and relationships did not suggest any shift in mineralization rates throughout the sequence. However, we only considered standing dead trees. Considering the complete range of dead wood (snags and logs), which represent a longer time scale relative to snags alone, would probably have highlighted one type of model more clearly. However, caution is required before extrapolating these relationships to logs as mineralization rates are reported to be much higher when boles are in contact with the forest floor (Krankina and Harmon 1995; Yatskov et al. 2003; Boulanger and Sirois 2006).

2.6.3 Differential mineralization rates within a snag

Studies have shown that density can be very heterogeneous within a dead bole (Creed et al. 2004) and even within a single piece of wood (Boddy 2001). In snags, Harmon (1982) reported no difference in mineralization rates at the base of stems in fire-killed snags (mostly hardwoods). However, Shorohova et al. (2008) reported higher wood density losses for stumps compared with logs and snags in Norway spruce (*Picea abies* L.), Scots pine (*Pinus sylvestris* L.), and two birch species. In our study, the only significant positional difference was found in trembling aspen, with more rapid loss of wood density at the base of the snag than at breast height. The lack of difference for conifers may be attributable in part to the base of conifer trees often being impregnated with phenolic compounds that prevent decay (Tarasov and Birdsey 2001).

2.6.4 Factors influencing snag mineralization

In boreal ecosystems, climate is the main factor that limits heterotrophic activity and, hence, decay (Trofymow et al. 2002). The very low mineralization rates in snags that were observed in both our study and elsewhere are attributable to two main factors. First, since snags eventually fall, the time frame available for sampling is shorter than in logs and might not allow detection of decreasing density (Yatskov et al. 2003). Second, when trees are standing, drying of the wood results in low moisture content, which limits metabolic processes that control decomposer activity, particularly fungi’s (Erickson et al. 1985; Harmon et al. 1986; Johnson and Greene 1991). Other factors influence microclimatic conditions that, in turn, influence the presence and activity of the decomposer community and, therefore, mineralization rates.

2.6.4.1 Saproxylic insect colonization

A relationship between saproxylic insect colonization and wood mineralization has often been suspected but has rarely been quantified. The association between cerambycid activity and higher mineralization rates found in the three snag species is likely explained by two differing colonization patterns.

In coniferous species, colonization by Cerambycidae is characterized by stress-host species and is concentrated in dying or recently dead trees (Saint-Germain et al. 2007). While fragmentation by gallery excavation likely exerts a minor effect on wood decomposition (Harmon et al. 1986, Zhong and Schowalter 1989), other aspects of this activity may more strongly influence the process. First, by penetrating the bark and/or the wood, larvae provide access to carbohydrate resources for decomposer microorganisms such as fungi and bacteria. Second, these galleries also allow moisture to penetrate the bole, creating a more favourable environment for decomposition (Rayner and Boddy 1988; Zhong and Schowalter 1989). Lastly, insects may act as vectors of decomposer spores and directly inoculate wood (Rayner and Boddy 1988; Zhong and Schowalter 1989).

Colonization of trembling aspen differs from that of conifers. Cerambycid beetles colonize aspen snags in middle- to late-stages of decay, when wood density has significantly decreased (Saint-Germain et al. 2007). The association between cerambycid activity and wood density might thus be inverted when compared with that of conifers, with advanced degree of decay favouring cerambycid colonization. This relationship is also suggested by our data, with highest activity for Cerambycidae in boles that exhibited the lowest wood densities (data not shown).

In our study, the multi-model inference approach indicated that the activity of Cerambycidae, but not that of Scolytinae, contributed to wood mineralization. Edmonds and Eglitis (1989) found similar results in Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco). Greater influence of Cerambycidae than Scolytinae activity on decay might be due to differential impacts of the wood-boring behaviour of each group: Cerambycidae make larger entry and exit holes, dig longer galleries, and penetrate deeper into the wood than Scolytinae, thereby exposing more internal wood surface area to fungi. They may also carry different assemblages of decay agents (Zhong and Schowalter 1989).

2.6.4.2 Growth and DBH

Negative, positive and insignificant correlations between diameter and dead wood decay rates have been documented in the literature. The vast majority of studies have concluded that large-diameter woody debris decay more slowly than smaller diameter material (Means et al. 1985; Harmon et al. 1986; Tarasov and Birdsey 2001; Mäkinen et al. 2006). This relationship has mainly been highlighted in large-diameter trees, but is more rarely observed in ecosystems with intermediate or small diameter trees (Foster and Lang 1982; Mattson et al. 1987; Johnson and Greene 1991; Tarasov and Birdsey 2001, Chapter 1). In this study, for trembling aspen, jack pine and balsam fir, the size effect might have been undetectable given the relatively narrow DBH range that was measured (Foster and Lang 1982; Mattson et al. 1987; Johnson and Greene 1991, Chapter 1).

In black spruce, DBH and growth were the factors most significantly influencing mineralization. Smaller snags and slowly grown trees were more resistant to decay than others. This result may be specific to sites where growth is strongly limited by climatic and edaphic conditions. In this study, black spruce was located in paludified and, therefore, very low productivity stands (Simard et al. 2007). This low productivity was manifested by slow growth, as individuals commonly sustained periods of growth for several years with radial increments of less than 1 mm y^{-1} (Table 2.1). Accordingly, DBH was low, despite an average age of individuals that exceeded 150 years (Table 2.1). With *Picea abies*, Edman et al. (2006) found that rates of wood density loss were lowest in slowly grown wood. Slowly grown wood has high density, has a high latewood-to-earlywood ratio and, thus, a higher concentration in lignin, which is often correlated with higher concentrations of defensive compounds, lower concentrations of nitrogen and amino acids, and lower porosity of the wood that limits penetration of fungal hyphae through the tissue. All of these factors limit fungi decay potential (see Edman et al. 2006 for a review).

Besides reflecting slow growth, DBH might have influenced the mineralization rate in another way. Spruce stands were very open as a result of the successional paludification process (Simard et al. 2007). Snags were thus more exposed to solar radiation and wind penetration, presumably enhancing desiccation of the wood. Furthermore, snags of black spruce were, on average, smaller than those of other species (Table 2.1), allowing the wood to dry out more rapidly (Rayner and Boddy 1988).

2.7 Conclusion

Results from this study clearly show that most tree species do experience mineralization while standing dead. Snags can experience a considerable decrease in wood density, sometimes by as much as half their initial value, and still maintain enough mechanical resistance to remain upright. In addition, although they may share similar environments, snags of different tree species responded in an individualistic manner to mineralization. Our results also show that mineralization is not only influenced by the post-mortem history of snags (time since death) but sometimes by features acquired while the tree was living (DBH, growth).

The microclimatic context in which dead trees decompose also seems to be an important factor to consider, and could explain why some studies have observed mineralization at the snag stage while others have not (Johnson and Greene 1991; Krankina and Harmon 1995; Yatskov et al. 2003). In this study, only a limited number of factors were considered, whereas the main agents of decay, fungi, were not. Further studies are needed to understand more thoroughly the mineralization process in snags, particularly with regards to biotic decomposer agents such as fungi.

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2.9 References

Alban, D.H. and Pastor, J. 1993. Decomposition of aspen, spruce, and pine boles on two sites in Minnesota. Can. J. For. Res. **23**: 235-242. 1744-1749.

Basham, J.T. 1991. Stem decay in living trees in Ontario's forests: a user's compendium and guide. Forestry Canada, Ontario Region, Great Lakes Forestry Centre, Sault Ste. Marie, ON. Information report O-X-408.

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

Blanchette, R. A. 1995. Degradation of the lignocellulose complex in wood. Can. J. Bot. **73**: S999-S1010.

Boddy, L. 2001. Fungal community ecology and wood decomposition processes in angiosperms: from standing tree to complete decay of coarse woody debris. Ecol. Bull. **49**: 43-56.

Bond-Lamberty, B., Wang, C. and Gower, S.T. 2002. Annual carbon flux from woody debris for a boreal black spruce fire chronosequence. Journal of Geophysical Research - Atmospheres **107**. Article 8220.

Bond-Lamberty, B. and Gower, S.T. 2008. Decomposition and fragmentation of coarse woody debris: Re-visiting a boreal black spruce chronosequence. Ecosystems **11**: 831-840.

Boulanger, Y. and Sirois, L. 2006. Postfire dynamics of black spruce coarse woody debris in northern boreal forest of Quebec. Can. J. For. Res. **36**: 1770-1780.

Brais, S., Paré, D. and Lierman, C. 2006. Tree bole mineralization rates of four species of the Canadian eastern boreal forest: implications for nutrient dynamics following stand-replacing disturbances. Can. J. For. Res. **36**: 2331-2340.

Burnham, K.P. and Anderson, D.R. 2002. Model selection and multimodel inference: a practical information-theoretic approach. 2nd ed. Springer-Verlag, New York, USA.

Creed, I.F., Webster, K.L. and Morrison, D.L. 2004. A comparison of techniques for measuring density and concentrations of carbon and nitrogen in coarse woody debris at different stages of decay. Can. J. For. Res. **34**: 744-753.

Dansereau, P.-R. and Bergeron, Y. 1993. Fire history in the southern boreal forest of northwestern Quebec. Can. J. For. Res. **23**: 25-32.

Drapeau, P., Nappi, A., Imbeau, L. and Saint-Germain, M. 2009. Standing dead wood for keystone bird species in the eastern boreal forest: Managing for snag dynamics. For. Chron. **85**: 227-234.

Edman, M., Möller, R. and Ericson, L. 2006. Effects of enhanced tree growth rate on the decay capacities of three saprotrophic wood-fungi. For. Ecol. Manage. **232**: 12-18.

Edmonds, R.L. and Eglitis, A. 1989. The role of the Douglas-fir beetle and wood borers in the decomposition of and nutrient release of Douglas-fir logs. Can. J. For. Res. **19**: 853-859.

Environment Canada. 2010. National Climate Data and Information Archive. Available at www.climate.weatheroffice.gc.ca/climate_normals/results_e.html, accessed 8 November 2010 [Verified 8 November 2010].

Erickson, H.E., Edmonds, R.L. and Peterson, C.E. 1985. Decomposition of logging residues in Douglas-fir, western hemlock, Pacific silver fir, and ponderosa pine ecosystems. Can. J. For. Res. **15**: 914-921.

Fahey, T.J. 1983. Nutrient dynamics of aboveground detritus in lodgepole pine (*Pinus contorta* spp. *latifolia*) ecosystems, southeastern Wyoming. Ecol. Mono. **53**: 51-72.

Farris, K.L., Huss, M.J. and Zack, S. 2004. The role of foraging woodpeckers in the decomposition of ponderosa pine snags. Condor **106**: 50-59.

Foster, J.R. and Lang, G.E. 1982. Decomposition of red spruce and balsam fir boles in the White Mountains of New Hampshire. Can. J. For. Res. **12**: 617-626.

Graham, R.L. and Cromack, K., Jr. 1982. Mass, nutrient content, and decay rate of dead boles in rain forests of Olympic National Park. Can. J. For. Res. 12: 511-521.

Grier, C.C. 1978. A *Tsuga heterophylla--Picea sitchensis* ecosystem of coastal Oregon: decomposition and nutrient balances of fallen logs. Can. J. For. Res. 8: 198-206.

Harmon, M.E. 1982. Decomposition of standing dead trees in the southern Appalachian Mountains. Oecologia **52**: 214-215.

Harmon, M.E., Franklin, J.F., Swanson, F.J., Sollins, P., Gregory, S.V., Lattin, J.D., Anderson, N.H., Cline, S.P., Aumen, N.G., Sedell, J.R., Lienkaemper, G.W., Cromack, K. Jr. and Cummins, K.W. 1986. Ecology of coarse woody debris in temperate ecosystems. Adv. Ecol. Res. **15**: 133-302.

Harmon, M.E., Krankina, O.N. and Sexton, J. 2000. Decomposition vectors: a new approach to estimating woody detritus decomposition dynamics. Can. J. For. Res. **30**: 76-84.

Harmon, M.E. and Sexton, J. 1996. Guidelines for measurements of woody detritus in forest ecosystems. Publication No. 20. U.S. Long Term Ecological Research Network Office, University of Washington, Seattle, WA.

Holmes, R.L. 1983. Computer-assisted quality control in tree-ring dating and measurement. Tree-Ring Bull. **43**: 69-78.

Jessome, J.P. 1977. Strength and related properties of woods grown in Canada. Eastern Forest Products Lab., Ottawa, ON. Forestry Technical Report 21.

Johnson, E.A. and Greene, D.F. 1991. A method for studying dead bole dynamics in *Pinus contorta* var. *latifolia* - *Picea engelmannii* forests. J. Veg. Sci. **2**: 523-530.

Kasischke, E.S. 2000. Processes influencing carbon cycling in the North American boreal forest. *In*: Kasischke, E.S. and Stocks, B.J. (eds.), Fire, climate change and carbon cycling in the boreal forest. Ecol. Stud. **138**:103-110.

Krankina, O. N. and Harmon, M. E. 1995. Dynamics of the dead wood carbon pool in northwestern Russian boreal forests. Water Air Soil Pollut. **82**: 227-238.

Kruys, N., Jonsson, B.G., and Ståhl, G. 2002. A stage-based matrix model for decay-class dynamics of woody debris. Ecol. Appl. **12**: 773–781.

Laiho, R. and Prescott, C.E. 2004. Decay and nutrient dynamics of coarse woody debris in northern coniferous forests: A synthesis. Can. J. For. Res. **34**: 763-777.

Lambert, R.L., Lang, G.E. and Reiners, W.A. 1980. Loss of mass and chemical change in decaying boles of a subalpine balsam fir forest. Ecology **61**: 1460-1473.

Mäkinen, H., Hynynen, J.S.J. and Sievänen, R. 2006. Predicting the decomposition of Scots pine, Norway spruce, and birch stems in Finland. Ecol. Appl. **16**: 1865-1879.

Mast, J.N. and Veblen, T.T. 1994. A dendrochronological method of studying tree mortality patterns. Phys. Geogr. **15**: 529-542.

Mattson, K.G., Swank, W.T. and Waide, J.B. 1987. Decomposition of woody debris in a regenerating, clear-cut forest in the Southern Appalachians. Can. J. For. Res. **17**: 712-721.

Means, J.E., Cromack, K. Jr. and MacMillan, P.C. 1985. Comparison of decomposition models using wood density of Douglas-fir logs. Can. J. For. Res. **15**: 1092-1098.

Miller, W.E. 1983. Decomposition rates of aspen bole and branch litter. For. Sci. **29**: 351-356.

Morin, H., Laprise, D. and Bergeron, Y. 1993. Chronology of spruce budworm outbreaks near Lake Duparquet, Abitibi region, Quebec. Can. J. For. Res. **23**: 1497-1506.

Naesset, E. 1999. Decomposition rate constants of *Picea abies* logs in southeastern Norway. Can. J. For. Res. **29**: 372-381.

Olson, J.S. 1963. Energy storage and the balance of producers and decomposers in ecological systems. Ecology **44**: 322-331.

Peterson, E.B. and Peterson, N.M. 1992. Ecology, management, and use of aspen and balsam poplar in the prairie provinces. Forestry Canada, Northwest Region. Northern Forestry Centre, Edmonton, AB. Special Report 1.

Putz, F.E., Coley, P.D., Lu, K., Montalvo, A. and Aiello, A.1983. Uprooting and snapping of trees: structural determinants and ecological consequences. Can. J. For. Res. **13**: 1011-1020.

Rayner, A.D.M. and Boddy, L. 1988. Fungal decomposition of wood: Its biology and ecology. John Wiley and Sons, Bath, UK.

Rinn, F. 1996. TSAP (Time series Analysis and Presentation) Version 3.0. Rinntech, Heidelberg, Germany.

Robitaille, A. and Saucier, J.-P. 1998. Paysages régionaux du Québec méridional. Les publications du Québec, Ste-Foy, QC, Canada.

Saint-Germain, M., Drapeau, P. and Hébert, C. 2004 Landscape-scale habitat selection patterns of *Monochamus scutellatus* (Coleoptera: Cerambycidae) in a recently burned black spruce forest. Environmental Entomology **33**: 1703-1710.

Saint-Germain, M., Drapeau, P. and Buddle, C. M. 2007. Host-use patterns of saproxylic phloeophagous and xylophagous Coleoptera adults and larvae along the decay gradient in standing dead black spruce and aspen. Ecography **30**: 737-748.

Shorohova, E.V. and Shorohov, A.A. 2001. Coarse woody debris dynamics and stores in a boreal virgin spruce forest. Ecol. Bull. **49**: 129-135.

Shorohova, E., Kapitsa, E. and Vanha-Majamaa, I. 2008. Decomposition of stumps 10 years after partial and complete harvesting in a southern boreal forest in Finland. Can. J. For. Res. **38**: 2414-2421.

Simard, M., Lecomte, N., Bergeron, Y., Bernier, P.-Y. and Paré, D. 2007. Forest productivity decline caused by successional paludification of boreal soils. Ecol. Appl. 17: 1619-1637.

Storaunet, K.O. and Rolstad, J. 2002. Time since death and fall of Norway spruce logs in old-growth and selectively cut boreal forest. Can. J. For. Res. **32**: 1801-1812.

Storaunet, K.O. and Rolstad, J. 2004. How long do Norway spruce snags stand? Evaluating four estimation methods. Can. J. For. Res. **34**: 376-383.

Tarasov, M.E. and Birdsey, R.A. 2001. Decay rate and potential storage of coarse woody debris in the Leningrad region. Ecol. Bull. **49**: 137-147.

Trofymow, J.A., Moore, T.R., Titus, B., Prescott, C., Morrison, I., Siltanen, M., Smith, S., Fyles, J., Wein, R., Camiré, C., Duschene, L., Kozak, L., Kranabetter, M. and Visser, S. 2002. Rates of litter decomposition over 6 years in Canadian forests: influence of litter quality and climate. Can. J. For. Res. **32**: 789-804.

Vallentgoed, J. 1991. Some important woodborers related to export restrictions. Forestry Canada, Forest Pest Leafl. 74.

Vincent, J.S. and Hardy, L. 1977. L'évolution et l'extinction des lacs glaciaires Barlow et Ojibway en territoire québécois. Géographie physique et Quaternaire **31**: 357-372.

Yatskov, M., Harmon, M.E. and Krankina, O.N. 2003. A chronosequence of wood decomposition in the boreal forests of Russia. Can. J. For. Res. **33**: 1211-1226.

Zhong, H. and Schowalter, T. D. 1989. Conifer bole utilization by wood-boring beetles in western Oregon. Can. J. For. Res. **19**: 943-947.

Table 2.1. Characteristics of sampled snags included in Akaike model selection.

Species	TSD (years) Mean ± SE (range)	DBH (cm) Mean ± SE (range)	Age (years) Mean ± SE (range)	Growth ($cm.y^{-1}$) Mean ± SE (range)	SCOL activity ($holes.m^{-2}$) Mean ± SE (range)	CER activity ($holes.m^{-2}$) Mean ± SE (range)
Trembling aspen (*n* = 50)	8.6 ± 0.9 (1 - 25)	16.6 ± 1.0 (7.8 - 34.3)	63.9 ± 2.8 (68 - 323)	0.26 ± 0.00 (0.14 - 0.50)	53.8 ± 22.4 (0 - 986.1)	9.5 ± 2.5 (0 - 61.0)
Jack pine (*n* = 37)	17.5 ± 1.5 (2 - 39)	14.3 ± 0.8 (7.1 - 29.3)	53.9 ± 1.6 (38 - 72)	0.26 ± 0.01 (0.18 - 0.46)	31.1 ± 8.0 (0 - 178.2)	17.2 ± 4.4 (0 - 121.6)
Balsam fir (*n* = 57)	18.3 ± 0.8 (4 - 31)	18.6 ± 0.8 (6.1 - 33.4)	63.9 ± 2.3 (37 - 170)	0.30 ± 0.01 (0.11 - 0.55)	251.7 ± 102.9 (0 - 5615.3)	30.0 ± 3.2 (0 - 102.9)
Black spruce (*n* = 63)	16.4 ± 1.4 (3 - 65)	12.2 ± 0.5 (5.7 - 23.6)	156.5 ± 5.5 (39 - 126)	0.08 ± 0.01 (0.04 - 0.11)	13.2 ± 6.0 (0 - 332.2)	6.6 ± 2.6 (0 - 149.8)

Table 2.2. Parameters of linear and negative exponential wood decay models.

Species	Linear model				Negative exponential model			
	m ± SE	Y_0	p	r^2	k ± SE	Y_0	p	r^2
Trembling aspen	-0.0103 ± 0.0002*a*	0.432	<0.001	0.455	0.0351 ± 0.0008	0.453	<0.001	0.479
Jack pine	-0.0058 ± 0.0002*b*	0.523	<0.001	0.436	0.0152 ± 0.0005	0.530	<0.001	0.418
Balsam fir	-0.0028 ± 0.0001*c*	0.352	0.007	0.119	0.0094 ± 0.0005	0.355	0.007	0.119
Black spruce	-0.0025 ± 0.0001	0.536	0.030	0.073	0.0065 ± 0.0003	0.539	0.031	0.073

Note: For linear model slopes (m), values followed by the same letter do not differ significantly among species ($p < 0.05$). Black spruce was not included in species comparisons as its site conditions differed greatly from the others.

Table 2.3. Parameters associated with wood decay according to multi-model inference.

Species	Parameter*	Model-averaged estimate	Unconditional SE
Trembling aspen (*n* = 50)	TSD (-)	-0.007827	0.002012
	CER (-)	-0.001280	0.000644
Jack pine (*n* = 37)	TSD (-)	-0.005326	0.001127
	CER (-)	-0.000857	0.000380
Balsam fir (*n* = 57)	TSD (-)	-0.002370	0.001012
	CER (-)	-0.000656	0.000253
Black spruce (*n* = 63)	GROWTH (-)	-1.448496	0.650578
	DBH (-)	-0.000870	0.003718

*TSD: Time since death; CER: Cerambycidae activity; GROWTH: Average growth; DBH: Diameter at breast height.

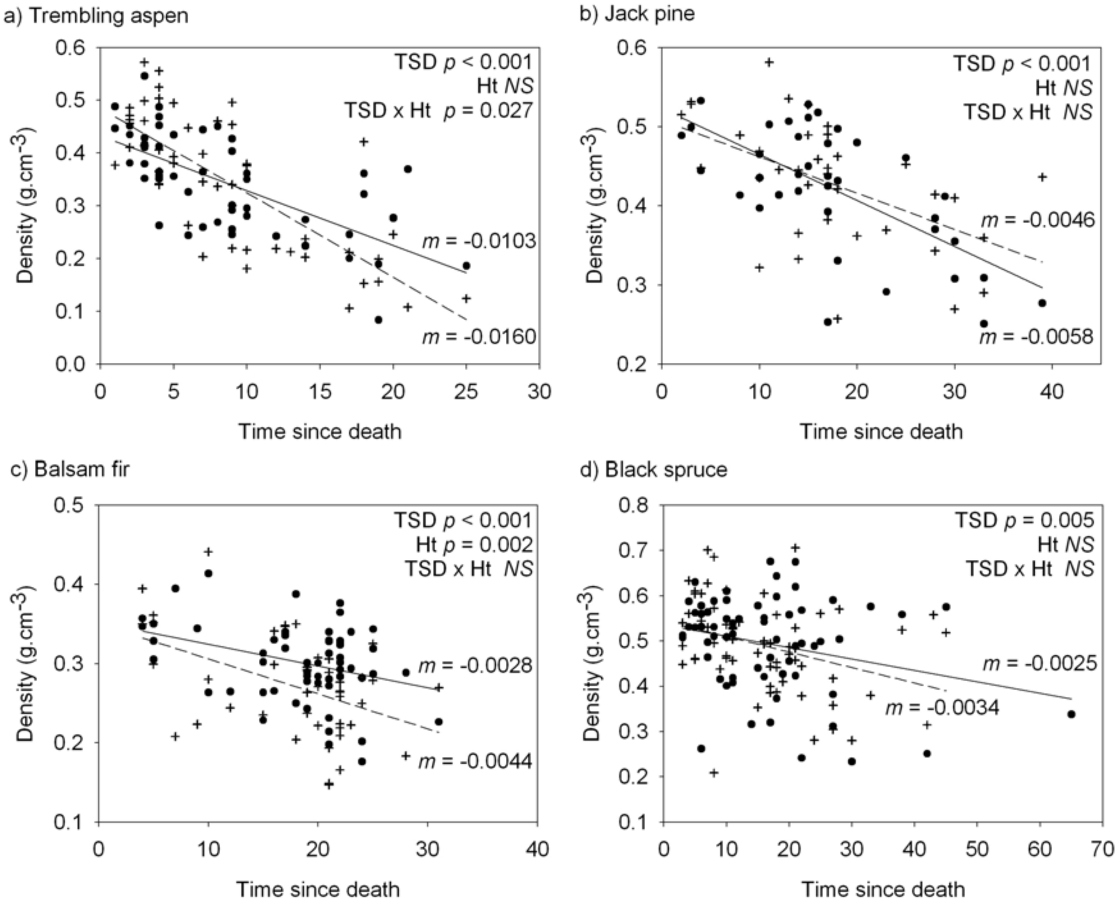

Figure 2.1. Linear relationship between wood density and time since death (TSD) at the tree base (+, ----) and at breast (•,——) height (Ht). Results from ANCOVA are presented in the upper right corner. Line slopes (m) are indicated. NS: not significant ($p > 0.05$).

CHAPITRE 3

TREE MORTALITY AND SNAG DYNAMICS IN NORTH AMERICAN BOREAL TREE SPECIES AFTER A WILDFIRE: A LONG-TERM STUDY

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3.1 Résumé

Nous avons étudié les patrons temporels de mortalité et la dynamique des arbres morts après feu sur une période de dix ans dans un dispositif de placettes permanentes établi immédiatement après feu en forêt boréale de l'est (Québec, Canada). La mortalité après feu, la persistance des chicots, les patrons de chute des arbres et les variables influençant la dynamique des chicots ont été examinés. Des analyses de survie ont été utilisées pour documenter 1- les courbes de survie des arbres situés dans les peuplements décidus et mixtes qui ont subit des feux de sévérité légère et modérée et 2- les courbes de persistance des chicots de pin gris (*Pinus banksiana* Lamb.), de peuplier faux-tremble (*Populus tremuloides* Michx) et d'épinette noire (*Picea mariana* Mill.).

Les patrons temporels de mortalité des trois espèces ont révélé que la mortalité était décalée dans le temps. La majeure partie de la mortalité a eu cours dans les deux années suivant le feu, mais le processus de mortalité s'est poursuivi jusqu'à la fin de la période d'étude de dix ans. Le pin gris était l'espèce la plus persistante comme chicot, suivi du peuplier faux-tremble et de l'épinette noire. Les facteurs influençant la persistance des chicots représentaient plusieurs échelles et étaient généralement spécifiques à chaque espèce. La sévérité du feu était le seul facteur influençant la persistance des chicots commun à toutes les espèces, les chicots situés dans des peuplements sévèrement brûlés étant moins susceptibles de tomber. La persistance sur pied des chicots de peuplier faux-tremble augmentait avec la surface terrière et le diamètre des tiges. La présence de coupes de récupération dans le paysage n'a affecté que l'épinette noire. Les patrons de chute différaient aussi selon les espèces. Le court-circuitage du stade de chicot (i.e. quand un arbre vivant tombe directement au sol) ainsi que le déracinement de chicots étaient communs.

La mortalité décalée dans le temps des arbres dans plusieurs peuplements jumelée à la persistance relativement élevée des chicots dix ans après feu a assuré un recrutement continu de bois mort frais qui a permis la présence d'une importante quantité de chicots ainsi que l'abondance simultanée de bois mort de différents stades de dégradation.

Mots-clés: Mortalité décalée, sévérité du feu, coupe de récupération, analyse de survie, Québec, peuplier faux-tremble, *Populus tremuloides* Michx., pin gris, *Pinus banksiana* Lamb., épinette noire, *Picea mariana* (Mill.) BSP.

3.2 Abstract

Temporal patterns of tree mortality and snag dynamics after fire were investigated over 10 years in a permanent plot design established immediately after a wildfire in an eastern boreal forest landscape of northwestern Quebec, Canada. Post-fire tree mortality, snag persistence, tree fall patterns and variables influencing snag dynamics were assessed. Survival analysis was used to examine: 1- survival curves of trees in deciduous and mixed stands that experienced low- and moderate-severity fires, and 2- persistence curves of snags of jack pine (*Pinus banksiana* Lamb.), trembling aspen (*Populus tremuloides* Michx.) and black spruce (*Picea mariana* Mill.).

Temporal patterns of tree mortality for the three species revealed that mortality was delayed through time. Most post-fire tree mortality occurred within 2 years following fire but continued until the end of the 10-year observation period. Jack pine was the most persistent snag species, followed by trembling aspen and black spruce. Factors influencing the persistence of snags were multi-scaled and generally species-specific. Fire severity was the only common factor influencing snag persistence among all species, with snags located in severely-burned stands being less susceptible to falling. Trembling aspen snag persistence increased with basal area and diameter. Salvage logging in the vicinity affected black spruce. Fall patterns also differed among species. Bypasses of the snag stage (i.e. when a living tree falls directly to the forest floor) as well as uprooting of snags were common.

The delayed tree mortality in many stands coupled with the relatively high persistence of snags 10 years after fire ensured a continuous input of fresh dead wood that led to the occurrence of a high density of snags and the simultaneous availability of dead wood at different stages of degradation.

Keywords: Delayed mortality, fire severity, salvage logging, survival analysis, Quebec, trembling aspen, *Populus tremuloides* Michx., jack pine, *Pinus banksiana* Lamb., black spruce, *Picea mariana* (Mill.) BSP.

3.3 Introduction

Wildfire is a major natural disturbance in North American boreal ecosystems (Johnson 1992; Payette 1992; Bergeron et al. 2004). Within large fires, burn severity may be highly heterogeneous as a result of stand, site, season and climate conditions (Turner et al. 1994; Kushla and Ripple 1997; Kafka et al. 2001; Oliveras et al. 2009). Initial tree mortality is usually massive and synchronous but its magnitude is influenced by fire severity (Hély et al. 2003). Some studies have highlighted the fact that tree mortality continues to occur in the mid- to long-term (Brown and DeByle 1987; Ryan et al. 1988; Harrington 1993; Keyser et al. 2006), but few studies have addressed the issue in boreal ecosystems (but see Brown and DeByle 1987).

The large number of dead trees produced by fire is related to many ecosystem processes that range from carbon and nutrient cycling (Kasischke 2000; Boulanger and Sirois 2006) to habitat creation for a wide diversity of organisms (Saint-Germain et al. 2004; Chambers and Mast 2005; Nappi and Drapeau 2009). Although a growing body of knowledge on snag dynamics, i.e. the transition from standing dead trees to logs, is available for late-seral forests (Lee 1998; Garber et al. 2005; Boulanger and Sirois 2006; Taylor and MacLean 2007; Aakala et al. 2008), persistence of fire-killed snags has received limited attention, especially in the eastern boreal forest (but see Boulanger and Sirois 2006). Environmental conditions such as humidity, temperature and solar insulation influence dead wood degradation (Erickson et al. 1985; Harmon et al. 1986; Naesset 1999; Boddy 2001). As these environmental conditions differ drastically between post-fire and late-seral forest stands, snag dynamics are likely to differ within these two environments. Furthermore, the influence of surrounding salvage logging on snag dynamics of unsalvaged stands has only rarely been assessed (Russell et al. 2006).

In this study we documented the fate of living and dead trees after a wildfire using a study design with permanent plots that offered a unique opportunity to follow simultaneously post-fire tree mortality and snag dynamics over a long period (10 years). First, we examined tree mortality at the stand scale with the specific objective of determining if and how temporal mortality patterns are related to stand composition and fire severity. Then, we analyzed snag dynamics for three species: trembling aspen (*Populus tremuloides* Michx.), jack pine (*Pinus banksiana* Lamb.) and black spruce (*Picea mariana* [Mill.] BSP). For each tree species, our specific objectives were to: 1- generate survival curves of snags after fire, 2- quantify the effect of tree-, stand- and landscape-level explanatory variables on snag persistence, and 3- establish fall pattern, i.e. the different paths a tree may take from standing to lying on the forest floor.

3.4 Methods

3.4.1 Study area

Sampling was conducted in an area where a wildfire covering 12 557 ha occurred in June 1997 near Val-Paradis, northwestern Quebec, Canada (49°09'N, 79°26'W). Lowland areas are covered by clay deposits originating from the proglacial Lake Barlow (Vincent and Hardy 1977) whereas tills and sandy fluvio-glacial deposits dominate uplands (Tremblay 1974). Elevation ranges from 440 to 537 m above sea level. The area is at the transition from mixed-wood to coniferous boreal forest (Gauthier et al. 2000) where black spruce (*Picea mariana* [Mill.] BSP), jack pine (*Pinus banksiana* Lamb.) and trembling aspen (*Populus tremuloides* Michx.) dominate. Paper birch (*Betula papyrifera* Marsh.) and balsam fir (*Abies balsamea* [L.] Mill.) were the main secondary species. According to the closest weather station located in La Sarre, climate is cold and continental, with a mean annual temperature of 0.7°C and mean total annual precipitation of 889.8 mm (1971-2000, Environment Canada 2010).

The fire was an intermittent crown fire and was extinguished on the third day (Hély et al. 2003). Various levels of fire intensity yielded highly variable degrees of severity within the fire. Intensive salvage logging by clear-cutting was conducted in 1997 and 1998 on 59% of the burned area and 92% of stands with commercial timber (Fig. 3.1). Pre-fire stand age varied from 63 to >150 years (Greene et al. 2004).

3.4.2 Data collection

A series of permanent sample plots was established a few weeks after the fire. Thirty-six (36) 0.04 ha plots (20 m x 20 m) were established, with a stratified sampling protocol that covered a combination of three crown fire severity classes (low: 0-25% stand mortality, moderate: 25-75%, high: 75-100%) and three stand composition classes (deciduous, mixed, coniferous) based on the canopy composition (relative basal area) prior to the fire. Deciduous stands were dominated by trembling aspen (> 70%), mixed stands were composed of 10-70% trembling aspen, with the rest being mostly jack pine and black spruce, and coniferous stands were dominated by jack pine, black spruce or a mix of these two species (see Table 3.1 in Greene et al. 2004 for a full description of sites composition). All plots had a minimal buffer zone of 10 m from salvage cut areas. Unfortunately, in 1997, seven plots were inadvertently salvage logged. Seven new plots were thus established in 1998 of which one plot (severely-burned coniferous) was logged in the following years, probably for firewood. Thus the final analysis was conducted on 35 plots.

All trees with diameter at breast height (DBH) greater than 5 cm were labeled. Standing dead trees (trees with no green foliage) were considered as snags when at least 1.3 m tall. A total of 2313 trees were surveyed over 10 years. Species, DBH, height, crown length, status (whether living or dead) and stem integrity (intact, broken, uprooted), were recorded in 1997 whereas these measurements were taken at the end of the summer for the re-established sites in 1998. Status and stem integrity of living trees and snags were reassessed in 1998, 1999, 2000, 2002, 2004 and 2006. In 2004 and 2006, the height of trees was measured and in 2004, percentage of residual bark was estimated.

3.4.3 Data analysis

In total, 2313 trees were surveyed from 1997 to 2006. To avoid any confusion regarding tree mortality and snag temporal dynamics, hereafter we will refer to the former as tree survival curves and to the latter as snag persistence curves. Survival time was calculated as the number of years from fire to tree death. As tree mortality rates varied between 98% and 100% per stand in the year of the fire in severely-burned stands, we only considered lightly- and moderately-burned stands in our temporal analysis of tree mortality. Persistence time of each snag was calculated as the number of years from tree death to snag fall. Trees that eventually died during the observation period were included in the snag persistence analysis (43% of all snags). When an individual was not found, whether because it was accidentally cut, the tag was lost or unreadable, or if a snag was still standing at the end of the observation period, the observation was considered as right-censored at the date of last census.

3.4.3.1 Survival analysis

Survival analysis provides an accurate and detailed representation of survival patterns. It has been used with tree mortality data (see Woodall et al. 2005 for a review) and more recently, in studies of snag dynamics (Lee 1998; Garber et al. 2005; Russell et al. 2006). Survival analysis makes it possible to compare whole survival distributions among different groups, handles censored-data and can be interpreted as a function of independent variables (Allison 1995).

Given that some visits were separated by more than 1 year, we used three scenarios: minimum, median and maximum time since death or fall of trees to compute survival functions. These functions were computed at the stand scale for the six possible composition/severity combinations for tree mortality data and for each species in snags. Significance of differences was assessed using the log-rank test statistics using the SAS LIFETEST procedure (Allison 1995, SAS Institute Inc.

2002). This survival analysis allowed us to test the null hypothesis that the survival curves are the same in two or more groups. For tree mortality, there was no difference between survival curves of minimum, median and maximum survival time ($p \geq 0.2918$ in all groups). There was no significant difference between snag persistence curves of minimum, median and maximum time since fall for jack pine and trembling aspen ($p = 0.7873$ and $p = 0.1870$, respectively). Differences were more marked in black spruce ($p = 0.0006$) but this result had no major biological significance: divergences were concentrated between 3 and 5 years after death and the proportion of standing dead stems was the same or almost identical from the beginning to the end of the observation period. We thus assumed the date of the event to be the midpoint of the interval and based further analyses on this assumption.

3.4.3.2 Variables influencing tree survival and snag persistence

The SAS LIFEREG procedure and the log-rank test statistics were used to test the influence of fire severity and stand composition on tree survival at the stand scale (all species included). This procedure uses the method of maximum likelihood to produce estimates of parametric regression models. We assessed the effect of tree-, stand- and landscape-level variables on snag persistence for each tree species using the following procedure: first, predictive variables were identified and computed if necessary. Tree-level variables were DBH (cm), height and crown length. Stand-level variables included pre-fire basal area (BA, m^2/ha, all species included), composition (COMP, three classes) and fire severity (SEV, three classes). The landscape-level variable was the proportion of salvage-logged area within a 100 m radius from the centre of the permanent plots (SALVG). It was calculated using salvage report maps (ESRI 2000). Percentage of salvage-logged area within 100 m from the centre of our permanent plots ranged from 0% to 98.7% (Average = 53.3%, SE = 4.5%).

Using multiple linear regressions, a list of models was then developed to assess the joint effect of tree-, stand- and landscape-level variables on snag persistence for each species. Models were based on variables known to be biologically meaningful with regard to snag fall (see Appendix B for the list of models). Variables were considered independent and therefore used in models when Pearson's correlation coefficient between two given variables was less than 0.5. In all species, DBH, height and crown length were all strongly correlated to each other (Pearson's correlation coefficient > 0.5, data not shown). Since DBH is the tree-level variable most widely used in snag dynamics studies and given that its variance was slightly higher than other variables (Table 3.1), we decided to systematically include this variable in our models. For jack pine, stand composition was not included since this species was mostly only present in coniferous stands. Models including each individual variable were added to the list. DBH was the only variable determined by tree life history and has been shown to affect snag persistence in many instances (see discussion), so we included it in many models. We considered SEV and SALVG as stand- and landscape-level factors likely to induce environmental changes following wildfire, and hence, affect snag persistence in remnant habitats. These two variables were thus also frequently included in the models, together or separately.

Third, we used the LIFEREG procedure to investigate whether the models suggested by that procedure were included in the listed models for each species and added them if they were not. The null and full models were also included. Finally, Akaike's information criterion (AIC) was used to select the best model, i.e. the most simple and parsimonious one (Burnham and Anderson 2002). For black spruce and trembling aspen, the AIC is expressed by:

$$\text{AIC} = -2(\text{log-likelihood}) + 2K$$

where K is the number of parameters in the model (including intercept, shape and scale).

For jack pine, the sample size was small relative to the number of parameters (i.e. n / number of parameters < 40). Hence, the second-order Akaike information criterion (AIC_c) was used (Burnham and Anderson 2002), as expressed by:

$$\text{AIC}_c = -2(\text{log-likelihood}) + 2K + 2K(K+1) / (n\text{-}K\text{-}1)$$

When several models competed for top rank ($\Delta\ \text{AIC}_c < 2$), indicating uncertainty regarding the best model, we used multi-model inference (Burnham and Anderson 2002). By computing a weighted average of the regression coefficients of a given variable for all models including that variable, model-averaged estimates and unconditional standard errors were generated and used to build a 95% confidence interval, enabling us to assess the magnitude of the effect of this specific variable.

3.4.3.3 Tree fall pattern

After removal of dead trees that were still standing at the end of the observation period and individuals that were not followed throughout the entire observation period (i.e. censored data) we investigated detailed fall pattern for each individual to reconstruct the successive transit from one status to another. Any combination (double or multiple) of the following status was considered as a separate fall pattern class: living, standing dead intact, standing dead broken, fallen broken at the base, fallen uprooted (ex.: living to standing dead intact to standing dead broken to fallen broken at the base).

As broken snags have been found to be more persistent than intact ones, we compared the interval from death to fall in snags that fell after breaking at the base versus snags that exhibited other fall patterns using a Wilcoxon rank sum test since the assumption of normality was not met even when the data were transformed.

3.5 Results

3.5.1 Survival curves of trees after fire

In the year of fire (1997), tree survival varied between 76% and 93% in lightly-burned stands and 52% and 63% in moderately-burned stands, depending on stand composition (Fig. 3.2). Tree survival generally dropped considerably the second year (1998) and continued to decrease less drastically in the 3 following years, particularly in lightly-burned stands (1998-2000). Although trees continued to die every year during the observation period in every stand type, tree mortality tended to stabilize during the last 5 years of observation (2002-2006), especially in moderately-burned stands.

The differences between initial tree survival (1997) and survival at the end of the observation period (2006) varied between 45% and 60% in low- and mid-severity fires. Even though high tree mortality occurred in all stand types, survival at the end of the observation period remained higher in low-severity fires than in moderate-severity ones.

Both fire severity and stand composition influenced tree survival rates (LIFEREG procedure, log rank test, $p \leq 0.0001$ and $p = 0.0021$ respectively). As expected, trees in lightly-burned stands were more likely to survive than those in moderately-burned stands, even in the long term (Fig. 3.2). Trees from deciduous stands generally had greater survival rates than those from mixed and coniferous stands whereas trees from mixed stands had lower survival rates than those from coniferous stands in which fire severity was low.

3.5.2 Persistence curves of snags after fire

Snag persistence curves differed significantly for each species (LIFETEST procedure, log rank test, $p < 0.0001$, Fig. 3.3). Jack pine snags were the most persistent, black spruce the least, while trembling aspen snags were intermediate. Both jack pine and trembling aspen snags exhibited a reverse sigmoid function with evident time lags, i.e. initial periods of high snag persistence during the first 3 years (> 85% persistence) followed by higher fall rates. Black spruce snags exhibited a more constant fall rate though time. Half-life of snags, the time required for half the stems to fall to the forest floor, was 4.4 years for black spruce, 7.5 years for trembling aspen and 8.3 years for jack pine. Survival analysis showed that 10 years after their death, 15.3% of black spruce snags, 20.1% of trembling aspen snags and 32.6% of jack pine snags were still standing. Given that tree mortality was delayed throughout the observation period, it is worth noting that these results are related to time since death, not time since fire. Moreover, these values must not be confused with the percentage of all dead trees that died during or after the fire and were still standing at the end of the observation period, which were somewhat higher.

Specifically, 22.1% of black spruce snags, 44.8% of trembling aspen snags and 61.9% of jack pine snags were still standing at the end of the observation period.

3.5.3 Variables influencing snag persistence

Multi-model inference showed that fire severity was the only factor common to all tree species that influenced snag persistence: snag fall was less when stand fire severity was higher (Table 3.2). For trembling aspen and jack pine, the difference was significant among all severity classes. In black spruce, the difference was significant only when comparing lightly- and severely-burned stands. No significant differences occurred between lightly- and moderately-burned or between moderately- and severely-burned stands. Fire severity was the only significant factor influencing snag persistence in jack pine.

Other factors influencing snag persistence were species-specific (Table 3.2). Variables from tree-, stand- and landscape scales were found to influence snag persistence in one species or another. For trembling aspen, large snags were more persistent than small ones, while snags located in stands with high basal area were more susceptible to fall. The only species for which the landscape-scale variable was significant was black spruce, with snags surrounded by a high proportion of salvage-logged burned stands being more susceptible to fall.

3.5.4 Tree fall patterns

All fall pattern classes representing at least 5% of stems in one species are presented in Fig. 3.4. In most cases, trees changed from a standing dead intact status to fallen, whether by breaking at the base or by uprooting (63% to 85% depending on species). Uprooting prevailed in black spruce (61%) whereas 81% of trembling aspen fell by breakage at the base. In jack pine, uprooting and breakage at the base were roughly equivalent (52% and 48%, respectively). Direct transit from living to fallen status, whether by breakage at the base or uprooting, was common in trembling aspen (26%) whereas it was close to 10% for the two other species. Snags of trembling aspen and black spruce that were already broken at some point along the bole and that fell by breaking at the base were at least two times more persistent than snags that experienced any other fall pattern (Table 3.3, p < 0.0001 in both species).

Double breakage, i.e. breakage at the base of a snag already broken, although not prevalent, was observed in 9% of trembling aspen snags and in 6% of cases in black spruce. Multiple breakage values are, however, more frequent. Indeed, height of snags was only measured during the two last surveys (2004 and 2006). The status of a broken snag from which the stem would have been broken a second time was considered as the same (standing broken) throughout the survey. For broken snags still standing in 2006 for which height was estimated in 2004, 11% of black spruce snags and 14% of trembling aspen snags experienced a reduction in height. Multiple breakages were uncommon in jack pine, as only one snag out of 53 experienced a height reduction during that interval.

3.6 Discussion

This study provides a unique dataset of trees that were repeatedly surveyed over a long time frame following a wildfire. A large number of trees were monitored yearly or every second year over a 10-year period. Many forest cover types representative of the boreal ecosystems of eastern North America were included in our study design that combined forest cover composition with fire severity classes. To our knowledge, our study is the first to provide such a detailed assessment of tree mortality and snag dynamics in the first years following fire in the boreal forest. Moreover, no other study on post-fire tree mortality or fire-killed snag dynamics provides such a large number of permanent study sites surveyed over a long time period.

3.6.1 Survival curves of trees after fire

Our results clearly show delayed mortality of tree species in boreal forest ecosystems following low- and moderate-severity wildfires. To our knowledge, our study is the first to provide a quantitative assessment of this phenomenon in boreal ecosystems. In studies conducted on 4- to 10-year post-fire periods, delayed tree mortality has been reported in low- to moderate-severity wildfires in aspen (Brown and DeByle 1987) and ponderosa pine (*Pinus ponderosa* Dougl.) stands (Keyser et al. 2006) as well as in Douglas-fir (*Pseudotsuga menziesii* Mirb.) (Ryan et al. 1988) and ponderosa pine stands (Harrington 1993) that experienced prescribed burning. In our study, we found roughly the same tree mortality pattern in all stand types: a strong pulse of mortality in the first 2 years after the fire, followed by a period of ongoing but low mortality in the following years. This pattern was also reported in the above studies.

For a given fire severity class, significant differences in survival curves were found across stand composition. However, these compositional differences were most likely attributable to the initial survival value. Indeed, when initial survival was higher in one stand type compared with another, survival at the end of the observation period was also usually higher. Furthermore, differential in survival (∆ initial-final survival value) was similar among severity classes (10% difference maximum).

Large boreal fires are generally considered to induce mortality of most trees (Johnson 1992). However, in the eastern Canadian boreal forest, partial tree mortality following wildfire has been shown to represent large proportions of fire perimeters (Bergeron et al. 2001, Kafka et al. 2001). When fire severity is heterogeneous, lightly- and moderately-burned stands exhibit an initial large amount of green tree retention. Nevertheless, delayed tree mortality may lead to a considerably lower rate of tree survival. For instance, in moderately-burned stands in our study, mortality increased by an additional 44% to 50% during the 5 years after fire, resulting in survivorship of 6% to 11% (Fig. 3.2). Consequently, stands initially classified moderately-burned would have been classified as severely-burned stands (tree survival ≤ 25%) if classification had been done 5 years after fire. Hence, tree mortality following fire is an ongoing process in areas where fire severity is low to moderate at the time of the fire event.

Tree survival tended to stabilize in the last years of our census, suggesting that trees that survived 10 years after fire will generally remain alive. These legacy trees will contribute to maintaining a forest cover, increasing structural diversity and providing dead wood as they progressively die in the regenerating stands.

3.6.2 Snag persistence after fire

Few quantitative data exist on the persistence of snags after wildfire for the species under study. Most studies were conducted in the western United States and present half-lives similar to those found in our study, even though snags sometimes exhibited much larger sizes (Dahms 1949; Everett et al. 1999; Passovoy and Fulé 2006; Russell et al. 2006). In the eastern boreal forest, three studies assessed post-fire snag persistence for the studied species. Using a chronosequence approach in black spruce forests, Boulanger and Sirois (2006) found a half-life of 16.2 years in post-fire stands located 500 km north of our study area. In Manitoba, Canada, Bond-Lamberty and Gower (2008) found that only 23% of black spruce snags had fallen from year one to year nine after fire. For jack pine, 86% to 100% of the snags were still standing 9 years after fire in burned stands located 350 km northeast of our study area (V.A. Angers, *unpublished data*). All studies found much longer persistence than what we reported. This will be discussed in greater detail in the next section.

For both jack pine and trembling aspen, the nearly yearly monitoring of tree fall within the first 10 years following the fire showed a reverse sigmoid curve exhibiting a period of high retention in the first years after death before the onset of higher rates of snag fall. This pattern is consistent with other studies conducted on fire-killed snags (Chambers and Mast 2005; Russell et al. 2006) or snags that died of other causes (Keen 1929; Cline et al. 1980; Lee 1998; Garber et al. 2005; Mäkinen et al. 2006; Taylor and MacLean 2007; Chapter 1). The 3-year lag time following death observed in our study is low but within the range of those obtained in other studies conducted on boreal tree species with similar DBH in mature forests (1-13 years; Lee 1998; Garber et al. 2005; Taylor and MacLean 2007; Chapter 1).

Fire-killed snags are generally considered to be less persistent when compared with snags from the same species killed by causes other than fire (Morrison and Raphael 1993). In our study, this was the case for the three species under investigation. Trembling aspen's half-life was up to three times less than reported half-lives for aspen snags in late-seral forests (Lee 1998; Vanderwel et al. 2006; Chapter 1). In black spruce, reported half-lives ranged from 18 to 40 years in late-seral forests (Aakala et al. 2008; Chapter 1) compared with 4.4 years in our study. As observed with other mortality causes, jack pine post-fire snags were the most persistent. In Chapter 1, we found half-lives of 26 years for jack pine snags sampled in late-seral forests, which is more than three times what was found in our study.

3.6.3 Factors influencing snag persistence

Variables from all scales (tree-, stand- and landscape-level) significantly influenced snag persistence in our study. However, explanatory variables differed among species.

Trembling aspen was the only species for which DBH had an influence on snag persistence, with larger DBH snags being more persistent than smaller ones. Numerous studies have reported that size is influential in post-fire snag persistence (Dahms 1949; Morrison and Raphael 1993; Everett et al. 1999; Chambers and Mast 2005; Russell et al. 2006). However, these studies were conducted in ecosystems where trees were much larger than those sampled in this study. In our study, the lack of a relationship between snag persistence and size observed in jack pine and black spruce corroborates our results for these species in late-seral stands of the same region (Chapter 1). This is probably related to the relatively narrow DBH range of jack pine and black spruce snags which impedes the detection of a size effect (Johnson and Greene 1991; Lee 1998; Kruys et al. 2002; Storaunet and Rolstad 2002). Trembling aspen exhibited a much higher average DBH and, hence, a wider range of DBH size than jack pine and black spruce (Table 3.1). Sampling larger jack pine and black spruce snags could potentially provide a better test of the size effect on snag persistence for these species.

In trembling aspen, snags in stands with high basal area (all species included) were more susceptible to fall. Trees growing in stands with low stem density experience continuous wind exposure and develop physical characteristics for wind firmness compared with those that grow in denser stands where wind exposure is lower because surrounding stems provide shelter (Mitchell 1995). When a disturbance opens the stands, as is the case with fire and salvage logging, trees grown in low-basal area stands may better resist wind exposure. Alternatively, Chambers and Mast (2005) found that snags with higher basal area in ponderosa pine stands in Arizona were less prone to fall.

For all species, snags located in severely-burned stands were less likely to fall compared with those in lightly-burned stands. To our knowledge, no other published study has reported that fire severity influences snag persistence. A possible explanation for such a pattern may be that biological agents such as fungi and saproxylic insects that initiate and maintain decaying activities in wood are less active on severely burned snags (Rayner and Boddy 1988; Saint-Germain et al. 2004) given their lower moisture content (Boulanger and Sirois 2006). In addition, wood desiccation of snags in severely-burned stands might be exacerbated by many factors including the relatively thin bark of the studied species (that does not provide sufficient insulation to protect subcortical tissues), the more rapid bark loss experienced by coniferous species compared with those from other fire severity classes ($p \leq 0.0015$, data not shown), and the sun- and wind-exposed conditions that occur when mortality is high.

Whereas we suggest that moisture level is likely to explain the differential persistence rates in post-fire snags observed in our study, it does not constitute a dominant factor in all situations. For instance, one could expect that the higher humidity levels in unburned mature stands would provide higher water content in snags that should lead to higher fall rates and shorter snag half-lives. This is not the case in unburned forests (Lee 1998; Vanderwel et al. 2006; Aakala et al. 2008; Chapter 1). The study by Morrison and Raphael (1993) in burned and unburned forests of California's Sierra Nevada also documented shorter snag half-lives of snags in burns when compared with unburned stands. Their interpretation of such patterns includes the direct effect of fire that weakens the base of the snag and more direct exposure to wind in comparison with snags surrounded by live trees.

In addition to being more exposed to wind in a burned landscape, our permanent plots were embedded in a heavily salvage-logged matrix where more than 90% of commercial timber was salvage logged using clear-cuts. Hence, even though we did not measure wind conditions, the removal of surrounding snags likely increased wind exposure and fall susceptibility for retention trees and snags of our permanent plots, at least to a level that might be close to what has been documented in forest edges of remnant habitats in boreal ecosystems under clear-cutting (Esseen 1994; Harper et al. 2004; Mascarúa López et al. 2006; see Ruel 1995 for a review). This could explain the remarkably low snag persistence rates in our study that were at least three times shorter than what was observed in stands that experienced high-severity fires with either unsalvaged or lightly salvage-logged surroundings (Boulanger and Sirois 2006, Bond-Lamberty and Gower 2008, V.A. Angers *unpublished data*).

Influence of salvage logging on snag persistence in residual burned stands has seldom been addressed. The only other results were reported by Russell et al. (2006), who found no significant differences in persistence rates of snags sharing the same characteristics in salvage-logged or unlogged sites. Burned stands from the Russell et al. (2006) study were salvage logged using partial cuts and composed of

Douglas-fir and ponderosa pine, two species that grow to larger diameters than the species in this study and that are not particularly susceptible to windthrow.

In our study, we found that black spruce snag persistence was reduced by nearby salvage logging. Because of its lateral and very shallow root system (Viereck and Johnston 1990), black spruce is particularly vulnerable to uprooting compared with the other species (Ruel 1995), as seen in tree fall pattern results (Fig. 3.4). In addition, superficial root mortality induced by fire (Smirnova et al. 2008) may have amplified this vulnerability.

Our results enabled us to highlight the vulnerability of black spruce snags to fall in a salvage-logged context, but did not allow us to distinguish the effect of fire from salvage logging on snag persistence nor to conclude that salvage logging has no effect on jack pine and trembling aspen. Both fire and salvage logging induce an opening of the canopy and a higher exposure to wind. In our study, in order to get enough variability to proceed with the modelling, we selected a 100 m radius around the plots to assess the influence of the surrounding landscape. However, a larger radius might be necessary to draw conclusions on the influence of the surrounding landscape. As much of the burned area was salvage logged, variability in the proportion of salvage-logged surroundings was low when considering a larger radius than what we used and no sites were located in a large, unsalvaged burned matrix. Sampling in a wildfire where spatial distribution of salvage-logged areas would be more variable and would include large patches of intact burns would allow us to assess the influence of fire alone as well as salvage logging on fall vulnerability. Unfortunately, extensive areas of burned forest that are accessible and have not been salvage logged are rare in Quebec (Jayen 2004, Nappi et al. 2004).

3.6.4 Tree fall patterns

The classic degradation process presented in decay classifications, i.e. transition from a living tree to an intact standing dead tree, to a shortened snag following successive breakages, and ending in a stump (e.g. Maser et al. 1979) represented a low proportion of snags in our data set (less than 10% in all species). This pattern was mostly observed in trembling aspen, a species with wood that decomposes more rapidly than coniferous species (Alban and Pastor 1993; Brais et al. 2006; Saint-Germain et al. 2007; Chapter 2) and develops extensive columns of decay within the stem (Basham 1991) that favour successive breakage. On the other hand, a relatively large proportion of trees from all species bypassed the snag stage, as they were either uprooted or broken at the base (below 1.3 m) while alive. Trembling aspen was the species exhibiting the most important deficit in snag recruitment, with a quarter of the fallen stems that fell while alive (mostly broken at the base).

Uprooting has been extensively studied in living trees (e.g. Smith et al. 1987; Ruel 1995) but has only seldom been reported in snags (Taylor and MacLean 2007; Y. Bergeron, pers. obs.). Our results not only document this possibility, but clearly show that it may be a common fall pattern for the fire-killed coniferous species studied, particularly for black spruce where it is dominant. Uprooting in snags may prevail following a disturbance causing massive mortality since the opening of the canopy likely allows wind to enter more freely within stands. In such cases, salvage logging becomes a second disturbance that increases the vulnerability of trees and snags to wind.

As also found in unburned mature stands in the same region (Chapter 1), jack pine consistently appeared to be highly breakage-resistant when compared with the other two species in burned plots. This might be explained by jack pine having the highest wood density, particularly in latewood, and the highest modulus of rupture of the studied species (Jessome 1977, Panshin and De Zeeuw 1980).

Several authors have reported that broken-topped snags are more likely to remain standing than others (Dahms 1949; Morrison and Raphael 1993; Chambers and Mast 2005). In our study, this was clearly the case for trembling aspen and black spruce (Table 3.3). Stability of broken-topped snags is likely enhanced because the loss of branches reduces wind stress and snow loading when the crown is partially or completely gone (Dahms 1949; Huggard 1999; Lee 1998).

3.7 Conclusion: Ecological and management implications

Although fire provides a strong and synchronized pulse of tree mortality, delayed mortality in years following fire also occurs and represents a significant portion of total mortality in stands affected by low- and mid-severity fires. In this study, tree mortality was still ongoing 10 years after the fire. In managed ecosystems where green retention is implemented, managers often face the hastened death of a number of residual trees in the years following harvesting (Esseen 1994, Vanha-Majamaa and Jalonen 2001). This retention approach has been criticized as managers often consider legacy trees as a waste. However, our study shows that mid- and long-term tree mortality in partially burned stands is a common process in deciduous, mixed as well as coniferous stands. Green retention and the potential death of legacy trees in even-aged stands could thus be considered to a certain extent as a surrogate of tree mortality and snag dynamics in early post-fire stands. Moreover, the rates at which trees die and snags break and fall after fire can have tremendous implications for several ecosystem processes, including carbon balance and key habitat attributes recruitment.

Considering dead wood dynamics, i.e. inputs and decomposition rate of dead trees, in assessments of regional and global carbon budgets is crucial as dead wood represents an important source of carbon. This is especially important after wildfire in boreal forests as a considerable amount of dead wood is produced and because this disturbance affects large parts of that biome (Kasischke 2000, Bond-Lamberty et al. 2002). Delayed mortality following fire as observed in this study does not only represent a larger total amount of carbon released than expected when considering initial mortality, but also influences the timing of the release by postponing some of it. Furthermore, as decomposition is more rapid in downed dead wood than in snags

(Harmon et al. 1986, Boulanger and Sirois 2006, Yatskov et al. 2003), the variability in snag persistence can also greatly influence carbon balance (Bond-Lamberty and Gower 2008) and can even make the difference between the stand being a carbon sink or source (Bond-Lamberty et al. 2004).

Spatial and temporal tree mortality patterns may also have major implications for various structural habitat attributes for a wide range of species associated with decaying, standing and fallen dead wood (Drapeau et al. 2009). Delayed tree mortality in lightly- and moderately-burned stands involves a delayed recruitment of snags and downed dead wood. In a forest matrix where fire severity is heterogeneous, this continuous input of fresh dead wood creates the simultaneous availability of dead wood of different degradation stages. This diversity of dead wood substrate can have a marked influence on the occurrence of organisms associated with specific decay classes (Nappi 2009) while allowing the prolonged persistence of species associated with recently dead trees in burned systems (Nappi et al. 2010). In ecosystems where nurse logs are important to seedling establishment and development, the delayed mortality and the recruitment of fallen snags over time may also influence regeneration patterns (Harmon et al. 1986).

Only large trembling aspen snags were found to be more persistent than small ones, and this result is likely due to the fast-growing potential of this species compared with black spruce and jack pine. In this regard, in ecosystems where trembling aspen is a companion of species growing more slowly, particularly when in association with conifers, large trembling aspen snags may represent key elements due to their greater persistence and to the fact that this species is preferentially used by primary excavators (Martin et al. 2004; Gasse *unpublished data*).

Finally, tree mortality and snag dynamics in this study were influenced by salvage logging, a management practice that is evolving worldwide in recently burned forests (Lindenmayer et al. 2004; Nappi et al. 2004; Schmiegelow et al. 2006). Hence, our results may be useful in a post-fire forest management strategy where planning includes both harvesting operations and the conservation of burned patches to ensure biodiversity and regeneration functions through snag conservation and recruitment (Drapeau et al. 2002; Nappi et al. 2004; Hannon and Drapeau 2005).

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3.9 References

Aakala T, Kuuluvainen T, Gauthier S, De Grandpré L (2008) Standing dead trees and their decay-class dynamics in the northeastern boreal old-growth forests of Quebec. Forest Ecology and Management 255, 410-420.

Alban DH, Pastor J (1993) Decomposition of aspen, spruce, and pine boles on two sites in Minnesota. Canadian Journal of Forest Research 23, 1744-1749.

Alison PD (1995) ‘Survival Analysis Using the SAS System, A Practical Guide.’ (SAS Institute: Cary, NC)

Basham, JT (1991) ‘Stem decay in living trees in Ontario's forests: a user's compendium and guide.’ Forestry Canada, Great Lakes Forestry Centre, Information Report O-X-408 (Sault Ste. Marie, ON)

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

Bergeron Y, Leduc A, Harvey BD, Gauthier S (2001) Natural fire regime: A guide for sustainable management of the Canadian boreal forest. Silva Fennica 36, 81-95.

Boddy L (2001) Fungal community ecology and wood decomposition processes in angiosperms: from standing tree to complete decay of coarse woody debris. Ecological Bulletins 49, 43-56.

Bond-Lamberty B, Wang C, Gower ST (2002) Annual carbon flux from woody debris for a boreal black spruce fire chronosequence. Journal of Geophysical Research 107, art. no. 8220.

Bond-Lamberty B, Wang C, Gower ST (2004) Net primary production and net ecosystem production of a boreal black spruce fire chronosequence. Global Change Biology 10, 483-487.

Bond-Lamberty B, Gower ST (2008) Decomposition and fragmentation of coarse woody debris: Re-visiting a boreal black spruce chronosequence. Ecosystems 11, 831-840.

Boulanger Y, Sirois L (2006) Postfire dynamics of black spruce coarse woody debris in northern boreal forest of Quebec. Canadian Journal of Forest Research 36,1770-1780.

Brais S, Paré D, Lierman C (2006) Tree bole mineralization rates of four species of the Canadian eastern boreal forest: implications for nutrient dynamics following stand-replacing disturbances. Canadian Journal of Forest Research 36, 2331-2340.

Brown JK, DeByle NV (1987) Fire damage, mortality and suckering in aspen. Canadian Journal of Forest Research 17, 1100-1109.

Burnham KP, Anderson DR (2002) 'Model selection and multimodel inference: a practical information-theoretic approach.' 2nd Edition. (Springer-Verlag: New York)

Chambers CL, Mast JN (2005) Ponderosa pine snag dynamics and cavity excavation following wildfire in northern Arizona. Forest Ecology and Management 216, 227-240.

Cline SP, Berg AB, Wight HM (1980) Snag characteristics and dynamics in Douglas-fir forests, western Oregon. Journal of Wildlife Management 44, 773-786.

Dahms WG (1949) 'How long do ponderosa pine snags stand?' USDA Forest Service, Pacific Northwest Forest and Range Experiment Station Research Note 57 (Portland, OR)

Drapeau P, Nappi A, Giroux J-F, Leduc A, Savard J-P (2002) Distribution patterns of birds associated with snags in natural and managed eastern boreal forests. In 'Proceedings of the Symposium on the Ecology and Management of Dead Wood in Western Forests'. (Technical Coordinators WF Laudenslayer, PJ Shea, BE Valentine, CP Weatherspoon, TE Lisle) pp. 193–205. USDA Forest Service, Pacific Southwest Research Station General Technical Report PSW-GTR 181 (Albany, CA)

Drapeau P, Nappi A, Imbeau L, Saint-Germain M (2009) Standing dead wood for keystone bird species in the eastern boreal forest: Managing for snag dynamics. The Forestry Chronicle 85, 227-234.

Environment Canada (2010) National Climate Data and Information Archive. Available at www.climate.weatheroffice.gc.ca/climate_normals/results_e.html [Verified 8 November 2010].

Erickson HE, Edmonds RL, Peterson CE (1985) Decomposition of logging residues in Douglas-fir, western hemlock, Pacific silver fir, and ponderosa pine ecosystems. Canadian Journal of Forest Research 15, 914-921.

ESRI (Environmental Systems Research Institute Inc.) (2000). ArcView GIS 3.2. ESRI, Redlands, CA.

Esseen P-A (1994) Tree mortality patterns after experimental fragmentation of an old-growth conifer forest. Biological Conservation 68, 19-28.

Everett R, Lehmkuhl J, Schellhaas R, Ohlson P, Keenum D, Riesterer H, Spurbeck, D (1999) Snag dynamics in a chronosequence of 26 wildfires on the east slope of the Cascade Range in Washington state, USA. International Journal of Wildland Fire 9, 223-234.

Garber SM, Brown JP, Wilson DS, Maguire DA, Heath LS (2005) Snag longevity under alternative silvicultural regimes in mixed-species forests of central Maine. Canadian Journal of Forest Research 35, 787-796.

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

Greene DF, Noël J, Bergeron Y, Rousseau M, Gauthier S (2004) Recruitment of Picea mariana, Pinus banksiana and Populus tremuloides across a burn severity gradient following wildfire in the southern boreal forest of Quebec. Canadian Journal of Forest Research 34, 1845-1857.

Hannon S, Drapeau P (2005) Bird responses to burning and logging in the boreal forest of Canada. Studies in Avian Biology 30, 97-115.

Harmon ME, Franklin JF, Swanson FJ, Sollins P, Gregory SV, Lattin JD, Anderson NH, Cline SP, Aumen NG, Sedell JR, Lienkaemper GW, Cromack K Jr, Cummins KW (1986) Ecology of coarse woody debris in temperate ecosystems. Advances in Ecological Research 15, 133-302.

Harper K, Lesieur D, Bergeron Y, Drapeau P (2004) Forest structure and composition at young fire and cut edges in black spruce boreal forest. Canadian Journal of Forest Research 34, 289-302.

Harrington MG (1993) Predicting Pinus ponderosa mortality from dormant season and growing season fire injury. International Journal of Wildland Fire 3, 65-72.

Hély C, Flannigan M, Bergeron Y (2003) Modelling tree mortality following wildfire in the southeastern Canadian mixed-wood boreal forest. Forest Science 49, 566-576.

Huggard DJ (1999) Static life-table analysis of fall rates of subalpine fir snags. Ecological Applications 9, 1009-1016.

Jayen K (2004) ‘Utilisation des cartes d'impact de feux pour estimer la sévérité des feux et rôle de la sévérité des feux dans le succès de la régénération en forêt boréale dans le nord-ouest du Québec.’ M.Sc. Thesis, Université du Québec à Montréal (Montréal, Canada).

Jessome JP (1977) ‘Strength and related properties of woods grown in Canada.’ Eastern Forest Products Lab., Ottawa, Forestry Technical Report 21. (Ottawa, Canada)

Johnson EA (1992) ‘Fire and vegetation dynamics - Studies from the North American boreal forest.’ Cambridge Studies in Ecology. (Cambridge University Press, Cambridge)

Johnson EA, Greene DF (1991) A method for studying dead bole dynamics in Pinus contorta var. latifolia - Picea engelmannii forests. Journal of Vegetation Science 2, 523-530.

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

Kasischke ES (2000). Processes influencing carbon cycling in the North American boreal forest. In ‘Fire, climate change and carbon cycling in the boreal forest.’ (Eds ES Kasischke, BJ Stocks). Ecological Studies 138: 103–110.

Keen FP (1929) How soon do yellow pine snags fall? Journal of Forestry 27, 735-737.

Keyser TL, Smith FW, Lentile LB, Shepperd WD (2006) Modeling postfire mortality of ponderosa pine following a mixed-severity wildfire in the Black Hills: The role of tree morphology and direct fire effects. Forest Science 52, 530-539.

Kruys N, Jonsson BG, Ståhl G (2002) A stage-based matrix model for decay-class dynamics of woody debris. Ecological Applications 12, 773-781.

Kushla JD, Ripple WJ (1997) The role of terrain in a fire mosaic of a temperate coniferous forest. Forest Ecology and Management 95, 97-107.

Lee P (1998) Dynamics of snags in aspen-dominated midboreal forests. Forest Ecology and Management 105, 263-272.

Lindenmayer DB, Foster DR, Franklin JF, Hunter ML, Noss RF, Schmiegelow FA, Perry D (2004) Salvage harvesting policies after natural disturbance. Science 303, 1303.

Mäkinen H, Hynynen JSJ, Sievänen R (2006) Predicting the decomposition of Scots pine, Norway spruce, and birch stems in Finland. Ecological Applications 16, 1865-1879.

Martin K, Aitken KEH, Wiebe KL (2004) Nest sites and nest webs for cavity nesting communities in interior British Columbia, Canada: nest characteristics and niche partitioning. The Condor 106, 5-19.

Mascarúa López L, Harper KA, Drapeau P (2006) Edge influence on forest structure in large forest remnants, cutblock separators, and riparian buffers in managed black spruce forests. Ecoscience 13, 226-233.

Maser C, Anderson R, Cromack K Jr, William JT, Martin RE (1979) Dead and down woody material. In ‘Wildlife habitats in managed forests, the Blue Mountains of Oregon and Washington’. (Ed J Thomas) pp. 78-95. USDA Forest Service, Agriculture Handbook 553. (Washington, DC)

Mitchell SJ (1995) The windthrow triangle: A relative windthrow hazard assessment procedure for forest managers. The Forestry Chronicle 71, 446-450.

Morrison ML, Raphael MG (1993) Modeling the dynamics of snags. Ecological Applications 3, 322-330.

Naesset E (1999) Decomposition rate constants of Picea abies logs in southeastern Norway. Canadian Journal of Forest Research 29, 372-381.

Nappi A (2009) ‘Sélection d’habitat et démographie du pic à dos noir dans les forêts brûlées de la forêt boréale’. Ph.D. thesis, Université du Québec à Montréal, Montréal, Canada. 220 p.

Nappi A, Drapeau P, Savard J-PL (2004) Salvage logging after wildfire in the boreal forest: Is it becoming a hot issue for wildlife? The Forestry Chronicle 80, 67-74.

Nappi A, Drapeau P (2009) Reproductive success of the black-backed woodpecker (Picoides arcticus) in burned boreal forests: Are burns source habitats? Biological Conservation 142, 1381-1391.

Nappi A, Drapeau P, Saint-Germain M, Angers VA (2010) Effect of fire severity on long-term occupancy of burned boreal conifer forests by saproxylic insects and wood-foraging birds. International Journal of Wildland Fire 19, 500-511.

Oliveras I, Gracia M, Moré G, Retana J (2009) Factors influencing the pattern of fire severities in a large wildfire under extreme meteorological conditions in the Mediterranean basin. International Journal of Wildland Fire 18, 755-764.

Panshin AJ, De Zeeuw C (1980) ‘Textbook of Wood Technology.’ 3rd Edition. (McGraw-Hill: New York)

Passovoy MD, Fulé PZ (2006) Snag and woody debris dynamics following severe wildfires in northern Arizona ponderosa pine forests. Forest Ecology and Management 223, 237-246.

Payette S (1992) Fire as a controlling process in the North American boreal forest. In 'A system analysis of the global boreal forest.' (Eds HH Shugart, R Leemans, GB Bonan) pp. 144-169. (Cambridge University Press: Cambridge)

Rayner ADM, Boddy L (1988) ‘Fungal decomposition of wood - Its biology and ecology.’ (John Wiley and Sons: Bath)

Ruel J-C (1995) Understanding windthrow: Silvicultural implications. The Forestry Chronicle 71, 434-445.

Russell RE, Saab VA, Dudley JG, Rotella JJ (2006) Snag longevity in relation to wildfire and postfire salvage logging. Forest Ecology and Management 232, 179-187.

Ryan KC, Peterson DL, Reinhardt ED (1988) Modeling long-term fire-caused mortality of Douglas-fir. Forest Science 34, 190-199.

Saint-Germain M, Drapeau P, Hébert C (2004) Xylophagous insect species composition and patterns of substratum use on fire-killed black spruce in central Quebec. Canadian Journal of Forest Research 34, 677-685.

Saint-Germain M, Drapeau P, Buddle CM (2007) Host-use patterns of saproxylic phloeophagous and xylophagous Coleoptera adults and larvae along the decay gradient in standing dead black spruce and aspen. Ecography 30, 737-748.

SAS Institute Inc. (2002) Version 9.1. (SAS Institute Inc.: Cary, NC.)

Schmiegelow FKA, Stepnisky DP, Stambaugh CA, Koivula M (2006) Reconciling salvage logging of boreal forests with a natural-disturbance management model. Conservation Biology 20, 971-983.

Smirnova, E, Bergeron, Y, Brais, S, Granström, A (2008) Postfire root distribution of Scots pine in relation to fire behaviour. Canadian Journal of Forest Research 38, 353-362.

Smith VG, Watts M, James DF (1987) Mechanical stability of black spruce in the clay belt region of northern Ontario. Canadian Journal of Forest Research 17, 1080-1091.

Storaunet KO, Rolstad J (2002) Time since death and fall of Norway spruce logs on old-growth and selectively cut boreal forest. Canadian Journal of Forest Research 32, 1801-1812.

Taylor SL, MacLean DA (2007) Dead wood dynamics in declining balsam fir and spruce stands in New Brunswick, Canada. Canadian Journal of Forest Research 37, 750-762.

Tremblay G (1974) ‘Géologie du Quaternaire, Région de Rouyn-Noranda et de l’Abitibi, comté Abitibi-est, Québec.’ Ministère des Richesses naturelles, Rapport intérimaire. (Québec, Canada)

Turner MG, Hargrove WW, Gardner RH, Romme WH (1994) Effects of fire on landscape heterogeneity in Yellowstone National Park, Wyoming. Journal of Vegetation Science 5, 731-742.

Vanderwel MC, Caspersen JP, Woods ME (2006) Snag dynamics in partially harvested and unmanaged northern hardwood forests. Canadian Journal of Forest Research 36, 2769-2779.

Vanha-Majamaa I, Jalonen J (2001) Green tree retention in Fennoscandian forestry. Scandinavian Journal of Forest Research 16, 79-90.

Viereck LA, Johnston WF (1990) Picea mariana (Mill.) B.S.P. Black spruce. In 'Silvics of North America: Vol 1 Conifers'. (Eds RM Burns, BH Honkala) pp. 227-237. USDA Forest Service Agriculture Handbook 654. (Washington, DC).

Vincent JS, Hardy L (1977) L'évolution et l'extinction des lacs glaciaires Barlow et Ojibway en territoire québécois. Géographie Physique et Quaternaire 31, 357-372.

Woodall CW, Grambsch PL, Thomas W, Moser WK (2005) Survival analysis for a large-scale forest health issue: Missouri oak decline. Environmental Monitoring and Assessment 108, 295-307.

Yatskov M, Harmon ME, Krankina ON (2003) A chronosequence of wood decomposition in the boreal forests of Russia. Canadian Journal of Forest Research 33, 1211-1226.

Table 3.1. Stand and tree characteristics of main tree species.

Species	Trembling aspen (*n* = 551) Mean ± SE (range)	Jack pine (*n* = 298) Mean ± SE (range)	Black spruce (*n* = 1314) Mean ± SE (range)
Tree-level variable			
DBH (cm)	21.2^a ± 0.3	13.9^b ± 0.3	11.9^c ± 0.1
	(5.0 - 48.0)	(5.8 - 42.2)	(5.0 - 38.0)
Height (m)	19.1^a ± 0.2	13.9^b ± 0.2	11.2^c ± 0.1
	(4.8 - 38.4)	(4.7 - 23.3)	(2.0 - 21.8)
Stand-level variable			
Pre-fire basal area (m^2 ha^{-1})*	35.2^a ± 2.1	33.0^a ± 2.4	34.2^a ± 1.6
	(20.3 - 57.0)	(23.5 - 57.0)	(23.5 - 57.0)

Note: Within a given species, values followed by the same lowercase letter do not differ significantly ($p < 0.0001$).
*All species included

Table 3.2. Parameters associated with snag persistence according to multi-model inference.

Species	Parameter[A]	Scale	Model-averaged estimate	Unconditional SE
Trembling aspen	DBH (+)	Tree	0.01340	0.00330
(*n* = 453)	SEV (L vs. H) (-)		-0.62727	0.08732
	SEV (L vs. M) (-)	Stand	-0.45616	0.07853
	SEV (M vs. H) (-)		-0.17111	0.05453
	BA (-)	Stand	-0.01888	0.00291
Jack pine	SEV (L vs. H) (-)		-0.57138	0.11133
(*n* = 244)	SEV (L vs. M) (-)	Stand	-0.27186	0.07562
	SEV (M vs. H) (-)		-0.35018	0.13229
Black spruce	SEV (L vs. H) (-)	Stand	-0.12372	0.05620
(*n* = 1039)	SALVG (-)	Landscape	-0.00677	0.00082

[A] DBH: Diameter at breast height; SEV: Fire severity; L: Low fire severity; M: Moderate fire severity; H: High fire severity; BA: Stand basal area (all species included); SALVG: Proportion of salvage-logged area in a 100 m radius.

Table 3.3. Persistence time as snags for fallen trembling aspen, jack pine and black spruce trees after fire according to specific fall patterns.

Mean interval from death to fall (years, Mean ± SE [range])	Trembling aspen (n = 124)	Jack pine (n = 60)	Black spruce (n = 677)
Standing dead broken snags that fell after breaking at the base	7.1^{a} ± 0.5 (3.5 - 8.5)	-[A]	6.9^{a} ± 0.4 (1.0 - 8.5)
All other fall patterns	2.9^{b} ± 0.2 (0.0 - 8.5)	4.2 ± 0.3 (0.0 - 8.5)	3.4^{b} ± 0.1 (0.0 - 8.5)

Note: Within a given species, values followed by the same lowercase letter do not differ significantly ($p < 0.0001$).

[A] Only one stem that fell after breaking at the base was previously standing dead broken.

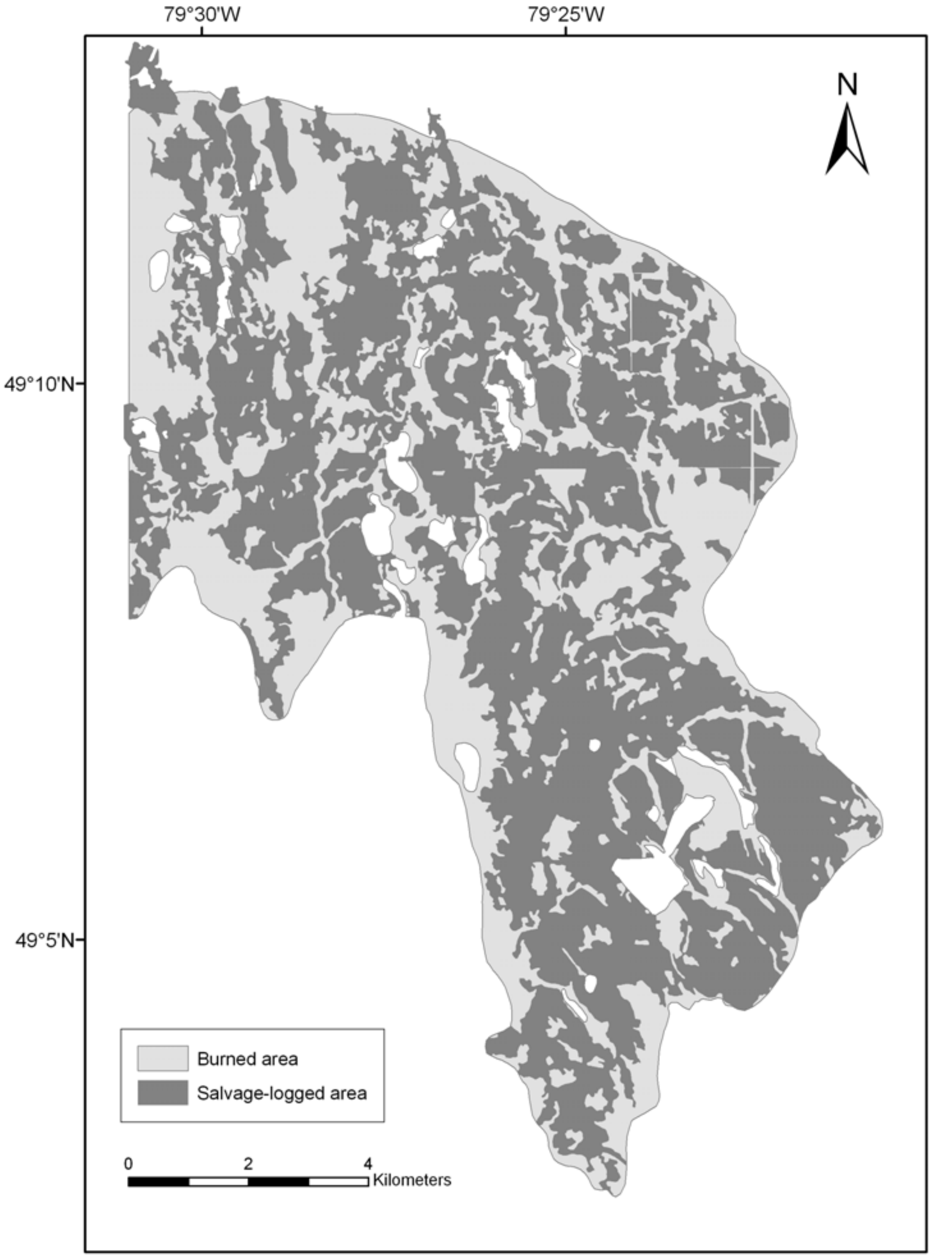

Figure 3.1. Location of salvage-logged areas within the wildfire.

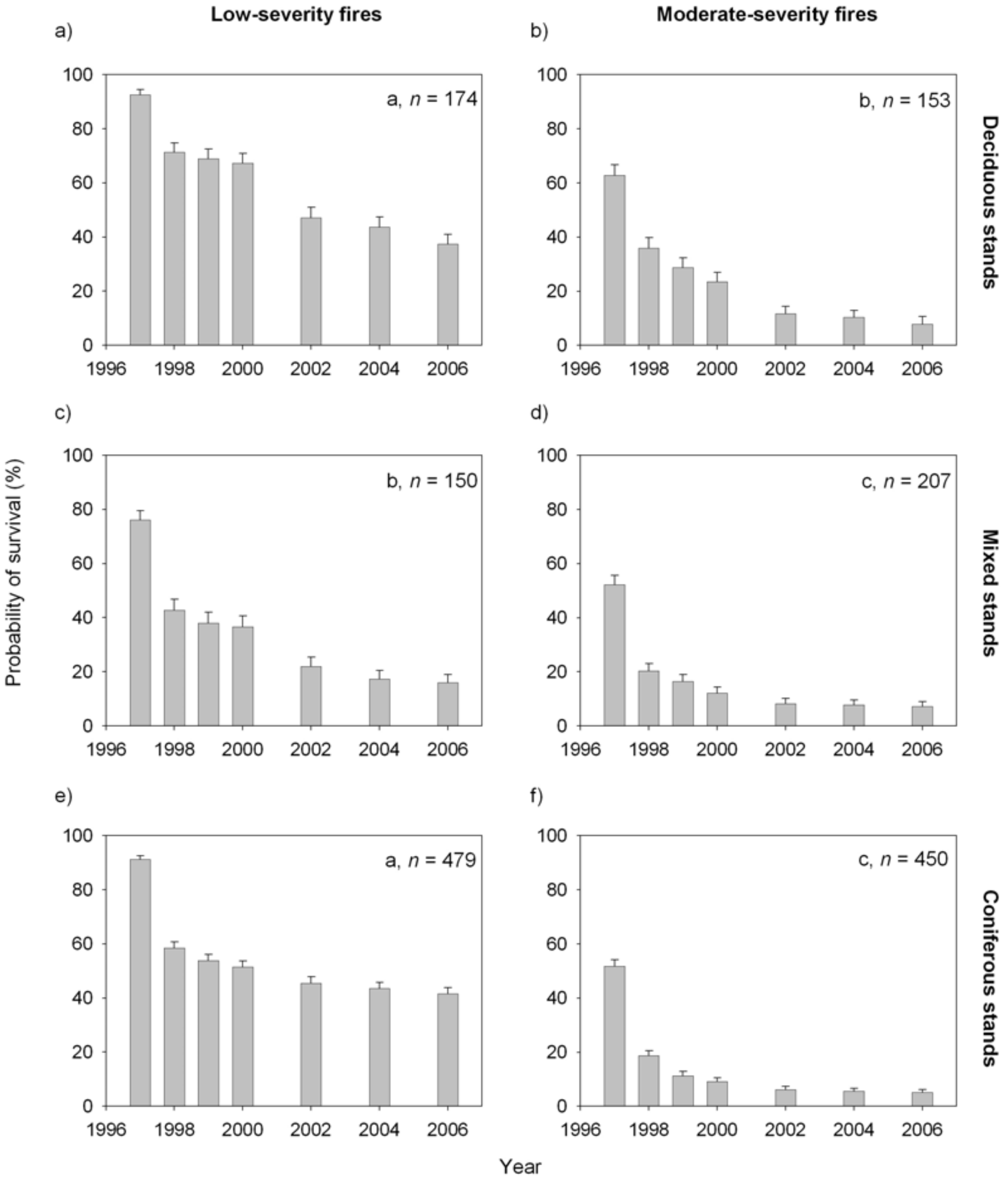

Figure 3.2. Survival probability (± SE) of trees after fire in a) lightly-burned deciduous stands, b) moderately-burned deciduous stands, c) lightly-burned mixed stands, d) moderately-burned mixed stands, e) lightly-burned coniferous stands and f) moderately-burned coniferous stands (see Methods for a description of composition and fire severity classes). Different letters indicate significantly different survival curves among stand types as tested using the LIFEREG procedure and log rank test (six combinations compared simultaneously). Survival probabilities are only presented for lightly- and moderately-burned stands as mortality was ≥ 98% the year of fire in severely-burned stands.

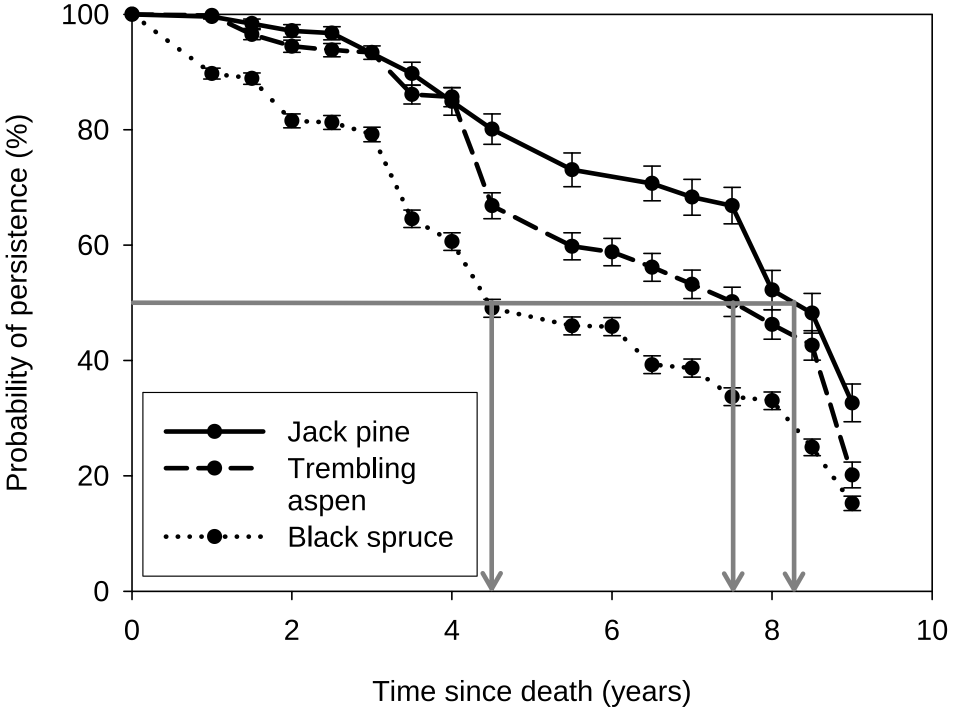

Figure 3.3. Probability of post-fire snag persistence over time in three species using the LIFETEST procedure and log rank test. Grey arrows indicate half-lives.

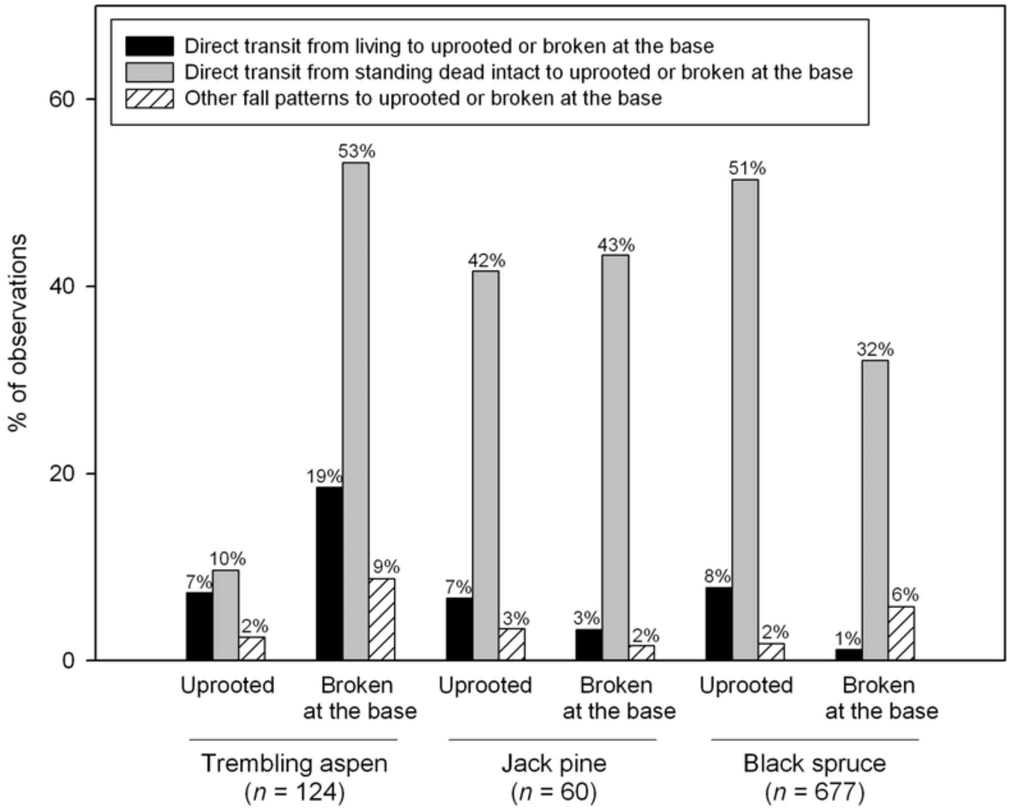

Figure 3.4. Main fall patterns in fallen trembling aspen, jack pine and black spruce trees after fire.

CHAPITRE 4

MORPHOLOGICAL ATTRIBUTES AND SNAG CLASSIFICATION OF FOUR NORTH AMERICAN BOREAL TREE SPECIES: RELATIONSHIPS WITH TIME SINCE DEATH AND WOOD DENSITY

Virginie-Arielle Angers, Yves Bergeron et Pierre Drapeau

4.1 Résumé

Les systèmes de classification de la dégradation des chicots basés sur des traits morphologiques sont largement utilisés mais ont rarement été mis en relation avec le temps écoulé depuis la mort de l'arbre ou la densité du bois. De plus, ces systèmes de classification reposent sur l'apparence globale des chicots alors que le potentiel prédictif de traits individuels a rarement été étudié.

Nous avons examiné quels traits morphologiques prédisent le mieux le temps écoulé depuis la mort (TDM) et la densité du bois chez les chicots de quatre espèces communes en forêt boréale de l'est de l'Amérique du Nord: le peuplier faux-tremble (*Populus tremuloides* Michx.), le sapin baumier (*Abies balsamea* [L.] Mill.), le pin gris (*Pinus banksiana*) et l'épinette noire (*Picea mariana* [Mill.] BSP). Nous avons aussi évalué dans quelle mesure un système de classification de la dégradation des chicots communément utilisé est représentatif du TDM et de la densité du bois. L'échantillonnage a été conduit dans le nord-ouest du Québec, au Canada. Pour chaque espèce, de 37 à 65 chicots ont été échantillonnés et le TDM a été déterminé par dendrochronologie.

Un premier jeu de régressions linéaires multiples a montré que le recouvrement d'écorce était le seul trait morphologique inclus dans les modèles de toutes les espèces et était le seul trait prédictif du TDM chez le sapin baumier. Chez les autres espèces, les autres traits prédictifs du TDM diffèrent. Un deuxième jeu de régressions linéaires multiples a montré que la combinaison des meilleurs traits prédictifs de la densité étaient aussi spécifique à chaque espèce et que la pénétrabilité du bois constituait un trait prédictif commun à toutes les espèces. Le stade de dégradation constituait un indicateur grossier de l'âge des chicots (i.e. TDM). L'âge moyen des chicots croissait généralement avec les stades de dégradation, mais des chevauchements significatifs dans les TDM de stades de dégradation adjacents ont été observés chez toutes les espèces. Le même phénomène a été observé relativement à la densité du bois.

Cette étude montre que le système de classification de la dégradation utilisé peut être utile lorsque des estimations grossières sont requises. Cependant, lorsque des estimations plus précises sont nécessaires, les modèles spécifiques à chaque espèce construits selon des traits morphologiques significatifs ne représentent pas des outils demandant plus de temps ou de ressource sur le terrain et procurent des estimations du TDM et de la densité plus précises.

Mots-clés: Bois mort, dendrochronologie, Québec, peuplier faux-tremble, *Populus tremuloides* Michx., sapin baumier, *Abies balsamea* (L.) Mill., pin gris, *Pinus banksiana* Lamb., épinette noire, *Picea mariana (*Mill.) BSP.

4.2 Abstract

Degradation classification systems of snags based on external morphological attributes are widely used but have rarely been related to elapsed time since death or wood density. Furthermore, these classification systems rely on the global aspect of snags, and the predictive ability of specific attributes has rarely been investigated.

We examined which morphological attributes best predicted time since tree death (TSD) and wood density in snags of four major boreal species in eastern North America: trembling aspen (*Populus tremuloides* Michx.), balsam fir (*Abies balsamea* [L.] Mill.), jack pine (*Pinus banksiana* Lamb.) and black spruce (*Picea mariana* [Mill.] BSP). We also investigated how a commonly used snag degradation classification system relates to TSD and wood density. Sampling was conducted in northwestern Quebec, Canada. For each species, 37 to 65 snags were sampled and TSD was determined using dendrochonology.

A first set of multiple linear regressions showed that bark cover was the only morphological attribute common to models of all species and was the sole predictive variable of TSD in balsam fir. In other species, other predictors of TSD varied. A second set of multiple linear regressions showed that the combination of predictors for wood density was also species-specific and that wood penetrability was a common predictor in all species. Degradation stage appeared as a rough indicator of snag age (i.e. TSD). Average TSD generally increased with degradation stage, but significant overlap in TSD between adjacent stages occurred in all species. The same was true for the relationship between degradation stage and wood density.

This study shows that the degradation classification system used can be helpful when rough estimates are needed. However, species-specific models built according to significant morphological attributes do not represent more time- and resource-consuming field assessments while providing more precise measurements of TSD and wood density.

Key words: Dead wood, decay, dendrochronology, Quebec, trembling aspen, *Populus tremuloides* Michx., balsam fir, *Abies balsamea* (L.) Mill., jack pine, *Pinus banksiana* Lamb., black spruce, *Picea mariana (*Mill.) BSP.

4.3 Introduction

Degradation classification systems of dead wood, i.e. deterioration classifications that are based on external morphological attributes, are used in a wide range of ecology studies in forest ecosystems. As different degradation stages are used by different organisms associated with dead wood, degradation classification has been extensively employed to assess habitat availability and quality (Kruys et al. 1999, Drapeau et al. 2002, Saint-Germain et al. 2007). It is has also been used to characterize forest ecosystems and assess ecosystem integrity (Spies et al. 1988, Rouvinen et al. 2002, Desponts et al. 2004). Dead wood plays important roles in physical and chemical processes such as carbon sequestration and nutrient cycling (Krankina and Harmon 1995, Brais et al. 2006, but see Laiho and Prescott 2004) and represents an important component of the aboveground biomass in disturbed and older forest ecosystems (Harmon et al. 1986). Consequently, degradation classification systems have also been used to assess the contribution of coarse woody debris to the biogeochemical dynamics and carbon balance in forest ecosystems (Means et al. 1992, Krankina and Harmon 1995, Bond-Lamberty et al. 2002, Creed et al. 2004). In many instances, degradation classification systems have been used as tools to roughly reconstruct temporal patterns of past tree mortality or disturbance events retrospectively (Lertzman and Krebs 1991, Groven et al. 2002, Rouvinen and Kouki 2002, Pham et al. 2004). Finally, snag dynamics have been modelled using transition rates between degradation stages based on residence time of snags in each degradation stage (Morrison and Raphael 1993, Kruys et al. 2002, Aakala et al. 2008).

In many instances, degradation classification systems are used to roughly describe the general characteristics of dead trees. On other occasions, they are used as proxies for time since tree death (TSD) or for wood properties. In the latter case, one assumes that degradation stages are correlated to the response variable. In this regard, several studies have explored the relationship between degradation stages and TSD, with correlations ranging from very weak (Mast and Veblen 1994, Daniels et al. 1997) to relatively strong (Huggard 1999, Campbell and Laroque 2007, DeLong et al. 2008). The same suite of conclusions has emerged regarding wood density (Yatskov et al. 2003, Creed et al. 2004, Saint-Germain et al. 2007). The significance of these relationships may be of great importance when conclusions are drawn on that basis.

Degradation classification systems for standing dead trees (snags) are based on a visual assessment that combines several morphological attributes, such as presence of branches, twigs and leaves, bark cover, stem integrity (intact, broken), and wood hardness. In most cases, these classifications are not species-specific and, on some occasions, they have been used across a wide range of ecosystems. For instance, the system developed by Thomas et al. (1979) has been used for coniferous species in the Pacific Northwest region of the United States, but it has since been applied to species from the eastern boreal forest of Canada (e.g., Harper et al. 2005, Taylor and MacLean 2007). This broad use of snag degradation classification systems suggests that all species roughly follow a common degradation pattern, starting from an intact dead tree that gradually loses its leaves, twigs and bark, and which eventually breaks at some point above ground level.

When assigning a snag to a degradation stage in the field based on its external appearance, observers are frequently challenged by the impossibility of selecting a single category for which all criteria are met. For instance, a snag may be broken and its wood may be relatively soft, which indicates an advanced degree of degradation or decomposition (i.e. degree of wood density loss), while it also bears all its bark, which suggests that the snag is not very old. This example suggests that some criteria may be more indicative than others. Relatively few studies have evaluated the relevance of specific criteria to predict TSD or wood density, but those that did found significant differences in the contribution of different morphological attributes (Yatskov et al. 2003, Newberry et al. 2004, Storaunet 2004, Waskiewicz et al. 2007).

In North American boreal forests, numerous degradation classification systems have been used and some relationships have been established between degradation stages and snag age (i.e. time elapsed since its death; Campbell and Laroque 2007, Taylor and MacLean 2007, Aakala et al. 2008), or wood density (Saint-Germain et al. 2007). However, for tree species in this region, the reliability of individual morphological attributes has never been assessed. For the eastern boreal forest, Imbeau and Desrochers (2002) developed a system that they adapted from Bergeron et al. (1997, Table 4.1, Fig. 4.1), which is now in common use (Roberge et Desrochers 2004, Gagné et al. 2007, Aakala et al. 2008, Vaillancourt et al. 2008).

This study examined relationships between external appearance, wood density, and TSD in snags of four of the main boreal species in eastern North America: trembling aspen (*Populus tremuloides* Michx.), balsam fir (*Abies balsamea* [L.] Mill.), jack pine (*Pinus banksiana* Lamb.) and black spruce (*Picea mariana* [Mill.] BSP). The specific objectives were to: 1- investigate what readily observed external morphological attributes are the best predictors of TSD and wood density, 2- assess to what extent Imbeau and Desrochers' degradation classification system was appropriate to the studied species, 3- evaluate the relationship between TSD and degradation stages of Imbeau and Desrochers' (2002) degradation classification system, and 4- examine the relationship between wood density and degradation stages.

4.4 Methods

4.4.1 Study area

Our study was conducted in northwestern Quebec (Canada), in the transition zone between the mixedwood and coniferous boreal forest. The region is part of a broad physiographic unit known as the Northern Clay Belt, which is characterized by flat topography and clay deposits originating from the proglacial lakes Barlow and

Ojibway (Vincent and Hardy 1977). Climate is cold and continental, with a mean annual temperature of 0.7°C and mean annual total precipitation of 889.8 mm (weather station of La Sarre, Environment Canada 2010). Two distinct areas were sampled.

For balsam fir, trembling aspen, and jack pine, sampling was conducted in the Lake Duparquet Research and Teaching Forest (LDRTF; 48°26'-48°29'N, 79°26'-79°18'W), which is located 45 km northwest of Rouyn-Noranda. The research forest is located in the Rouyn-Noranda ecological region, within the balsam fir-white birch (*Betula papyrifera* Marsh.) bioclimatic domain (Robitaille and Saucier 1998), where associations of balsam fir, black spruce, white spruce (*Picea glauca* [Moench] Voss), paper birch, and trembling aspen dominate. The disturbance regime includes recurrent wildfires (Dansereau and Bergeron 1993) and periodic outbreaks (Morin et al. 1993) of spruce budworm (*Choristoneura fumiferana* [Clem.]).

For black spruce, sampling was conducted in coniferous forest 120 km further north (49°25'-49°50'N, 79°18'-78°41'W), in the Lake Matagami Lowland ecological region. This area is within the black spruce–feathermoss (*Pleurozium schreberi* [Brid.] Mitt.) bioclimatic domain (Robitaille and Saucier 1998). The disturbance regime is characterized by large stand-replacing fires (Bergeron et al. 2004), with return intervals long enough for successional paludification processes to take place, organic deposits to accumulate, and low productivity open forests to develop (Simard et al. 2007).

Detailed stand characteristics are provided in Chapter 1, and include tree composition, stand age, past harvesting activities, snag density, species-specific annual mortality, and snag fall rates.

4.4.2 Field methods

Data collection was conducted during the summers of 2004 and 2005. Seventeen stands were selected, based on species composition, surficial material type (glaciolacustrine clay in LDRTF, glaciolacustrine clay overlain by a thick organic layer in black spruce stands), drainage class (mesic sites in LDRTF, subhydric sites in black spruce stands), and age (mature to overmature stands).

In each stand, a 20 m x 20 m plot was established randomly, at least 50 m from any edge (road, cut, different stand). Every snag was identified. These were trees without green foliage that were at least 1.3 m tall, and which had a diameter at breast height (DBH) ≥ 5 cm. Leaning dead trees were considered as snags if their angle from the ground was > 45^o (Harmon and Sexton 1996). To fulfill sampling requirements for some specific attributes (e.g. snags of advanced degradation stages based on their external appearance), additional snags were sampled in the area surrounding the plots. A total of 216 snags were sampled (see Table 4.2 for distribution among species). Characterization of snags included species, DBH (± 0.1 cm), height (± 0.1 m), stem integrity (whether intact or broken), presence of dead leaves, twigs and branches (3 categories: abundant, partial, absent), and bark cover (10% categories). Wood penetrability was also assessed, using a knife that was pushed into the wood in several locations around the bole between 1 and 1.3 m, always by the same observer to limit bias (4 categories: 1- hard wood, blade can not penetrate into the sample; 2- blade can only slightly penetrate the sample [≤ 0.5 cm]; 3- blade penetrates the periphery of the bole, centre hard; 4- soft wood, blade easily penetrates the bole). Mean snag DBH ranged from 12.2 ± 0.5 (SE) cm (black spruce) to 18.6 ± 0.8 cm (balsam fir). Jack pine and trembling aspen were intermediate with average DBH of 14.3 ± 0.8 cm and 16.6 ± 1.0 cm, respectively.

Cross-sections that were ≈ 5 cm thick were taken from all snags. Fragile samples were taped with thread-enforced tape and cut using a fine-toothed bow saw to minimize fragmentation. To optimize the chances of successful crossdating, three cross-sections were taken from each bole when possible: at the base, breast height and near the top (around 3 m from top for intact trees and near the point of breakage for broken trees). This sampling procedure 1- reduced the risk of crossdating failure due to advanced decay, 2- validated year of death with multiple crossdated sections, and 3- increased capture of the last ring produced in stressed trees (Mast and Veblen 1994; V.A. Angers *unpublished data*). For broken trees, if the fallen tree top was reliably identifiable, a cross-section was also taken to maximize crossdating success. In boles with advanced decay, heights at which cross-sections were taken varied, depending on bole periphery preservation to maximize crossdating success.

4.4.3 Tree ring analysis

All cross-sections were dried and sanded until xylem cells were clearly visible. When necessary, hot glue was used to consolidate fragmented samples prior to sanding. Ring width was measured for each cross-section along two radii (one when decay impeded ring visibility elsewhere on the cross-section) using a Velmex micrometer (0.001 mm precision; Velmex incorporated, Bloomfield, New York, USA).

Year of death was considered as the year of the last ring produced. To establish year of death, each individual tree ring series that was generated by all sampled cross-sections was crossdated against master series constructed for balsam fir, jack pine, and trembling aspen from nearby living trees in LDRTF (Chapter 1) and from a master chronology developed for black spruce (Simard et al. 2007). Crossdating was performed using marker years, and verified with COFECHA (Holmes 1983) and TSAP (Rinn 1996) programs, with the latter being used for visually comparing the pattern generated by each tree ring series and the average of the master series. When discrepancies in years of death were obtained for cross-sections belonging to the same dead tree, the most recent year was retained. Of the 216 snags collected in the field, only five could not be successfully crossdated. These were excluded from the analysis because cross-sections were too decayed to perform measurements, cross-sections were too young (not enough rings) for reliable crossdating, or because snags had their periphery eroded and, thus, their outmost rings were possibly missing, impeding an accurate assessment of year of death. TSD was calculated as the difference between year of sampling and year of death.

4.4.4 Wood density analysis

All cross-sections were oven-dried at 60°C and weighed to the nearest 0.01 g until weight was stable for at least 24 hours. Bark was stripped and dry volume was calculated assuming a cylindrical shape:

$$V = \pi \times \left(\frac{d_{\min} + d_{\max}}{4} \right)^2 \times \left(\frac{t_{\min} + t_{\max}}{2} \right)$$

where V (cm^3) is the calculated volume, $d_{\min}$ and $d_{\max}$ (cm) are the minimum and maximum cross-sectional diameters, and $t_{\min}$ and $t_{\max}$ (cm) are the minimum and maximum cross-sectional thicknesses, with d and t being measured to the nearest 1 mm. Wood density (g.cm^{-3}) was calculated as the ratio of dry mass to dry volume.

4.4.5 Data analysis

4.4.5.1 Morphological attribute predictors of TSD and wood density

Several discrete variables (i.e. dead leaves, twigs, branches) lacked observations in some classes in some species. When there were fewer then five observations in a given class, we merged adjacent classes and reconfigured that variable classification system for data analysis (Table 4.2). For bark cover, we used the median of the original classes being merged to designate the resulting class. In all discrete variables, this merging step yielded a two- or three-class system. Classification reconfiguration was done separately for each species. Most discrete data were transformed to a binary form. In cases where observations were almost all concentrated in one class, the variable was excluded from the analysis (i.e. presence of dry leaves in all species, stem integrity in balsam fir, presence of branches in jack pine). In balsam fir, all bark cover classes (10%) were represented and that variable was thus considered to be continuous.

To evaluate residual height in broken snags, we first estimated the original height by regressing DBH against height of unbroken snags and surrounding living trees (n = 25 to 69, depending on species). Using the logarithmic relationships generated from these data (all r^2 were $\geq$ 0.67, data not shown), the percentage of estimated original height (%Height) was computed as the ratio of observed snag height to estimated original height.

For each species, two sets of multiple linear regressions were conducted to examine the ability of these variables to predict a) TSD and b) wood density of snags. Candidate variables that were tested are presented in Table 4.2. When preliminary observations of the data indicated non-linear relationships between variables, the response variable was transformed or a morphological attributes classification was adapted. Forward and mixed stepwise procedures were used and yielded the same models. A variance inflation factor (VIF) was calculated for each predictor to ensure that there was no collinearity between explanatory variables introduced together in models. All resulting VIF values were < 4.0.

4.4.5.2 Linkages between degradation classification system, TSD, and wood density

After assessing all morphological attributes that were observed in the field, snags were assigned to a degradation stage according to Imbeau and Desrochers' classification system (Imbeau and Desrochers 2002, Table 4.1, Fig. 4.1). When different variables suggested assignment to two or more degradation stages, we classified the snag into the median class suggested by all attributes.

To assess to what extent Imbeau and Desrochers' (2002) degradation classification system was appropriate to the studied species, an inconsistency index was calculated for each species as the percentage of snags that could have been placed in more than one degradation stage if each criterion was considered individually. We also calculated the inconsistency index for each degradation stage to examine if some stages were more problematic than others.

As very few observations occurred in degradation stages 7 and 8 (the last snag stages), we merged them. Apart from one trembling aspen snag, this was not due to the impossibility to crossdate snags in an advanced degradation stage because of incomplete ring measurements; rather, this was due to their scarcity in the field (see Discussion).

For each species, the relationship between TSD and degradation stage was tested using a one-way analysis of variance (ANOVA), followed by post hoc Tukey's HSD tests. Relationships between wood density and degradation stage were tested in the same way.

All statistical analyses were done using JMP 7.0 software (SAS Institute Inc.). Prior to all regressions and analyses of variance, assumptions of normality and homoscedasticity were verified and the data were transformed if necessary.

4.5 Results

4.5.1 Morphological attribute predictors of TSD and wood density

To predict TSD, four models corresponding to the four species studied were generated. All models were significant ($p < 0.0001$) and the percentage of variance explained by models varied from 33% to 65%, depending on species (Table 4.3). All models included different groups of morphological attributes which best predicted

TSD (Table 4.4). The number of predictive variables also differed among species: trembling aspen and black spruce models included as many as four variables, whereas balsam fir included only one (Table 4.4). For all models, confidence intervals varied as a function of TSD (Fig. 4.2). In black spruce, the age of the oldest snags (≥ 30 years old) was consistently underestimated.

Bark cover was the only variable common to all species models predicting TSD (Table 4.4). Bark cover alone explained almost 45% of variance in balsam fir (Table 4.3), and no other variable significantly contributed to the model. Balsam fir was the only species for which the whole bark cover gradient was covered. In this case, the relationship between bark cover and TSD was nonlinear (bark cover remained almost entire until about 15 years after death and then declined rapidly), so TSD was square-transformed (i.e. TSD^2). In addition to the models proposed, some shortcuts could be derived from observed bark loss patterns. For example, all snags that still bore at least 90% of their bark had been dead less than 10 years in trembling aspen and less than 15 years in balsam fir. In jack pine, bark cover did not generally decrease below 80% until more than 20 years had elapsed following death.

Stem integrity was included in models for trembling aspen and black spruce (Table 4.4), whereas wood penetrability was included in models for trembling aspen and jack pine. Twig presence was a significant predictor for jack pine and black spruce, whereas %Height (black spruce) and presence of branches (trembling aspen) were included in only one model.

When investigating morphological attributes that best predicted wood density, most models explained a large proportion of variance, ranging from 54% to 64% in jack pine, trembling aspen, and black spruce (Table 4.5). In balsam fir, the model explained a significant but much lower percentage of the variance (17%). As with TSD, species generally featured different combinations and numbers of variables, ranging from one in balsam fir and black spruce to three in jack pine (Table 4.6). In most species, confidence intervals enlarged as wood density decreased (Fig. 4.3).

Wood penetrability was a significant predictor for all species, whereas bark cover was significant for trembling aspen and jack pine, and stem integrity for jack pine only (Table 4.6).

4.5.2 Appropriateness of Imbeau and Desrochers' degradation classification system to the studied species

Application of Imbeau and Desrocher's degradation classification system appeared to be problematic. In most instances, a single snag included characteristics of two or more adjacent classes, placing the onus on the observer to decide the final assignment. The inconsistency index varied from 49% in black spruce to 95% in balsam fir. Trembling aspen and jack pine were in an intermediate position with 60% and 76% of inconsistencies, respectively. Except for balsam fir, the inconsistency index was generally lowest in degradation stage 4 (first snag stage, Figure 4.1), varying between 0% and 19%.

4.5.3 Linkages between degradation classification system, TSD, and wood density

Degradation stage appeared to be a rough indicator of snag age. For each species, analysis of variance showed that significant differences in mean TSD existed among degradation stages ($p \leq 0.0004$ in all species, Fig. 4.4), with average age generally increasing with degradation stages. However, overlap in TSD between adjacent degradation stages occurred in all species, as Tukey's tests indicated that there was no significant difference in average age between adjacent classes on many occasions. Indeed, when grouping degradation stages to create significantly distinct groups, the number of classes decreased. Three grouped degradation stages were significantly distinct in balsam fir (stages 4, 5, 6-7) and jack pine snags (stages 4, 5, 6-8) whereas only two groups were significantly distinct in trembling aspen and black spruce (4-5, 6-8; $p \leq 0.0001$ in all species).

Although trembling aspen exhibited a consistently lower average age in all degradation stages when compared with other species (Fig. 4.4), the difference was not always significant, suggesting that this deciduous species did not progress through degradation stages much more rapidly than did the coniferous species. Among coniferous species, the progression through degradation stages was similar, with no significant distinction in TSD, regardless of the degradation stage considered.

Significant differences in wood density were observed between the extreme stages of degradation within a given species, but the intermediate stages overlapped (Fig. 4.5). As with TSD, grouping degradation stages to create significantly distinct groups also reduced the number of classes. Three grouped degradation stages were significantly distinct in trembling aspen (4, 5-6, 7-8) and balsam fir (stages 4, 5-6, 7) whereas only two groups were significantly distinct in jack pine (4-5, 6-8) and black spruce (4-6, 7-8; $p \leq 0.0003$ in all species). Within a given degradation stage, wood density often varied from species to species, with the species-specific differences lessening with progression through degradation stages.

4.6 Discussion

4.6.1 Morphological attribute predictors of TSD and wood density

To our knowledge, this is the first study that examines what assemblages of individual morphological attributes best predict TSD in snags of species from the eastern boreal forests of North America. Our models clearly show that the combinations of morphological attributes related to TSD of snags differ from one species to another.

Bark cover was, however, a common predictor of TSD for all species and this single criterion was found to be a better predictor than any combination of morphological attributes in balsam fir. Waskiewicz et al. (2007) also found that bark loss was the most useful predictor of age in ponderosa pine (*Pinus ponderosa* Dougl.) snags from Northern Arizona, whereas Newberry et al. (2004) reported that bark-related variables were included among the variables predicting TSD in interior spruce (*P. glauca* x *P. engelmannii* Parry ex Engelm.) and subalpine fir (*Abies lasiocarpa* [Hook.] Nutt.) found in sub-boreal spruce forests in British Columbia.

Bark cover was a good predictor of TSD when compared with other morphological attributes because trees that die of causes unrelated to fire usually enter the snag stage with all their bark intact, and residual bark cover can be estimated regardless of stem integrity or residual height of a snag. This type of relationship is not always as simple with other variables. For instance, the presence of branches and twigs can be misleading if assessed when a snag is broken below crown height (Storaunet 2004). This may be the result of bole breakage that is unrelated to TSD and not because of snag aging.

Presence of branches and presence of twigs were not consistently significant in our models, but one or the other was significant for three species. Examining morphological attributes predicting TSD, Newberry et al. (2004) reported that branch remains (four categories) and fine branch flexibility (three categories) significantly contributed to predicting TSD. Storaunet (2004), using Norway spruce (*P. abies* [L.] Karst) in Norway and DeLong et al. (2008, studying the same species and region as Newberry et al. 2004) found branch order classification (5 classes) to be a better predictor of TSD than bark cover. In our study, branches and twigs were classified into two categories, which may not have been sufficiently refined for these variables to be significant predictors in our models.

Stem integrity and/or %Height were significant predictive variables of TSD in trembling aspen and black spruce only (Table 4.4). Stem integrity appeared to be a straightforward indicator of TSD in trembling aspen: of all snags observed in this species, intact snags were always 10 years old or younger (Chapter 1, Fig. 4.3a).

This is consistent with previous findings suggesting that trembling aspen was resistant to breaking at the base (Chapter 1) and prone to successive breakages along the bole (Chapter 3) in the first years following death.

Stem integrity and %Height act as important criteria in a number of degradation classification systems, including that of Imbeau and Desrochers (Thomas et al. 1979, Cline et al. 1980). However, these variables must be used with caution as they can be misleading. Waskiewicz et al. (2007) incidentally reported that bole breakage may not be related to snag age. Old snags can indeed be classified in an advanced degradation stage based on these criteria as a result of aging and successive breakages through time, but young snags that are broken in the lower part of the stem before death, at the moment of death, or shortly after death may also be classified in the later degradation stages and remain in that category until they finally collapse to the forest floor. This early low breakage pattern did not seem to occur in jack pine and balsam fir. In the case of jack pine, this response is probably due to its high breakage resistance and to the fact that snags seemed to fall by breaking under 1.3 m or uprooting instead of decreasing their height progressively through intermediate breakages (Chapters 1 and 3). In balsam fir, spruce-budworm induced mortality left most balsam fir trees intact (Chapter 1). If other mortality causes were involved, such as breakage in the lower part of the bole induced by wind in trees with mechanical weakness caused by advanced butt rot, as is often the case with balsam fir (Basham 1991), the pattern of early low breakage could be observed.

In this study, the cause of tree death was relatively homogenous within each species (Chapter 1). Relevant criteria for classifying snags found in this study may become irrelevant when the cause of death alters the external appearance of snags. For instance, in this study, jack pine retained most of its bark in the first 20 years after death, with 89% of snags bearing 90% or more of their bark. In fire-killed trees, this variable would become useless and misleading as fire often causes the bark to shed and fall rapidly (Boulanger and Sirois 2006). In a site located about 70 km north of the study area (Chapter 3), only 20% of fire-killed snags still bore 90% or more of their bark seven years after fire (data not shown).

In the only other study that examined predictive morphological attributes of wood density in coarse woody debris (including snags), Yatskov et al. (2003) also found predictors of wood density to change from taxon to taxon among five major taxa from the boreal forest of Russia. As expected, wood penetrability was the common predictive variable of wood density of the four studied species. Of all variables assessed in our study, wood penetrability is the only one that relates to the internal properties of a snag. This variable emerged even though the sampling procedure used only assesses penetrability of the peripheral part of the bole. Wood density can be very heterogeneous within a bole (Creed et al. 2004) and even within a single piece of wood (Boddy 2001); our sampling procedure was not designed to detect inner decay that may occur in many species, whereas the wood density measurement does assess it. In balsam fir, the low degree of variability in wood density as compared to other species contributed to the poor predictive ability of the model. Indeed, the density of almost all of the samples ranged between 0.2 and 0.4 g.cm^{-3} (Chapter 2, Fig. 4.1c). Accordingly, balsam fir shared the narrowest range of wood penetrability classes of all species with black spruce (only 2 classes after merging, Table 4.2) and a great majority of observations were concentrated in wood penetrability class 1-2 (75% of observations, Table 4.2) as a result of a relatively synchronous spruce budworm-related mortality (Chapter 1). Bark cover was the second most represented variable in models and also emerged as an important predictor in the study by Yatskov et al. (2003) for their coniferous species.

4.6.2 Appropriateness of Imbeau and Desrochers' degradation classification system to the studied species

The high inconsistency index in snags classification suggests that assigning a snag to a degradation stage may often be subjective, as it leaves a lot of room for interpretation (Creed et al. 2004, Waskiewicz et al. 2007). This situation also likely means that some criteria may not be appropriate for some species. It is surprising to note that, although initially designed for coniferous species, Imbeau and Desrochers' degradation classification system describes fairly well the degradation of the only deciduous species sampled in this study, trembling aspen. The low inconsistency index found in the first degradation stage in most species is likely due to the relatively low variation in morphological attributes found at this stage.

4.6.3 Linkages between degradation classification system, TSD, and wood density

Regarding relationships between degradation stages and TSD, as well as wood density, our results are generally consistent with other studies. In several degradation classification systems, tree species and regions of the world, most authors have found a rough correspondence between degradation stages and TSD, with snags that were classified in first degradation stages generally tending to have been dead for a shorter period of time than those in more advanced stages (Mast and Veblen 1994, Daniels et al. 1997, Huggard 1999, Mäkinen et al. 2006, Taylor and MacLean 2007, Aakala et al. 2008, DeLong et al. 2008). Good relationships have been reported (Huggard 1999, Campbell and Laroque 2007, DeLong et al. 2008), but the variation in TSD within each category and overlap between categories were commonly so high (Mast and Veblen 1994, Daniels et al. 1997, Huggard 1999, Waskiewicz et al. 2007, Aakala et al. 2008, DeLong et al. 2008) that some authors consider degradation classifications based on external appearance of snags as poor indicators of TSD (Mast and Veblen 1994, Daniels et al. 1997).

In boreal ecosystems, the loss of wood density in fallen boles through time has received extensive attention (Krankina and Harmon 1995, Naesset 1999, Yatskov et al. 2003, Mäkinen et al. 2006). Snag wood decomposition, however, has been less frequently studied, especially in the eastern boreal forest of North America (Boulanger and Sirois 2006, Saint-Germain et al. 2007). This paucity of data is mostly because standing dead trees are in a transitory stage and generally decompose far more slowly than boles that are in contact with the forest floor (Krankina and Harmon 1995, Yatskov et al. 2003, Boulanger and Sirois 2006).

Most studies regarding decomposition of wood along a degradation gradient have been performed on logs (Bond-Lamberty et al. 2002, Creed et al. 2004, see Yatskov et al. 2003 for a review). Different patterns that are influenced by tree species morphology and physiology emerge from these studies, from linear wood density loss to differential decomposition rates that depend on degradation stages (Yatskov et al. 2003). In our study as well as in the two reported studies that examined the relationship between wood density and degradation stages in snags, results are generally similar to those regarding TSD: Degradation stages of snags provide a rough approximation of wood density but so much overlap exists between degradation stages (Mäkinen et al. 2006, Saint-Germain et al. 2007) that classification systems are often reduced to two or three distinct classes, which may be of little help in the end. This is in large part due to the fact that a degradation classification represents a discrete tool to assess a continuous phenomenon, i.e. density loss (Creed et al. 2004), and that the range of wood densities in snags is much narrower than in logs.

In all species, relatively few snags in degradation stages 7 and 8 were observed. Many dead trees fall to the forest floor before they reach these stages, as the mechanical stability of snags usually decreases with the progression of time and snags are thus more susceptible to falling (Aakala et al. 2008). Also, in our case, stand history might explain their scarcity in jack pine. Indeed, jack pine stands were relatively young (≈ 80 years, Chapter 1) and, as jack pine is the most fall-resistant snag species of those studied (Chapter 1), few snags were old enough to have developed characteristics of later degradation stages. The same rationale applies when considering the very low representation of jack pine snags with wood penetrability class 4 (Table 4.2).

Snags of boreal deciduous species are generally known to deteriorate faster than coniferous species. This has been documented with respect to degradation rates (i.e. the rates at which snags fall to the forest floor, Mäkinen et al. 2006) and wood decomposition rates (i.e. the rates at which snag wood loses its density; Alban and Pastor 1993, Yatskov et al. 2003, Mäkinen et al. 2006). Mäkinen et al. (2006) also reported lower average TSD of silver birch (Betula pendula Roth.) snags when compared with Scots pine (Pinus sylvestris L.) and Norway spruce (P. abies) snags in each degradation stage, but did not present comparison tests. Examining the same species as in the present study, Angers et al. (Chapters 1 and 2) found that trembling aspen snags fall and decompose more rapidly than the other three conifer species. Differences in progression rates through the degradation stages between species or groups of species were not that straightforward in the present study. As the degradation classification system that we used integrates both degradation and, indirectly, wood decomposition through penetrability class, one would expect the system to adequately expose differences between species. Nevertheless, trembling aspen did not progress faster through degradation classes with respect to TSD or density loss. This might be due to the limitation of the degradation system to express this process, but also to the high variability in TSD and wood density as well as the low number of observations in certain classes, which may have prevented clear differences from emerging.

4.7 Conclusion

Results from this study clearly showed that the degradation classification of Imbeau and Desrochers (2002), which is consistent with many other systems, is limited in terms of its power to predict TSD and wood density. Assignment to a single degradation stage that was based on several criteria appeared to be problematic and only two to three classes were distinct and these varied among species. These problems are of minor importance when rough approximations are required, but this classification tool rapidly becomes ineffective when more precise estimations are needed, as often occurs for modelling purposes. Species-specific models built according to significant morphological attributes do not require more time- and resource-consuming field assessments and provides continuous and as well as more precise measurements of TSD and wood density.

The inclusion of multiple species in this study enabled us to highlight the differences in the response of each species through out their degradation. Although common morphological attributes were significant predictors for the two sets of models that we developed, the combinations of predictive variables and the rates at which these attributes changed were species-specific. As discussed in Chapters 1, 2, and 3 for degradation pathways and mineralization rates, our results suggest that each species exhibits an individualistic response to the environment during its lifetime (Gleason 1926, Whittaker 1957) and after death, as each decomposes. In this regard, the development of species-specific decay classification systems or predictive models that combine significantly related predictive variables would be beneficial to all studies where a rapid and relatively accurate approximation of TSD or residual density in snags is required.

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4.9 References

Aakala T., Kuuluvainen T., Gauthier S. and L. De Grandpré. 2008. Standing dead trees and their decay-class dynamics in the northeastern boreal old-growth forests of Quebec. Forest Ecology and Management 255: 410-420.

Alban D.H. and J. Pastor. 1993. Decomposition of aspen, spruce, and pine boles on two sites in Minnesota. Canadian Journal of Forest Research 23: 1744-1749.

Basham J.T. 1991. Stem decay in living trees in Ontario's forests: a user's compendium and guide. Information report O-X-408. Forestry Canada, Great Lakes Forestry Centre, Sault Ste- Marie, ON.

Bergeron D., Darveau M., Desrochers A. and J.-P.L. Savard. 1997. Impact de l'abondance des chicots sur les communautés aviaires et la sauvagine des forêts conifériennes et feuillues du Québec méridional. Série de rapports techniques no 271F. Service canadien de la faune, Environnement Canada, Ste-Foy, Qc.

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

Bescond H. 2002. Reconstitution de l'historique de l'exploitation forestière sur le territoire de la forêt d'enseignement et de recherche du lac Duparquet au cours du 20ème siècle et influence sur l'évolution des peuplements forestiers. Mémoire de MSc en biologie, Université du Québec à Montréal.

Boddy L. 2001. Fungal community ecology and wood decomposition processes in angiosperms: from standing tree to complete decay of coarse woody debris. Ecological Bulletins 49: 43-56.

Bond-Lamberty B., Wang C., and S.T. Gower. 2002. Annual carbon flux from woody debris for a boreal black spruce fire chronosequence. Journal of Geophysical Research – Atmosphere 108, art. no. 8220.

Boulanger Y. and L. Sirois. 2006. Postfire dynamics of black spruce coarse woody debris in northern boreal forest of Quebec. Canadian Journal of Forest Research 36: 1770-1780.

Brais S., Paré D. and C. Lierman. 2006. Tree bole mineralization rates of four species of the Canadian eastern boreal forest: implications for nutrient dynamics following stand-replacing disturbances. Canadian Journal of Forest Research 36: 2331-2340.

Campbell L.J. and C.P. Laroque. 2007. Decay progression and classification in two old-growth forests in Atlantic Canada. Forest Ecology and Management 238: 293-301.

Cline S.P., Berg A.B. and H.M. Wight. 1980. Snag characteristics and dynamics in Douglas-fir forests, western Oregon. Journal of Wildlife Management 44: 773-786.

Creed I.F., Webster K.L. and D.L. Morrison. 2004. A comparison of techniques for measuring density and concentrations of carbon and nitrogen in coarse woody debris at different stages of decay. Canadian Journal of Forest Research 34: 744-753.

Daniels L.D., Dobry J., Klinka K. and M.C. Feller. 1997. Determining year of death of logs and snags of *Thuja plicata* in southwestern coastal British Colombia. Canadian Journal of Forest Research 27: 1132-1141.

Dansereau P.-R. and Y. Bergeron. 1993. Fire history in the southern boreal forest of northwestern Quebec. Canadian Journal of Forest Research 23: 25-32.

DeLong S.C., Sutherland G.D., Daniels L.D., Heemskerk B.H. and K.O. Storaunet. 2008. Temporal dynamics of snags and development of snag habitats in wet spruce-fir stands in east-central British Columbia. Forest Ecology and Management 255: 3613-3620.

Desponts M., Brunet G., Bélanger L. and M. Bouchard. 2004. The eastern boreal old-growth balsam fir forest: a distinct ecosystem. Canadian Journal of Botany 82: 830-849.

Drapeau P., Nappi A., Giroux J.-F., Leduc A. and J.-P. Savard. 2002. Distribution patterns of birds associated with snags in natural and managed eastern boreal forests. pp. 193–205 *In:* Laudenslayer W.F., Shea P.J., Valentine B.E., Weatherspoon C.P. and T.E. Lisle (Technical Coordinators). Proceedings of the Symposium on the Ecology and Management of Dead Wood in Western forests. USDA Forest Service, Pacific Southwest Research Station General Technical Report PSW-GTR 181, Albany, CA.

Environment Canada 2010. National Climate Data and Information Archive. Available at www.climate.weatheroffice.gc.ca/climate_normals/results_e.html, accessed 8 November 2010 [Verified 8 November 2010].

Gagné C., Imbeau L. and P. Drapeau. 2007. Anthropogenic edges: Their influence in the American three-toed woodpecker (*Picoides dorsalis*) foraging behaviours in managed boreal forests of Quebec. Forest Ecology and Management 252: 191-200.

Gleason H.A. 1926. The individualistic concept of the plant association. Bulletin of the Torrey Botanical Club 53: 1-20.

Groven R., Rolstad J., Storaunet K.O. and E. Rolstad. 2002. Using forest stand reconstructions to assess the role of structural continuity for late-successional species. Forest Ecology and Management 164: 39-55.

Harmon M.E., Franklin J.F., Swanson F.J., Sollins P., Gregory S.V., Lattin J.D., Anderson N.H., Cline S.P., Aumen N.G., Sedell J.R., Lienkaemper G.W., Cromack K.Jr. and K.W. Cummins. 1986. Ecology of coarse woody debris in temperate ecosystems. Advances in Ecological Research 15: 133-302.

Harmon M.E. and J. Sexton. 1996. Guidelines for measurements of woody detritus in forest ecosystems. U.S. Long Term Ecological Research Network Office, University of Washington, Seattle, WA. LTER Publ. No. 20.

Harper K.A., Bergeron Y., Drapeau P., Gauthier S., and L. De Grandpré. 2005. Structural development following fire in black spruce boreal forest. Forest Ecology and Management 206: 293-306.

Holmes R.L. 1983. Computer-assisted quality control in tree-ring dating and measurement. Tree-ring Bulletin 43: 69-78.

Huggard D.J. 1999. Static life-table analysis of fall rates of subalpine fir snags. Ecological Applications 9: 1009-1016.

Imbeau L. and A. Desrochers. 2002. Foraging ecology and use of drumming trees by three-toed woodpeckers. Journal of Wildlife Management 66: 222-231.

Krankina O.N. and M.E. Harmon. 1995. Dynamics of the dead wood carbon pool in northwestern Russian boreal forests. Water, Air, and Soil Pollution 82: 227-238.

Kruys N. and B.G. Jonsson. 1999. Fine woody debris is important for species richness on logs in managed boreal spruce forests of northern Sweden. Canadian Journal of Forest Research 29: 1295-1299.

Kruys N., Jonsson B.G. and G. Ståhl. 2002. A stage-based matrix model for decay-class dynamics of woody debris. Ecological Applications 12: 773-781.

Laiho R. and C.E. Prescott. 2004. Decay and nutrient dynamics of coarse woody debris in northern coniferous forests: A synthesis. Canadian Journal of Forest Research 34: 763-777.

Lecomte N., Simard M. and Y. Bergeron. 2006. Effects of fire severity and initial tree composition on stand structural development in the coniferous boreal forest of northwestern Québec, Canada. Ecoscience 13: 152-163.

Lertzman K.P. and C.J. Krebs. 1991. Gap-phase structure of a subalpine old-growth forest. Canadian Journal of Forest Research 21: 1730-1741.

Mast J.N. and T.T. Veblen. 1994. A dendrochronological method of studying tree mortality patterns. Physical Geography 15: 529-542.

Means J.E., MacMillan P.C. and K.Jr. Cromack. 1992. Biomass and nutrient content of Douglas-fir logs and other detrital pools in an old-growth forest, Oregon, U.S.A. Canadian Journal of Forest Research 22: 1536-1546.

Morin H., Laprise D., and Y. Bergeron. 1993. Chronology of spruce budworm outbreaks near Lake Duparquet, Abitibi region, Quebec. Canadian Journal of Forest Research 23: 1497-1506.

Mäkinen H., Hynynen J.S.J. and R. Sievänen. 2006. Predicting the decomposition of Scots pine, Norway spruce, and birch stems in Finland. Ecological Applications 16: 1865-1879.

Morrison M.L. and M.G. Raphael. 1993. Modeling the dynamics of snags. Ecological Applications 3: 322-330.

Naesset, E. 1999. Relationship between relative wood density of *Picea abies* logs and simple classification systems of decayed coarse woody debris. Scandinavian Journal of Forest Research 14: 454-461.

Newberry J.E., Lewis K.J. and M.B. Walters. 2004. Estimating time since death of *Picea glauca* x *P. engelmannii* and *Abies lasiocarpa* in wet cool sub-boreal spruce forest in east-central British Columbia. Canadian Journal of Forest Research 34: 931-938.

Pham A.T., De Grandpré L., Gauthier S. and Y. Bergeron. 2004. Gap dynamics and replacement patterns in gaps of the northeastern forest of Quebec. Canadian Journal of Forest Research 34: 353-364.

Rinn, F. 1996. TSAP (Time series Analysis and Presentation) Version 3.0. Rinntech, Heidelberg, Germany.

Roberge J.M. and A. Desrochers. 2004. Comparaison des caractéristiques des gros chicots entre une sapinière primitive et une sapinière aménagée sur la péninsule gaspésienne, Québec. Canadian Journal of Forest Research 34: 1-5.

Robitaille A. and J.-P. Saucier. 1998. Paysages régionaux du Québec méridional. Les publications du Québec, Ste-Foy, Qc.

Rouvinen S. and J. Kouki. 2002. Spatiotemporal availability of dead wood in protected old-growth forests: A case study from boreal forests in eastern Finland. Scandinavian Journal of Forest Research 17: 317-329.

Rouvinen S., Kuuluvainen T. and L. Karjalainen. 2002. Coarse woody debris in old *Pinus sylvestris* dominated forests along a geographic and human impact gradient in boreal Fennoscandia. Canadian Journal of Forest Research 32: 2184-2200.

Saint-Germain M., Drapeau P. and C.M. Buddle. 2007. Host-use patterns of saproxylic phloeophagous and xylophagous Coleoptera adults and larvae along the decay gradient in standing dead black spruce and aspen. Ecography 30: 737-748.

SAS Institute. 2002. Version 9.1. SAS Institute Inc., Cary, NC.

Simard M., Lecomte N., Bergeron Y., Bernier P.-Y. and D. Paré. 2007. Forest productivity decline caused by successional paludification of boreal soils. Ecological Applications 17: 1619-1637.

Spies T.A., Franklin J.F. and T.B. Thomas. 1988. Coarse woody debris in Douglas-fir forests of western Oregon and Washington. Ecology 69: 1689-1702.

Storaunet K.O. 2004. Models to predict time since death of *Picea abies* snags. Scandinavian Journal of Forest Research 19: 250-260.

Taylor S.L. and D.A. MacLean. 2007. Dead wood dynamics in declining balsam fir and spruce stands in New Brunswick, Canada. Canadian Journal of Forest Research 37: 750-762.

Thomas J.W., Anderson R.G., Maser C. and E.L. Bull. 1979. Snags. pp. 60-77 *In:* J.W. Thomas (Ed.). Wildlife habitats in managed forests: the Blue Mountains of Oregon and Washington. Agriculture Handbook 553, USDA Forest Service, Washington, DC.

Vaillancourt M.-A., Drapeau P., Gauthier S. and M. Robert. 2008. Availability of standing trees for large cavity-nesting birds in the eastern boreal forest of Québec, Canada. Forest Ecology and Management 255: 2272-2285.

Vincent J.S. and L. Hardy. 1977. L'évolution et l'extinction des lacs glaciaires Barlow et Ojibway en territoire québécois. Géographie physique et Quaternaire 31: 357-372.

Waskiewicz J.D., Fulé P.Z. and P. Beier. 2007. Comparing classification systems for Ponderosa pine snags in Northern Arizona. Western Journal of Applied Forestry 22: 233-240.

Whittaker R.H. 1957. Recent evolution of ecological concepts in relation to the eastern forests of North America. American Journal of Botany 44: 197-206.

Yatskov M., Harmon M.E. and O.N. Krankina. 2003. A chronosequence of wood decomposition in the boreal forests of Russia. Canadian Journal of Forest Research 33: 1211-1226.

Table 4.1. Imbeau and Desrochers' decay classification system for snags (Imbeau and Desrochers 2002, adapted from Bergeron et al. 1997). Classes 1 to 3 refer to living trees and are not shown.

Snag decay class	**Criteria**
4	Recently dead, hard wood, firm bark cover, 0% green foliage, small twigs still remaining
5	Hard wood, no dead foliage, no small twigs
6	Hard wood, loose bark cover, broken top, height still more than 50% of what is observed on trees with the same DBH
7	Soft, decomposed wood, broken top with height less than 50% of what is observed on trees with the same DBH
8	Height < 2 m

Table 4.2. Synthesis of candidate morphological attributes tested in models predicting time since death and wood density, together with discrete variable reconfiguration.

Species	Morphological attributes	Number of classes	New classes	*N*
Trembling aspen (*n* = 52)				
	Stem integrity	2	Intact, broken	19, 33
	Wood penetrability	3	1, 2, 3-4	17, 23, 12
	Bark cover	3	50%*, 90%, 100%	7, 6, 39
	Branches	2	Absent, partial or abundant	22, 30
	Twigs	2	Absent, partial or abundant	34, 18
	%Height	Continuous	-	52
Balsam fir (*n* = 57)				
	Wood penetrability	2	1-2, 3-4	46, 11
	Bark cover	Continuous	-	57
	Branches	2	Partial, abundant	8, 49
	Twigs	2	Absent or partial, abundant	26, 31
	%Height	Continuous	-	57
Jack pine (*n* = 37)				
	Stem integrity	2	Intact, broken	32, 5
	Wood penetrability	3	1, 2, 3-4	15, 15, 7
	Bark cover	3	45%*, 90%, 100%	10, 13, 14
	Twigs	2	Absent or partial, abundant	7, 30
	%Height	Continuous	-	37
Black spruce (*n* = 65)				
	Stem integrity	2	Intact, broken	20, 45
	Wood penetrability[†]	3	1, 2, 3-4	21, 26, 18
	Wood penetrability[‡]	2	1-2, 3-4	47, 18
	Bark cover	3	50%*, 90%, 100%	8, 14, 43
	Branches	2	Absent or partial, abundant	11, 54
	Twigs	2	Absent or partial, abundant	31, 34
	%Height	Continuous	-	65

*Based on the median of the original classes being merged

[†] Used in modelling of best predictors of TSD.

[‡] Used in modelling of best predictors of wood density. Classes 1 and 2 were merged because wood density of both classes was so similar that no transformation could linearise relationship between wood density and degradation classes.

Table 4.3. Summary of multiple linear regression statistics predicting time since death in four boreal tree species.

	Trembling aspen	**Balsam fir**	**Jack pine**	**Black spruce**
n	52	57	37	65
F-ratio	12.4	45.6	23.3	8.8
p	< 0.0001	< 0.0001	< 0.0001	< 0.0001
R^2 adj.	0.528	0.443	0.650	0.329

Table 4.4. Multiple linear regression results predicting time since death (TSD) in four boreal tree species.

Morphological attributes	**Coefficient**	**SE**	***t*-Value**	***p***
Trembling aspen				
Intercept	20.679	0.806	6.00	< 0.0001
Stem integrity	-8.218	0.437	-4.40	< 0.0001
Wood penetrability1	-6.292	0.419	-3.51	0.0010
Wood penetrability2	-4.300	0.375	-2.68	0.0102
Branches	5.283	0.388	3.18	0.0026
Bark cover	-0.086	0.009	-2.32	0.0247
Balsam fir				
Intercept	602.926	0.263	15.59	< 0.0001
Bark cover*	-4.096	0.004	-6.75	< 0.0001
Jack pine				
Intercept	40.409	0.633	11.96	< 0.0001
Wood penetrability1	-6.627	0.347	-3.58	0.0011
Twigs	-9.693	0.468	-3.88	0.0005
Bark cover	-0.152	0.008	-3.64	0.0009
Black spruce				
Intercept	35.707	7.425	4.81	< 0.0001
%Height	0.156	0.075	2.08	0.0418
Stem integrity	-10.484	4.273	-2.45	0.0171
Twigs	-11.226	3.388	-3.31	0.0016
Bark cover	-0.212	0.078	-2.71	0.0089

* TSD was square-transformed to fit a linear relationship with bark cover.

Table 4.5. Summary of multiple linear regression statistics predicting wood density in four boreal tree species.

	Trembling aspen	**Balsam fir**	**Jack pine**	**Black spruce**
n	52	57	37	64*
F-ratio	31.03	12.38	15.07	115,22
p	< 0.0001	0.0009	< 0.0001	< 0.0001
R^2 adj.	0.638	0.169	0.540	0.644

*One observation was excluded from the analysis because of erroneous wood density.

Table 4.6. Multiple linear regression results predicting wood density in four boreal tree species.

Morphological attributes	**Coefficient**	**SE**	***t*-Value**	***p***
Trembling aspen				
Intercept	0.228	0.046	4.96	< 0.0001
Wood penetrability1	0.106	0.019	5.58	< 0.0001
Wood penetrability3-4	-0.079	0.020	-3.85	0.0003
Bark cover	0.001	0.0005	2.13	0.0385
Balsam fir				
Intercept	0.312	0.007	46.69	< 0.0001
Wood penetrability	-0.053	0.015	-3.52	0.0009
Jack pine				
Intercept	0.213	0.038	5.56	< 0.0001
Stem integrity	0.107	0.027	3.90	0.0005
Wood penetrability1	0.052	0.019	2.74	0.0099
Bark cover	0.001	0.0004	2.95	0.0058
Black spruce				
Intercept	0.362	0.015	24.47	< 0.0001
Wood penetrability	0.187	0.017	10.73	< 0.0001

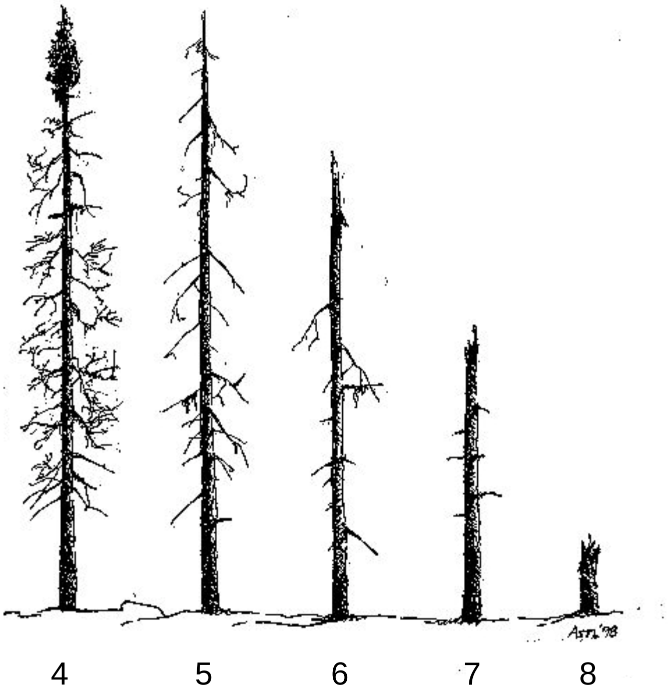


Figure 4.1. Visual representation of Imbeau and Desrochers' decay classification system for snags (Imbeau and Desrochers 2002, adapted from Bergeron et al. 1997). Classes 1 to 3 refer to living trees and are not shown. Reproduced with permission of the authors and The Journal of Wildlife Management, The Wildlife Society, Allen Press Publishing Services.

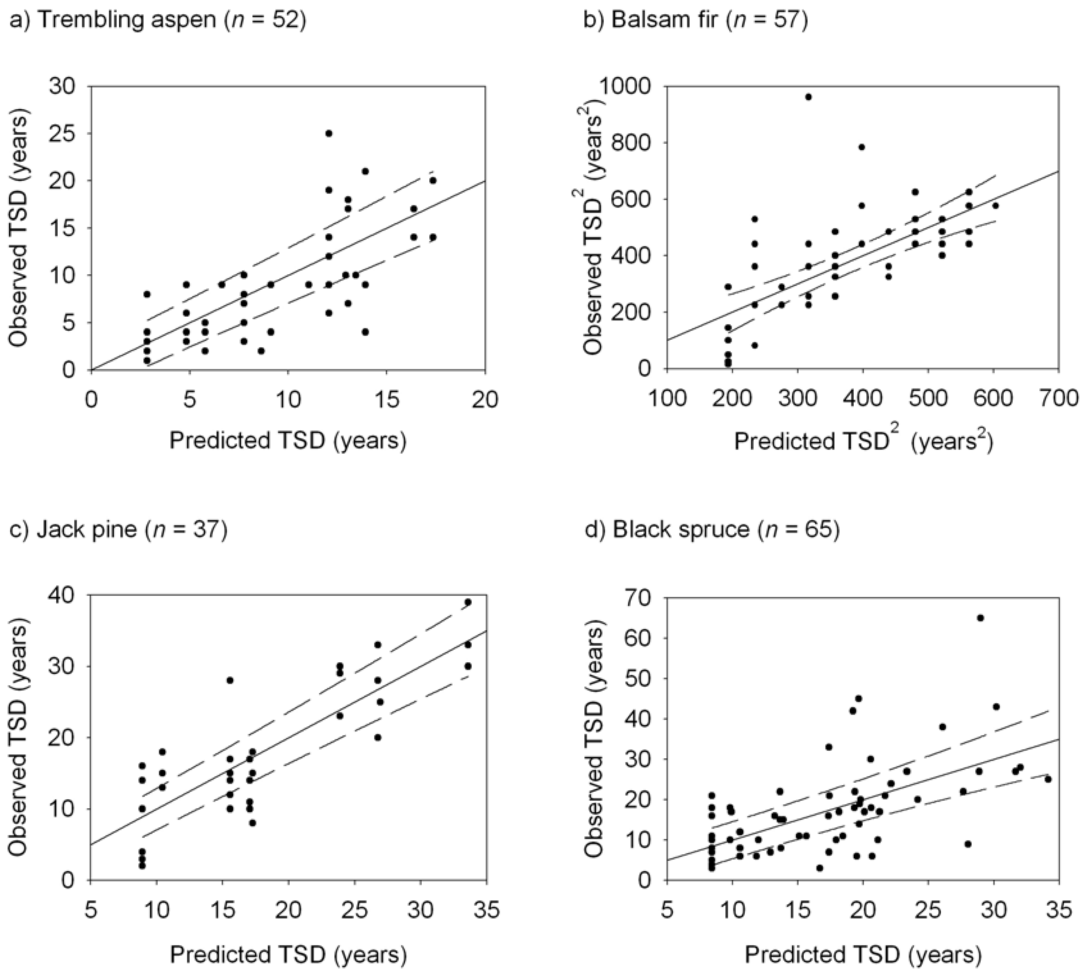
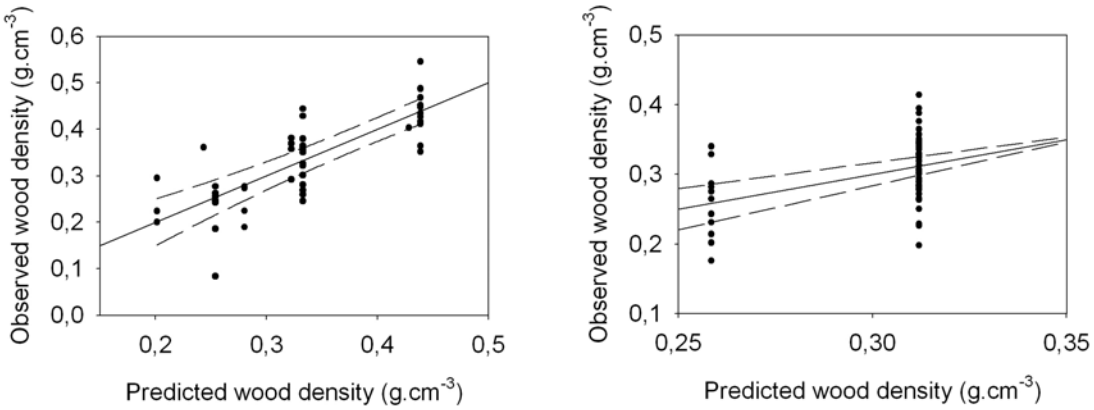


Figure 4.2. Regression between observed and predicted time since death (TSD, full line) and 95% confidence bands (dashed lines) in four boreal tree species.

a) Trembling aspen (*n* = 52) b) Balsam fir (*n* = 57)



c) Jack pine (*n* = 37) d) Black spruce (*n* = 64)

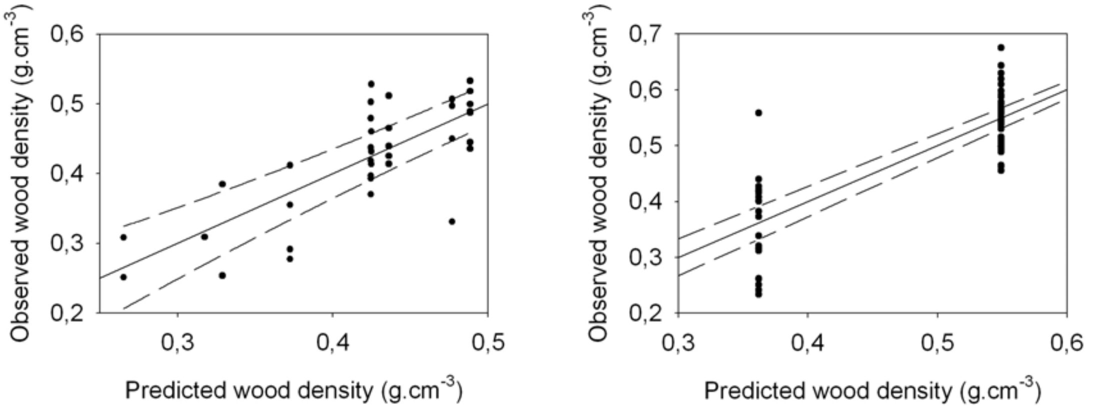


Figure 4.3. Regression between observed and predicted wood density (full line) and 95% confidence bands (dashed lines) in four boreal tree species. One observation was excluded from the analysis in black spruce (erroneous wood density, *n* = 64).

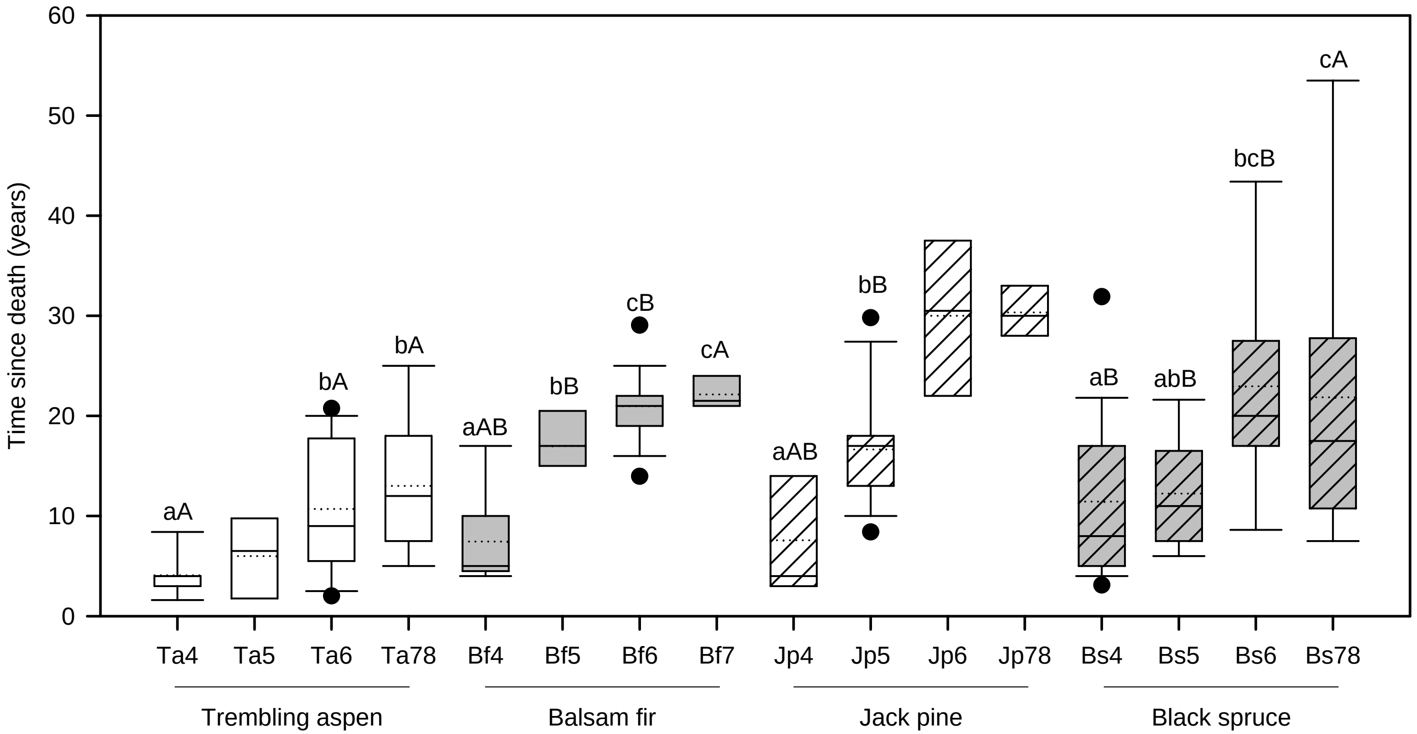


Figure 4.4. Box plots showing time since death according to degradation stages for four boreal tree species. Boundaries of the box indicate the 25th and 75th percentiles, the full line within the box marks the median, the dotted line within the box marks the mean, the error bars indicate 90th and 10th percentiles and the dots indicate 5th and 95th percentiles. Different lower-case letters indicate significantly different values among degradation classes within a given species while different upper-case letters indicate significantly different values among species within a given degradation class, following ANOVA and Tukey's HSD post-hoc tests ($p < 0.05$). When n included fewer than four observations, no means comparisons were conducted. Decay classes 7 and 8 were merged because of too few observations. There were no snags in degradation class 8 for balsam fir.

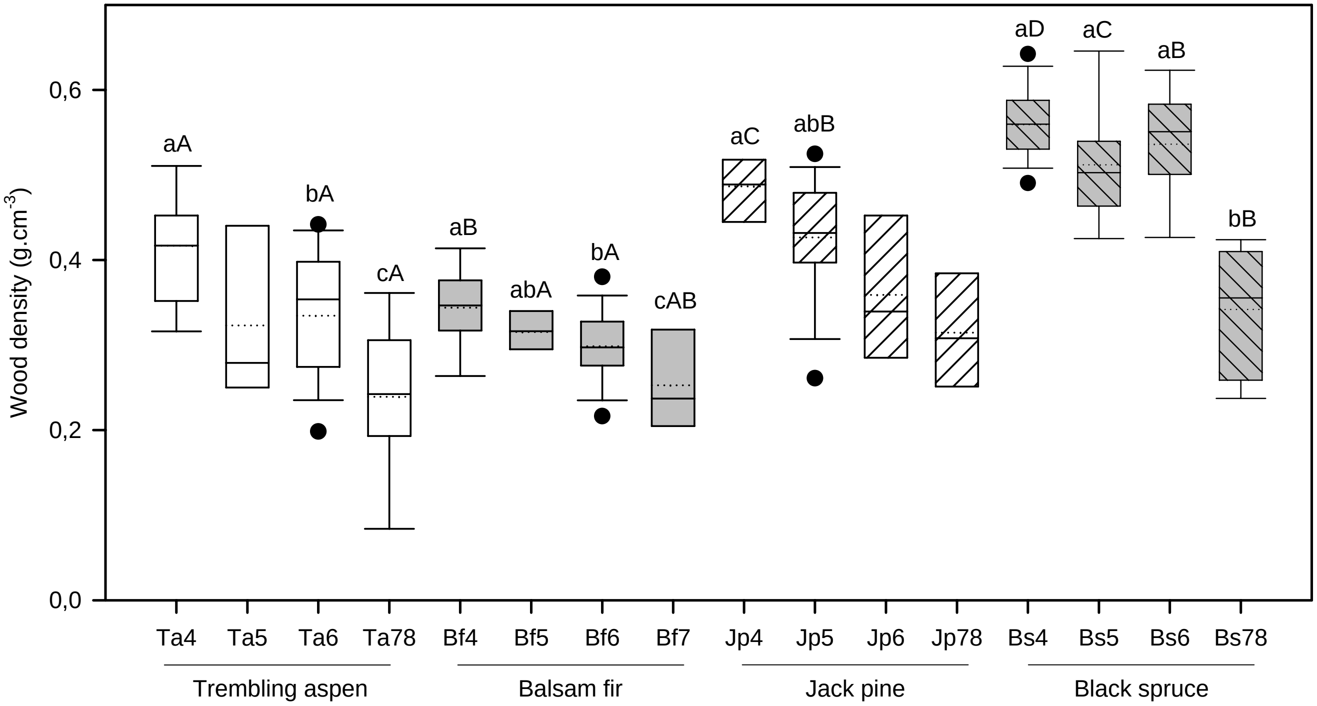


Figure 4.5. Box plots showing wood density according to degradation stages for four boreal tree species. Boundaries of the box indicate the 25th and 75th percentiles, the full line within the box marks the median, the dotted line within the box marks the mean, the error bars indicate 90th and 10th percentiles and the dots indicate 5th and 95th percentiles. Different lower-case letters indicate significantly different values among degradation classes within a given species while different upper-case letters indicate significantly different values among species within a given degradation class following ANOVA and Tukey's HSD post-hoc tests ($p < 0.05$). When n included fewer than four observations, no means comparisons were conducted. One observation was excluded from the analysis (erroneous wood density, $n = 64$ in black spruce). Degradation classes 7 and 8 were merged because of too few observations. There were no snags in degradation class 8 for balsam fir.

CONCLUSION GÉNÉRALE

Le bois mort constitue une composante clé des écosystèmes forestiers. Afin de bien comprendre les processus écologiques liés au bois mort, il est nécessaire de connaître les patrons de dégradation et de décomposition qui le caractérisent et les mécanismes sous-jacents. Or, pour la forêt boréale de l’est de l’Amérique du Nord, plusieurs lacunes restaient à combler en ce sens. Cette étude visait donc à documenter la dynamique des arbres morts sur pied, en termes de dégradation et de décomposition, et les facteurs qui l’influencent.

La première partie de cette conclusion consiste en un retour sur les principaux résultats obtenus dans cette thèse pour établir des liens entre les chapitres. Je propose ensuite quelques perspectives de recherche sur les enjeux relatifs au bois mort.

Retour sur les principaux résultats

Mortalité des arbres et patrons de recrutement du bois mort

Le recrutement en bois mort est directement lié à la mortalité des arbres et aux processus qui y mènent, notamment en regard des perturbations naturelles. En forêt boréale, on distingue deux stades évolutifs où de forts taux de recrutement sont observés. Lors de l’initiation des peuplements, suite à une perturbation naturelle sévère, le recrutement est massif et relativement synchronisé dans le temps. Au stade suranné, alors que le temps écoulé depuis la dernière perturbation dépasse l’espérance de vie des individus des espèces qui formaient la première cohorte, les perturbations secondaires, comme les épidémies légères ou les chablis partiels, constituent les principales sources de mortalité.

La thèse a entre autres porté sur ces deux stades évolutifs. La réponse des arbres morts à une perturbation sévère, le feu, est présentée au chapitre 3 tandis que la dynamique du bois mort dans des forêts arrivées au stade suranné ainsi qu'à d'autres stades évolutifs est abordée aux chapitres 1 et 2.

Mortalité et recrutement suite au feu

Les résultats du chapitre 3 relatifs à la mortalité décalée des tiges après feu représentent une contribution particulièrement importante, tant du point de vue de l'écologie des feux que de celui de la dynamique du bois mort. En effet, ils remettent en cause la perception répandue selon laquelle les tiges qui survivent à des feux de sévérité légère ou modérée persistent généralement dans les années qui suivent. Nos résultats suggèrent en effet que cette classification initiale sous-évalue grandement l'impact réel du feu à moyen terme puisque lorsque l'on considère la mortalité qui a cours dans les quelques années qui suivent le feu, on arrive à une classification bien différente, avec des taux de mortalité beaucoup plus élevés. Par exemple, dans les feux classés comme étant de sévérité modérée, la survie a connu une baisse variant de 44% à 55% selon les quadrats sur une période de cinq ans. Si la classification avait eu lieu cinq ans après feu, ces peuplements auraient été classés comme sévèrement brûlés, le pourcentage d'arbres toujours vivants oscillant entre 6% et 11%. Des conclusions similaires existent dans la littérature pour les régions du centre et du nord-ouest des États-Unis (Brown et DeByle 1987, Ryan *et al.* 1988, Harrington 1993, Keyser *et al.* 2006), mais à notre connaissance, le chapitre 3 constitue la première étude présentant une mesure quantitative et détaillée à long terme de la mortalité après feu en forêt boréale qui documente une mortalité décalée dans le temps chez ces écosystèmes. Qui plus est, l'ampleur du dispositif à l'étude (neuf traitements, plus de 2000 tiges) et la durée du suivi (10 ans) en font l'étude la mieux documentée sur le sujet.

Par rapport aux feux où la mortalité est sévère, le décalage de la mortalité dans le temps et le recrutement de bois mort que j'ai observé dans les feux légers et modérés assure une disponibilité de bois récemment mort dans les années qui suivent le feu. Cette situation présente de nombreuses conséquences.

D’une part, cette diversité de substrat permet la présence simultanée d’organismes associés à des classes de dégradation spécifiques (Nappi 2009) ainsi que la persistance prolongée d’espèces inféodées aux arbres récemment morts, notamment des insectes saproxyliques et des oiseaux prédateurs de ces insectes (Nappi *et al.* 2010). Ensuite, dans les écosystèmes où les arbres morts constituent un substrat préférentiel pour l’établissement et le développement de semis, la mortalité décalée et la chute de chicots étalée dans le temps peuvent aussi influencer les patrons de régénération (Harmon *et al.* 1986).

Finalement, comme le bois mort représente une importante source de carbone, les patrons de mortalité et de dégradation influencent grandement les bilans de carbone.

La mortalité décalée dans le temps représente en effet de plus grandes quantités de carbone émises que ce qui est estimé tout de suite après feu et influence le patron temporel de ces émissions. De plus, comme la décomposition du bois mort est plus rapide au sol que chez les chicots (Harmon *et al.* 1986, Boulanger and Sirois 2006, Yatskov *et al.* 2003), la variabilité dans la persistance des chicots sur pied peut influencer le bilan de carbone (Bond-Lamberty and Gower 2008) et peut même faire passer le statut d’un peuplement de source à puits de carbone (Bond-Lamberty *et al.* 2004).

D’autre part, comme la mortalité a semblé se stabiliser dans les dernières années de suivi, on suppose que les arbres qui ont survécu aux dix premières saisons de croissance resteront généralement vivants à moyen terme et mourront de causes autres que le feu. Ces arbres contribueront ainsi à maintenir un certain couvert forestier et une diversité dans la structure du peuplement. À moyen ou long terme, ces arbres survivants contribueront également au recrutement en bois mort et permettront la présence de bois mort frais alors que celui généré lors du feu sera dans un état de dégradation et de décomposition plus avancé.

Mortalité et recrutement liés à d'autres causes

Au chapitre 1, des patrons de mortalité variaient en fonction des stades évolutifs des peuplements étudiés et des perturbations passées. Les peuplements de pin gris et d'épinette noire ont présenté un recrutement relativement constant pendant la période à l'étude bien que les causes de mortalité aient différé. Dans le cas du pin gris, un peu plus de 80 ans s'étaient écoulés depuis le dernier feu et la mortalité était vraisemblablement due à l'auto-éclaircie des tiges. Dans le cas de l'épinette noire, les sites étant tous âgés de plus de 165 ans, la mortalité était vraisemblablement due à la sénescence, bien que le passage de la tordeuse des bourgeons de l'épinette ait possiblement favorisé la mortalité. Dans le cas du peuplier faux-tremble, deux causes de mortalité semblent avoir eu cours pendant la période à l'étude. L'auto-éclaircie est probablement responsable de la constance de la mortalité, alors que l'épidémie de livrée des forêts (*Malacosoma disstria* Hbn.) s'est traduite par une augmentation de la mortalité à la fin des années 1990. Cette perturbation secondaire ponctuelle serait responsable du fait que la mortalité n'est pas significativement continue pour le peuplier faux-tremble. Dans le cas de ces trois espèces, les patrons de recrutement du bois mort induisent une disponibilité relativement constante de ce dernier et une diversification des stades de dégradation (Kneeshaw et Bergeron 1998, Harper *et al.* 2002, Desponts *et al.* 2004, Pham *et al.* 2004, Aakala *et al.* 2008, Vaillancourt *et al.* 2008).

Toujours au chapitre 1, le cas du sapin baumier présente une situation intermédiaire entre la mortalité massive liée aux perturbations sévères et la mortalité continue liée à l'auto-éclaircie ou à la sénescence. Lors de la dernière épidémie de tordeuse des bourgeons de l'épinette, cette espèce a présenté un fort pic de mortalité sur un peu plus de cinq ans. Grâce à la survie partielle du sapin et à la présence d'espèces compagnes moins affectées par l'épidémie, de telles perturbations ponctuelles n'engendrent pas nécessairement le retour au stade initial du peuplement mais génèrent un important pic de recrutement de bois mort.

Dégradation des chicots en forêt verte et brûlée

Au chapitre 1, comme on ne disposait pas d'un dispositif expérimental où plusieurs stades évolutifs étaient représentés pour une même espèce et où les causes individuelles de mortalité sont très difficiles à déterminer avec exactitude, il a été impossible de comparer les trajectoires de dégradation des arbres selon des causes de mortalité pour une même espèce. Il est cependant possible de mettre en relation les courbes de persistance présentées aux chapitres 1 et 3 qui sont très contrastantes. Chez le peuplier faux-tremble, le pin gris et l'épinette noire, on observe en effet une chute des chicots beaucoup plus précoce après feu qu'en forêt verte, avec des demi-vies 2 à 4 fois plus courtes selon les espèces.

Cette différence est-elle attribuable à l'influence du feu, de la coupe de récupération ou d'une combinaison des deux perturbations? Dans le cas du feu comme dans celui de la coupe de récupération, l'ouverture du peuplement et l'exposition accrue au vent qui en résulte favorisent vraisemblablement la chute des arbres et des chicots. La probabilité accrue de chute des chicots due à l'effet d'ouverture du peuplement a été documentée suite au feu (Morrison et Raphael 1993), à des coupes partielles (Garber *et al.* 2005, Vanderwel *et al.* 2006) et a été suggérée par une abondance accrue de bois mort au sol en bordures de coupes totales (Harper *et al.* 2004, Mascarúa López *et al.* 2006, Gagné *et al.* 2007). D'autre part, trois autres sources suggèrent que la coupe de récupération ait pu avoir une influence significative dans l'accélération de la chute des chicots. En effet, dans des brûlis non récupérés en pessière noire, Boulanger et Sirois (2006) ont observé une demi-vie de 16 ans dans des peuplements situés à 500 km au nord de notre aide d'étude et Bond-Lamberty and Gower (2008), au Manitoba, ont évalué que 77% des chicots toujours debout un an après feu étaient encore sur pied neuf ans plus tard. Ces mesures correspondent à une persistance trois fois plus longue que dans notre étude. Chez le pin gris, au cours d'une étude parallèle à mon doctorat menée dans des brûlis situés à 350 km au nord-est de notre aire d'étude, j'ai observé que 86% à 100% des chicots issus du feu étaient toujours debout neuf ans après feu, ce qui correspond à une persistance 2,5 fois plus élevée (données non publiées).

Dans le contexte de cette thèse, il a été impossible de départager l'influence du feu de celui de la coupe de récupération. Les coupes de récupération ont touché une très grande proportion des superficies brûlées et ont été distribuées relativement uniformément sur le territoire (Figure 3.1), résultant en des superficies récupérées adjacentes à nos placettes d'étude qui étaient élevées et peu variables d'une placette à une autre dans notre aire d'étude. Si l'étude avait été menée dans une région où des portions importantes de brûlis avaient été laissées intactes, on aurait eu une plus grande variabilité dans la proportion de superficies récupérées et on aurait davantage pu démarquer l'influence du feu de celle de la coupe de récupération.

Spécificité des patrons de dégradation et de décomposition des arbres morts

L'une des grandes forces de cette étude est d'avoir examiné plusieurs espèces à la fois, ce qui a permis de mettre en lumière les différences qui existent entre elles. La plupart des travaux sur la dynamique des arbres morts ne se sont penchés que sur une ou deux espèces à la fois, et comme les études sont menées dans des contextes géographiques, climatiques et avec des méthodologies différentes, il est délicat d'établir des comparaisons fines entre les espèces. Nos résultats corroborent toutefois ceux rapportés dans des études récentes, notamment en regard des demi-vies (Lee 1998 et Vanderwel *et al.* 2006 chez le peuplier faux-tremble en forêt verte; Garber *et al.* 2005 et Taylor et MacLean 2007 chez le sapin baumier en forêt verte; Boulanger et Sirois 2006 et Bond-Lamberty et Gower 2008 pour l'épinette noire après feu) et des taux de décomposition des chicots (Saint-Germain *et al.* 2007 chez le peuplier faux-tremble et l’épinette noire). À notre connaissance, les résultats présentés pour la dégradation et la décomposition de chicots de pin gris et pour la décomposition de chicots de sapin baumier sont les premiers rapportés dans la littérature.

Le contexte édaphique dans lequel se trouve l’épinette noire aux chapitres 1 et 2 rend les comparaisons directes avec les autres espèces risquées, mais comme l’espèce est peu présente sur sites mésiques dans la sapinière à bouleau blanc, il aurait été difficile de trouver des peuplements comparables dans ce domaine bioclimatique. La dynamique des chicots d’épinette noire documentée dans cette thèse est toutefois représentative pour le grand territoire que représente la ceinture d’argile. Par ailleurs, les hypothèses avancées au chapitre 2 relativement à l’influence prédominante du contexte environnemental représentent des pistes d’explication potentiellement applicables à d’autres écosystèmes où les conditions environnementales limitent l’activité des organismes décomposeurs, comme les zones arides, les forêts de haute altitude ou les zones humides limitant l’activité aérobique.

La principale conclusion qui émane de cette thèse concerne les différences qui existent entre chaque espèce. De la même manière que les espèces présentent une autécologie qui leur est propre pendant leur vie, i.e. une manière de répondre à leur milieu (Gleason 1926, Whittaker 1957), cette individualité perdure après la mort et se traduit par une dynamique spécifique à chaque espèce. Ces différences entre espèces sont observables dans tous les chapitres, que ce soit en regard des trajectoires de dégradation des tiges (chapitres 1 et 3), de la décomposition du bois (chapitre 2) ou des indicateurs morphologiques de l’état d’un chicot (chapitre 4). Cette conclusion est aussi valable pour les facteurs qui influencent la dégradation (chapitre 3) et la décomposition (chapitre 2) du bois mort. Bien que certains facteurs soient communs à toutes les espèces, les combinaisons de facteurs explicatifs s’avèrent être spécifiques aux espèces. Le bois mort ne peut donc pas être considéré comme un substrat uniforme et la spécificité des espèces peut avoir d'importantes conséquences pour plusieurs fonctions écologiques remplies par cet attribut clé de la forêt boréale.

Le nombre élevé de réplicats dont on disposait au chapitre 3 a permis d'évaluer la contribution de facteurs potentiellement explicatifs de la dégradation des chicots aux échelles du peuplement et du paysage. Pour toutes les espèces, un ou plusieurs de ces facteurs s'est avéré explicatif, ce qui suggère que la dynamique des arbres morts ne doit pas être envisagée strictement du point de vue de l'individu mais aussi de son environnement immédiat et d'un contexte plus élargi.

Lien entre la dégradation et la décomposition des chicots

Comme la densité du bois influence la résistance mécanique des tiges et donc leur susceptibilité au bris (Panshin et de Zeeuw 1980, Putz *et al.* 1983, Basham 1991), on s'attendait à ce que la perte de densité du bois des chicots soit corrélée à leur chute et que les espèces dont la décomposition est lente soient aussi les plus persistantes sur pied. Règle générale, les résultats des différents chapitres convergents quant au lien entre la dégradation des chicots et la perte de densité de leur bois. Par exemple, le peuplier faux-tremble se dégrade (chapitres 1 et 3) et se décompose (chapitre 2) généralement plus rapidement que les conifères. Le sapin baumier présente la densité initiale la plus faible (chapitre 2) et est aussi l'espèce la plus susceptible au bris le long de la tige, comme en témoigne la figure 1.3 où l'on voit que sur 28 tiges, une seule est toujours entière (chapitre 1).

Le résultat en apparence le plus contradictoire concerne le pin gris. Au chapitre 1, il apparaît clairement comme l'espèce de chicot la plus persistante (Figure 1.2) et la plus résistante au bris (Figure 1.3), et on suggère même que sa longévité serait sous-estimée. Au chapitre 3, bien que sa persistance soit plus faible (Figure 3.2), on arrive aux mêmes conclusions. Au chapitre 2, c'est l'espèce qui présente la densité initiale la plus élevée des espèces échantillonnées à la FERLD et dans conditions similaires, Jessome (1977) a documenté que le bois du pin gris était le plus dense et présentait la plus grande résistance mécanique (module de rupture) des espèces à l'étude. Dans ce contexte, comment expliquer que le pin gris soit l'espèce résineuse qui présente la perte de densité du bois la plus rapide au chapitre 2 (Figure 2.1)? L'espèce la plus résistante à la chute et au bris dans le temps ne devrait-elle pas être aussi celle dont la perte de densité du bois est la plus lente? Il est vrai que les résultats obtenus pour l'épinette noire au chapitre 1 ne sont vraisemblablement pas comparables à ceux des espèces échantillonnées à la FERLD en raison des conditions édaphiques et climatiques observées en pessière paludifiée (chapitre 2), mais il reste que la perte de densité du sapin est beaucoup moins rapide que celle du pin gris.

La solution à cette apparente contradiction réside probablement dans les caractéristiques de l'anatomie du bois des différentes espèces. Contrairement aux deux autres conifères, les cernes annuels du pin gris sont caractérisés par une transition abrupte du bois initial au bois final, alors que le sapin baumier et l'épinette noire présentent une transition graduelle (Panshin et de Zeeuw 1980). Cette transition abrupte s'accompagne généralement d'une densité particulièrement élevée dans le bois final. Si la densité moyenne du bois, calculée sur les disques entiers, diminue plus rapidement chez le pin gris que chez le sapin baumier, il est probable que cette perte de densité soit plus faible dans le bois final et/ou que la densité relative du bois final soit tout de même encore assez élevée pour retarder le bris. Autrement dit, les cylindres concentriques formés par le bois final à densité relativement plus élevée conféreraient une meilleure résistance mécanique que chez les espèces à transition graduelle.

Perspectives de recherche

Bien que cette thèse ait répondu à plusieurs questions, de nombreuses autres ont été soulevées et mériteraient d'être approfondies. Voici quelques perspectives de recherche émergeantes parmi celles-ci.

Modélisation de la dégradation et de la décomposition des arbres morts

Les taux de chute et de minéralisation présentés dans cette thèse sont le résultat de travaux empiriques. Comme on l'a exposé plus tôt, ils sont entre autres influencés par plusieurs facteurs, dont les causes de mortalité, le stade successionnel, l'historique des peuplements et les conditions environnementales à l'échelle du peuplement et du paysage. Bien que dans plusieurs cas nos résultats posent les bases des patrons de dégradation et de décomposition de quatre espèces très communes, ils sont difficilement généralisables à l'ensemble de la forêt boréale. En ce sens, le développement de modèles plus généraux devrait être envisagé. Ces modèles pourraient être bonifiés ponctuellement par des études empiriques comme celle-ci, mais leur calibration devrait reposer sur des analyses de données prélevées à une échelle beaucoup plus grande. Par exemple, Vanderwel *et al.* (2006) ont développé un modèle de dégradation des arbres morts en forêt feuillue basé sur les données recueillies dans le réseau de parcelles permanentes du ministère des Ressources naturelles de l'Ontario.

Influence des champignons saproxyliques sur la dynamique des arbres morts

Dans cette étude, l'activité des insectes saproxyliques de la famille des Cérambycidés a été associée à une perte accélérée de la densité du bois des chicots chez le sapin baumier et le pin gris (chapitre 2). Plusieurs pistes d'explication ont été suggérées pour expliquer le phénomène (exportation de matériel lors de l’excavation des galeries, porte d’entrée pour l’humidité ambiante, accès facilité aux microorganismes décomposeurs, inoculation de spores de champignons saproxyliques par les insectes) mais n’ont pas pu être vérifiées. La plupart de ces pistes d’explications sont relatives à la mise en place de conditions favorables à la colonisation et au développement des champignons saproxyliques. Or, alors qu’ils sont directement responsables de la minéralisation du bois, leur contribution aux processus de dégradation et de décomposition n’a pas pu être évaluée dans cette étude.

L’occurrence des champignons saproxyliques est très forte en forêt boréale, notamment pour les champignons dits de carie. Ceci s’explique probablement par le fait que la plupart des espèces forestières boréales de l’est de l’Amérique y sont relativement peu résistantes (Boulet 2003). Les mécanismes de défense des arbres font en sorte que ces champignons saproxyliques colonisent la tige en suivant un patron vertical de dispersion (Shigo et Marx 1977), d’où la création de colonnes de bois décomposé ou de cheminées complètement vides entourées de bois sain (Manion 1991, Hennon et DeMars 1997). Règle générale, l’action des champignons de carie se fait à long terme et n’entraîne pas la mort directe de l’arbre. L’intégrité structurale de la tige est cependant compromise, ce qui la rend plus vulnérable aux agents mécaniques tels le vent et le poids de la neige ou du verglas qui favorisent son déracinement ou son bris, selon que la carie soit présente au niveau des racines, de la souche ou du tronc (Whitney 1989, Whitney *et al.* 2002, Hennon et McClellan 2003). L’activité des champignons saproxyliques influence la dynamique des arbres morts sur plusieurs plans. D’une part, lorsque la chute survient alors que la tige colonisée est vivante, l’arbre passe directement au stade de bois mort au sol sans passer par le stade de chicot. Ensuite, la probabilité de chute est accrue dès la première année qui suit la mort chez les tiges colonisées avant leur mort. Finalement, les champignons saproxyliques peuvent aussi influencer la trajectoire de chute des chicots. Par exemple, chez le peuplier faux-tremble, la carie la plus courante est causée par le polypore du tremble et s’introduit en hauteur pour ensuite se développer à la verticale. Il peut donc en résulter des bris successifs le long de la tige à mesure que la carie progresse vers le bas.

La raison pour laquelle très peu d'études ont évalué la contribution des champignons saproxyliques dans les processus de dégradation et de décomposition des arbres morts est sans doute liée au fait que ce sont des éléments difficilement observables et quantifiables. En effet, comme leur action est concentrée à l'intérieur du tronc, il est difficile d'évaluer l'état interne de la tige en l'observant de l'extérieur. Plusieurs auteurs se sont basés sur les fructifications apparentes comme indicateurs des communautés fongiques (ex.: Renvall 1995, Johannesson et Stenlid 1999, Rouvinen *et al.* 2002, Senecal *et al.* 2004, Hill *et al.* 2005). Cependant, comme ces dernières n'apparaissent que dans des conditions environnementales spécifiques, qu'elles ne sont pas toujours pérennes et que leur apparition peut survenir longtemps après la colonisation, cette méthode d'inventaire ne permet pas de caractériser la composition complète des communautés fongiques des troncs. La diversité des espèces de champignons peut conséquemment être grandement sous-estimée (Rayner et Boddy 1988, Hennon et DeMars 1997, Johannesson et Stenlid 1999, Boulet 2003). La culture de spores ou l'analyse moléculaire sont plus fiables (Johannesson et Stenlid 1999, Worrall *et al.* 2005) mais requièrent beaucoup plus d'investissements.

L'activité des champignons saproxyliques expliquant probablement une partie importante de la variance non expliquée observée dans les études sur le bois mort, on ne pourra pas interpréter de manière satisfaisante les patrons de dégradation et de décomposition observés sans en connaître davantage sur les organismes qui sont responsables de ces processus.

Influence de l'aménagement forestier sur la dynamique des arbres morts

À l'exception du contexte de récupération du chapitre 3, cette thèse a été réalisée dans des écosystèmes forestiers qui n'ont pas, ou très peu, été soumis à des perturbations anthropiques directes (Tableau 1.1). Or, l'aménagement forestier qui a cours sur la majorité des territoires forestiers productifs a vraisemblablement un impact majeur sur le recrutement et la dynamique du bois mort. L'influence de l'aménagement a été étudiée à quelques reprises, mais de nombreux points restent à éclaircir, notamment en regard de la dynamique des arbres morts dans les systèmes aménagés et de l'influence que peuvent avoir ces changements sur les fonctions du bois mort.

La plupart des études se sont penchées sur l'abondance et les caractéristiques du bois mort des forêts aménagées par rapport aux forêts non-aménagées. Les stades évolutifs des peuplements où l'on retrouve les plus fortes concentrations en bois mort sont aussi ceux qui font l'objet d'une récolte prioritaire lors des opérations de récolte. Aussi, les coupes de récupération réduisent considérablement l'abondance locale de grandes concentrations de bois mort tandis que les coupes totales surviennent lorsque que les peuplements sont mûrs ou surannés, éliminant ainsi le potentiel de recrutement de bois mort lié à la mortalité due à la sénescence et aux perturbations secondaires (Hunter 1990). Par rapport aux forêts non aménagées, les forêts de seconde venue présentent généralement des volumes de bois mort inférieurs (Linder et Östlund 1998, Sturtevant *et al.* 1997, Drapeau *et al.* 2002, Desponts *et al.* 2002, 2004, Vaillancourt *et al.* 2008) et des caractéristiques de bois mort différentes. Ainsi, la taille des arbres morts est habituellement plus faible en forêt aménagée (Fridman et Walheim 2000) et la représentativité de tous les stades de dégradation peut être affectée, les stades avancés étant sous représentés (Essen *et al.* 1997, Roberge et Desrochers 2004). L'incidence de ces changements sur les fonctions que peut remplir le bois mort commence à être documentée, mais devrait faire l'objet d'une programmation de recherche approfondie.

Plusieurs pays ont adopté des politiques de rétention des arbres vivants et morts au sein des parterres de coupe afin de maintenir les fonctions associées au bois mort dans les écosystèmes aménagés. Ces éléments de rétention peuvent prendre diverses formes : arbres individuels, bouquets d'arbres, îlots, bandes de forêt, etc. Il existe encore malheureusement très peu de connaissances sur la dynamique des chicots dans ces systèmes. Les résultats du chapitre 3 ainsi que les résultats d'études ayant caractérisé la chute d'arbres vivants dans les milieux adjacents à de récentes coupes totales (Mascarúa López *et al.* 2006, Bladon *et al.* 2008) ou suite à des coupes avec rétention (Bebber *et al.* 2005) suggèrent que les taux de chute des chicots seraient accélérés, notamment en raison de l'ouverture subite du peuplement et de l'exposition au vent, mais les trajectoires de chute des arbres vivants et des chicots en milieu aménagé restent à documenter.

Dynamique et fonctions différentielles des feuillus en forêt boréale

Cette thèse a mis en lumière plusieurs aspects qui différencient la dynamique du peuplier faux-tremble de celle des conifères à l'étude (taux de chute, trajectoires de chute, taux de décomposition, facteurs qui influencent ces paramètres). Selon la littérature disponible, qui provient surtout du nord-ouest de l'Europe, les principaux genres décidus boréaux que sont les peupliers et les bouleaux présentent une dynamique bien différente de celle des conifères (Krankina et Harmon 1995, Yatskov *et al.* 2003, Mäkinen *et al.* 2006). Pour des raisons de temps disponible, on a dû exclure le bouleau blanc de cette étude, malgré le peu de documentation disponible concernant la dynamique de cette espèce. Comme il s'agit d'une espèce très abondante en forêt boréale mixte, à la fois comme espèce dominante en début de succession que comme espèce compagne en sapinière, il serait particulièrement intéressant de mener le même genre d'étude afin de pouvoir documenter sa dynamique.

Non seulement les feuillus boréaux présentent-ils une dynamique du bois mort différente de celle des conifères, mais plusieurs études ont mis en lumière les rôles fonctionnels particuliers des feuillus. D’une part, leur croissance généralement rapide leur permet d’atteindre de forts diamètres en relativement peu de temps par rapport aux conifères (Julien et Darveau 2005), ce qui en fait des arbres d’intérêt faunique particulièrement recherchés par les espèces utilisatrices de cavités qui sont contraintes par leur taille (Martin *et al.* 2004, Gasse 2007, Drapeau *et al*. 2009).

D’autre part, certaines espèces feuillues présentent des patrons de décomposition du bois qui en font des habitats distinctifs. Par exemple, les peupliers développent des colonnes de pourriture à l’intérieur du tronc qui favorisent la création naturelle ou l’excavation de cavités et par conséquent la présence d’utilisateurs de cavités. Martin et Eadie (1999) et Martin *et al.* (2004) ont d’ailleurs montré le rôle clé du peuplier faux-tremble pour les espèces qui forment le réseau de nidification de la faune cavicole (nest-web) des forêts mixtes du nord de la Colombie-Britannique.

Finalement, le bois des feuillus représente un substrat prisé par plusieurs espèces de champignons saproxyliques et d’invertébrés, tant chez les tiges vivantes (voir Niemelä 1997 pour une revue) que chez les tiges mortes (Martikainen *et al.* 1996, 1998, Siitonen *et al.* 2001). Les communautés associées aux arbres morts décidus sont particulièrement riches en espèces (Kaila *et al.* 1994, Martikainen *et al.* 1998), sont différentes de celles associées aux conifères (Saint-Germain *et al.* 2007) et ce substrat est essentiel à plusieurs espèces qui en sont dépendantes (Martikainen *et al.* 1996, 1998, Siitonen *et al.* 2001). Ces arbres sont à la base de réseaux trophiques très développés: des champignons saproxyliques s’y installent alors que les arbres sont toujours vivants, des insectes saproxyliques se nourrissent du bois, des champignons ou d’autres insectes, et des oiseaux, notamment des pics, se nourrissent des insectes (Virkkala *et al.* 1993, Kaila *et al.* 1994, Martikainen *et al.* 1996, 1998, Siitonen *et al.* 2001, Nappi 2009).

Tous ces éléments font en sorte que malgré leur faible abondance relative, les feuillus boréaux et le bois mort feuillu représentent des éléments clés pour une gamme très étendue d'organismes (Martikainen *et al.* 1998, Gasse 2007, Drapeau *et al*. 2009). En Scandinavie, comme l'historique d'aménagement forestier intensif a entraîné une diminution marquée de l'abondance de feuillus (Virkkala *et al.* 1993) ainsi qu'une raréfaction du bois mort dans le paysage (Linder et Östlund 1998), on a observé un déclin allant jusqu'à l'extinction régionale, voire nationale, de nombreuses espèces et on a ainsi pu documenter les associations entre plusieurs d'entre elles et les arbres feuillus ainsi que le rôle fonctionnel particulier des feuillus (Martikainen *et al.* 1996, 1998, Siitonen *et al.* 2001). Pour la forêt boréale de l'est de l'Amérique du Nord, l'aménagement forestier ayant été beaucoup moins intensif, on n'a pas encore documenté des patrons similaires, mais les connaissances sont plus partielles et demandent à être étoffées.

La répartition holarctique des genres *Populus* et *Betula* et la similarité des patrons de dégradation et de décomposition observés en forêt boréale nord-américaine et scandinave suggèrent que ces espèces ne jouent pas un rôle différentiel à une échelle locale ou régionale mais bien à l'échelle holarctique.

REFERENCES CITEES DANS LA THESE

Aakala, T., Kuuluvainen, T., Gauthier, S., et De Grandpré, L. 2008. Standing dead trees and their decay-class dynamics in the northeastern boreal old-growth forests of Quebec. Forest Ecology and Management 255: 410-420.

Alban, D.H. et Pastor, J. 1993. Decomposition of aspen, spruce, and pine boles on two sites in Minnesota. Canadian Journal of Forest Research 23: 1744-1749.

Allison, P.D. 1995. Survival Analysis Using the SAS System, a Practical Guide. SAS Institute, Cary, NC.

Angers, V.-A. 2009. L'enjeu écologique du bois mort – Complément au Guide pour la description des principaux enjeux écologiques dans les plans régionaux de développement intégré des ressources et du territoire. Ministère des Ressources naturelles et de la Faune, Direction de l'environnement et de la protection des forêts.

Angers, V.-A., Messier, C., Beaudet, M., et Leduc, A. 2005. Comparing composition and structure in old-growth and harvested (selection and diameter-limit cuts) northern hardwood stands in Quebec. Forest Ecology and Management 217: 275-293.

Basham, J.T. 1991. Stem decay in living trees in Ontario's forests: a user's compendium and guide. Forestry Canada, Ontario region, Great Lakes Forestry Centre, Information report O-X-408.

Bebber, D.P., Cole, W.G., Thomas, S.C., Balsillie, D., et Duinker, P. 2005. Effects of retention harvests on structure of old-growth *Pinus strobus* L. stands in Ontario. Forest Ecology and Management 205: 91-103.

Béland, M., Bergeron, Y. et Zarnicovan, R. 1999. Natural regeneration of jack pine following harvesting and site preparation in the Clay Belt of northwestern Quebec. The Forestry Chronicle 75: 821-831.

Berg, A.B., Ehnström, B., Gustafsson, L., Hallingbäck, T., Jonsell, M., et Weslien, J. 1994. Threatened plant, animal, and fungus species in Swedish forests: Distribution and habitat associations. Conservation Biology 8: 718-731.

Bergeron, D., Darveau, M., Desrochers, A., et Savard, J.-P.L. 1997. Impact de l'abondance des chicots sur les communautés aviaires et la sauvagine des forêts conifériennes et feuillues du Québec méridional. Service canadien de la faune, région du Québec, Environnement Canada, Série de rapports techniques no 271F.

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

Bergeron, Y., Leduc, A., Harvey, B.D. and Gauthier, S. 2001. Natural fire regime: A guide for sustainable management of the Canadian boreal forest. Silva Fennica 36: 81-95.

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

Bergeron, Y. et Charron, D. 1994. Postfire stand dynamics in a southern boreal forest (Québec): A dendroecological approach. Ecoscience 1: 173-184.

Bescond, H. 2002. Reconstitution de l'historique de l'exploitation forestière sur le territoire de la forêt d'enseignement et de recherche du lac Duparquet au cours du 20ème siècle et influence sur l'évolution des peuplements forestiers. Mémoire de maîtrise, Université du Québec à Montréal.

Bladon, K.D., Lieffers, V.J., Silins, U., Landhäusser, S.M., et Blenis, P.V. 2008. Elevated mortality of residual trees following structural retention harvesting in boreal mixedwoods. The Forestry Chronicle 84: 70-75.

Blais, J.R. 1981. Mortality of balsam fir and white spruce following a spruce budworm outbreak in the Ottawa River watershed in Quebec. Canadian Journal of Forest Research 11: 620-629.

Blanchette, R. A. 1995. Degradation of the lignocellulose complex in wood. Cananadian Journal of Botany 73: S999-S1010.

Boddy, L. 2001. Fungal community ecology and wood decomposition processes in angiosperms: from standing tree to complete decay of coarse woody debris. Ecological Bulletins 49: 43-56.

Boddy, L. et Watkinson, S.C. 1995. Wood decomposition, higher fungi, and their role in nutrient redistribution. Canadian Journal of Botany 73: S1377-S1383.

Bond-Lamberty, B. et Gower, S.T. 2008. Decomposition and fragmentation of coarse woody debris: Re-visiting a boreal black spruce chronosequence. Ecosystems 11: 831-840.

Bond-Lamberty, B., Wang, C. et Gower, S.T. 2004. Net primary production and net ecosystem production of a boreal black spruce fire chronosequence. Global Change Biology 10: 483-487.

Bond-Lamberty, B., Wang, C. et Gower, S.T. 2002. Annual carbon flux from woody debris for a boreal black spruce fire chronosequence. Journal of Geophysical Research - Atmospheres 107, art. no. 8220.

Bouchard, M. 2001. Les communautés d'insectes décomposeurs léiodides dans des sapinières de la Gaspésie. Le Naturaliste Canadien 125: 126-130.

Boulanger, Y. et Sirois, L. 2006. Postfire dynamics of black spruce coarse woody debris in northern boreal forest of Quebec. Canadian Journal of Forest Research 36: 1770-1780.

Boulet, B. 2003. Les champignons des arbres de l'Est de l'Amérique du Nord. Les Publications du Québec, Ste-Foy, Qc.

Brais, S., Paré, D., et Lierman, C. 2006. Tree bole mineralization rates of four species of the Canadian eastern boreal forest: implications for nutrient dynamics following stand-replacing disturbances. Canadian Journal of Forest Research 36: 2331-2340.

Brown, J.K. et DeByle, N.V. 1987. Fire damage, mortality and suckering in aspen. Canadian Journal of Forest Research 17: 1100-1109.

Bull, E. 1983. Snag habitat management. USDA Forest Service, General Technical Report RM-99.

Bull, E.L., Parks, C.G. et Torgersen, T.R., 1997. Trees and Logs Important to Wildlife in the Interior Columbia River Basin. USDA Forest Service General Technical Report no 391.

Burnham, K. P. et Anderson, D. R. 2002. Model selection and multimodel inference: a practical information-theoretic approach. 2nd ed. Springer-Verlag, New York.

Campbell, L.J. et Laroque, C.P. 2007. Decay progression and classification in two old-growth forests in Atlantic Canada. Forest Ecology and Management 238: 293-301.

Candau, J.N., Abt, V. et Keatley, L. 2002. Bioclimatic analysis of declining aspen stands in northeastern Ontario. Ontario forest research institute Forest Research Report 154.

Chambers, C.L. et Mast, J.N. 2005. Ponderosa pine snag dynamics and cavity excavation following wildfire in northern Arizona. Forest Ecology and Management 216: 227-240.

Churchill, G.B., John, H.H., Duncan, D.P. et Hodson, A.C. 1964. Long-term effects of defoliation of aspen by the forest tent caterpillar. Ecology 45: 630-633.

Cline, S.P., Berg, A.B., et Wight, H.M. 1980. Snag characteristics and dynamics in Douglas-fir forests, western Oregon. Journal of Wildlife Management 44: 773-786.

Cooke, B.J. et Lorenzetti, F. 2006. The dynamics of forest tent caterpillar outbreaks in Québec, Canada. Forest Ecology and Management 226: 110-121.

Courteau, M., Darveau, M., et Savard, J.-P.L. 1997. Effet des coupes forestières sur la disponibilité de sites de nidification pour le garrot à œil d'or (*Bucephala clangula*) en sapinière boréale. Service canadien de la faune, Série de rapport techniques no 270.

Creed, I. F., Webster, K. L. et Morrison, D. L. 2004. A comparison of techniques for measuring density and concentrations of carbon and nitrogen in coarse woody debris at different stages of decay. Canadian Journal of Forest Research 34: 744-753.

Crête, M., Brais, S., Campagna, M., Darveau, M., Desponts, M., Déry, S., Drapeau. P., Drolet, B., Jetté, J.-P., Maisonneuve, C., Nappi, A., et Petitclerc, P. 2004. Pourquoi et comment maintenir du bois mort dans les forêts aménagées du Québec - Avis scientifique. Société de la faune et des parcs du Québec, Direction du développement de la faune et du ministère des Ressources naturelles du Québec, Direction de l'environnement forestier.

Dahms, W.G. 1949. How long do ponderosa pine snags stand? USDA Forest Service, Research Note 57.

Daniels, L.D., Dobry, J., Klinka, K., et Feller, M.C. 1997. Determining year of death of logs and snags of *Thuja plicata* in southwestern coastal British Colombia. Canadian Journal of Forest Research 27: 1132-1141.

Dansereau, P.-R. et Bergeron, Y. 1993. Fire history in the southern boreal forest of northwestern Quebec. Canadian Journal of Forest Research 23: 25-32.

Darveau, M. et Desrochers, A. 2001. Le bois mort et la faune vertébrée - État des connaissances au Québec. Rapport préparé pour le ministère des Ressources naturelles, Université Laval, Centre de recherche en biologie forestière.

DeGraaf, R.M., Yamasaki, M., Leak, W.B., et Lanier, J.W. 1992. New England wildlife: management of forest habitats. USDA Forest Service General Technical Report NE-144.

DeLong, S.C., Sutherland, G.D., Daniels, L.D., Heemskerk, B.H., et Storaunet, K.O. 2008. Temporal dynamics of snags and development of snag habitats in wet spruce-fir stands in east-central British Columbia. Forest Ecology and Management 255: 3613-3620.

DeLong, S.C., Daniels, L.D., Heemskerk, B., et Storaunet, K.O. 2005. Temporal development of decaying log habitats in wet spruce-fir stands in east-central British Columbia. Canadian Journal of Forest Research 35: 2841-2850.

Desponts, M., Brunet, G., Bélanger, L., et Bouchard, M. 2004. The eastern boreal old-growth balsam fir forest: a distinct ecosystem. Canadian Journal of Botany 82: 830-849.

Desponts, M., Desrochers, A., Bélanger, L., et Huot, J. 2002. Structure de sapinières aménagées et anciennes du massif des Laurentides (Québec) et diversité des plantes invasculaires. Canadian Journal of Forest Research 32: 2007-2093.

Desponts, M., Brunet, G., et Bélanger, L. 2001. Diversité structurale et biodiversité des plantes invasculaires de la sapinière à bouleau blanc de la Gaspésie. Le Naturaliste Canadien 125: 168-174.

Doyon, F., Gagnon, D., et Giroux, J.-F. 2005. Effect of strip and single-tree selection cutting on birds and their habitat in a southwestern Quebec northern hardwood forest. Forest Ecology and Management 209: 101-115.

Doyon, F., Savard, J.-P.L., Gagnon, D., et Giroux, J.-F. 1999. Snag characteristics and use as woodpecker drilling sites in harvested and non-harvested northern hardwood forests. pp. 103-114 *In:* Diamond, A. W. et Nettleship, D. N. (Éditeurs). Biology and conservation of forest birds. Society of Canadian Ornithologists, Fredericton, New-Brunswick.

Drapeau, P., Nappi, A., Imbeau, L., et Saint-Germain, M. 2009. Standing dead wood for keystone bird species in the eastern boreal forest: Managing for snag dynamics. The Forestry Chronicle 85: 227-234.

Drapeau, P., Leduc, A., Bergeron, Y., Gauthier, S., et Savard, J.-P. 2003. Les communautés d'oiseaux des vieilles forêts de la pessière à mousse de la ceinture d'argile: Problèmes et solutions face à l'aménagement forestier. The Forestry Chronicle 3: 531-540.

Drapeau P., Nappi A., Giroux J.-F., Leduc A. et Savard, J.-P. 2002. Distribution patterns of birds associated with snags in natural and managed eastern boreal forests. pp. 193–205 *In:* Laudenslayer W.F., Shea P.J., Valentine B.E., Weatherspoon C.P. et T.E. Lisle (Technical Coordinators). Proceedings of the Symposium on the Ecology and Management of Dead Wood in Western forests. USDA Forest Service, Pacific Southwest Research Station General Technical Report PSW-GTR 181.

Drapeau, P., Leduc, A., Savard, J.-P., et Bergeron, Y. 2001. Les oiseaux forestiers, des indicateurs des changements des mosaïques forestières boréales. Le Naturaliste Canadien 125: 41-46.

Dynesius, M. et Jonsson, B.G. 1991. Dating uprooted trees: comparison and application of eight methods in a boreal forest. Canadian Journal of Forest Research 21: 655-665.

Edman, M., Möller, R. et Ericson, L. 2006. Effects of enhanced tree growth rate on the decay capacities of three saprotrophic wood-fungi. Forest Ecology and Management 232: 12-18.

Edmonds, R. L. et Eglitis, A. 1989. The role of the Douglas-fir beetle and wood borers in the decomposition and nutrient release of Douglas-fir logs. Canadian Journal of Forest Research 19: 853-859.

Environment Canada 2010. National Climate Data and Information Archive. Available at www.climate.weatheroffice.gc.ca/climate_normals/results_e.html, [Visité le 8 novembre 2010].

Erickson, H. E., Edmonds, R. L. et Peterson, C. E. 1985. Decomposition of logging residues in Douglas-fir, western hemlock, Pacific silver fir, and ponderosa pine ecosystems. Canadian Journal of Forest Research 15: 914-921.

ESRI (Environmental Systems Research Institute Inc.) 2000. ArcView GIS 3.2. ESRI, Redlands, CA.

Essen, P.-A.1994. Tree mortality patterns after experimental fragmentation of an old-growth conifer forest. Biological Conservation 68: 19-28.

Evans, K.E. et Conner, R.N. 1979. Snag management. pp. 214-225 *In:* DeGraaf, R.M. (ed). Management of north central and northeastern forests for nongame birds. USDA Forest Service, General Technical Report NC-51.

Everett, R., Lehmkuhl, J., Schellhaas, R., Ohlson, P., Keenum, D., Riesterer, H., et Spurbeck, D. 1999. Snag dynamics in a chronosequence of 26 wildfires on the east slope of the Cascade Range in Washington states, USA. International Journal of Wildland Fire 9: 223-234.

Fahey, T. J. 1983. Nutrient dynamics of aboveground detritus in lodgepole pine (*Pinus contorta* spp. *latifolia*) ecosystems, southeastern Wyoming. Ecological Monographs 53: 51-72.

Farris, K.L., Huss, M.J., et Zack, S. 2004. The role of foraging woodpeckers in the decomposition of ponderosa pine snags. Condor 106: 50-59.

Fenton, N., Lecomte, N., Légaré, S. et Bergeron, Y. 2005. Paludification in black spruce (*Picea mariana*) forests of eastern Canada: Potential factors and management implications. Forest Ecology and Management 213: 151-159.

Foster, J.R. et Lang, G.E. 1982. Decomposition of red spruce and balsam fir boles in the White Mountains of New Hampshire. Canadian Journal of Forest Research 12: 617-626.

Frank, R.M. 1990. Balsam fir. *In:* Burns, R.M., Honkala, B.H. (Éditeurs). Silvics of North America: Vol 1 Conifers. USDA Forest Service Agriculture Handbook 654.

Franklin, J.F., Spies, T.A., Van Pelt, R., Carey, A.B., Thornburgh, D.A., Berg, D.R., Lindenmayer, D.B., Harmon, M.E., Keeton, W.S., Shaw, D.C., Bible, K. et Chen, J. 2002. Disturbances and structural development of natural forest ecosystems with silvicultural implications, using Douglas-fir forests as an example. Forest Ecology and Management 155: 399-423.

Franklin, J.F., Cromack, J.F., Dension, W., McKee, A., Maser, C., Sedell, J., Swanson, F., et Juday, G. 1981. Ecological characteristics of old-growth Douglas-fir forests. USDA Forest Service General Technical Report PNW-118.

Fridman, J. et Walheim, M. 2000. Amount, structure, and dynamics of dead wood on managed forestland in Sweden. Forest Ecology and Management 131: 23-36.

Gagné, C., Imbeau, L. et Drapeau, P. 2007. Anthropogenic edges: Their influence in the American three-toed woodpecker (*Picoides dorsalis*) foraging behaviours in managed boreal forests of Quebec. Forest Ecology and Management 252: 191-200.

Garber, S.M., Brown, J.P., Wilson, D.S., Maguire, D.A. et Heath, L.S. 2005. Snag longevity under alternative silvicultural regimes in mixed-species forests of central Maine. Canadian Journal of Forest Research 35: 787-796.

Gasse, A. 2007. Importance des arbres de grande taille en forêt boréale mixte sur la distribution des oiseaux cavicoles ainsi que sur les patrons d'alimentation du grand pic (*Dryocopus pileatus*). Mémoire de maîtrise, Université du Québec à Montréal.

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

Gleason, H.A. 1926. The individualistic concept of the plant association. Bulletin of the Torrey Botanical Club 53: 1-20.

Gore, A.P., Johnson, E.A. et Lo, H.P. 1985. Estimating the time a dead tree has been on the ground. Ecology 66: 1981-1983.

Graham, R.L., et Cromack, K., Jr. 1982. Mass, nutrient content, and decay rate of dead boles in rain forests of Olympic National Park. Canadian Journal of Forest Research 12: 511-521.

Greene, D.F., Noël, J., Bergeron, Y., Rousseau, M. et Gauthier, S. 2004. Recruitment of *Picea mariana*, *Pinus banksiana* and *Populus tremuloides* across a burn severity gradient following wildfire in the southern boreal forest of Quebec. Canadian Journal of Forest Research 34: 1845-1857.

Grier, C.C. 1978. A *Tsuga heterophylla* - *Picea sitchensis* ecosystem of coastal Oregon: decomposition and nutrient balances of fallen logs. Canadian Journal of Forest Research 8: 198-206.

Groven R., Rolstad J., Storaunet K.O. et Rolstad, E. 2002. Using forest stand reconstructions to assess the role of structural continuity for late-successional species. Forest Ecology and Management 164: 39-55.

Hannon, S. et Drapeau, P. 2005. Bird responses to burning and logging in the boreal forest of Canada. Studies in Avian Biology 30: 97-115.

Harmon, M.E. 2001. Moving towards a new paradigm for woody detritus management. Ecological Bulletins 49: 269-278.

Harmon, M.E. 1982. Decomposition of standing dead trees in the southern Appalachian mountains. Oecologia 52: 214-215.

Harmon, M.E., Krankina, O.N. et Sexton, J. 2000. Decomposition vectors: a new approach to estimating woody detritus decomposition dynamics. Canadian Journal of Forest Research 30: 76-84.

Harmon, M.E. et Sexton, J. 1996. Guidelines for measurements of woody detritus in forest ecosystems. U.S. Long Term Ecological Research Network Office, University of Washington, Seattle, WA. LTER Publ. No. 20.

Harmon, M.E., Franklin, J.F., Swanson, F.J., Sollins, P., Gregory, S.V., Lattin, J.D., Anderson, N.H., Cline, S.P., Aumen, N.G., Sedell, J.R., Lienkaemper, G.W., Cromack, K.Jr. et Cummins, K.W. 1986. Ecology of coarse woody debris in temperate ecosystems. Advances in Ecological Research 15: 133-302.

Harper, K.A., Bergeron, Y., Drapeau, P., Gauthier, S. et De Grandpré, L. 2005. Structural development following fire in black spruce boreal forest. Forest Ecology and Management 206: 293-306.

Harper, K., Lesieur, D., Bergeron, Y. et Drapeau, P. 2004. Forest structure and composition at young fire and cut edges in black spruce boreal forest. Canadian Journal of Forest Research 34: 289-302.

Harper, K., Boudreault, C., De Grandpré, L., Drapeau, P., Gauthier, S. et Bergeron, Y. 2003. Structure, composition and diversity of old-growth black spruce boreal forest of the Clay Belt region in Quebec and Ontario. Environmental Review 11: S79-S98.

Harper, K.A., Bergeron, Y., Gauthier, S. et Drapeau, P. 2002. Post-fire development of canopy structure and composition in black spruce forests of Abitibi, Québec: A landscape scale study. Silva Fennica 26: 249-263.

Harrington, M.G. 1993. Predicting *Pinus ponderosa* mortality from dormant season and growing season fire injury. International Journal of Wildland Fire 3: 65-72.

Harvey, B. D. et Brais, S. 2007. Partial cutting as an analogue to stem exclusion and dieback in trembling aspen (*Populus tremuloides*) dominated boreal mixedwoods: implications for dead wood dynamics. Canadian Journal of Forest Research 37: 1525-1533.

Hély, C., Flannigan, M. et Bergeron, Y. 2003. Modelling tree mortality following wildfire in the southeastern Canadian mixed-wood boreal forest. Forest Science 49: 566-576.

Hély, C., Bergeron, Y. et Flannigan, M.D. 2000. Coarse woody debris in the southeastern Canadian boreal forest: composition and load variations in relation to stand replacement. Canadian Journal of Forest Research 30: 674-687.

Hennon, P.E. et McClellan, M.H. 2003. Tree mortality and forest structure in the temperate rain forest of southeast Alaska. Canadian Journal of Forest Research 33: 1621-1634.

Hennon, P.E. et DeMars, D.J. 1997. Development of wood decay in wounded western hemlock and Sitka spruce in southeast Alaska. Canadian Journal of Forest Research 27: 1971-1978.

Hill, S.B., Mallik, A.U. et Chen, H.Y.H. 2005. Canopy gap disturbance and succession in trembling aspen dominated boreal forests in northeastern Ontario. Canadian Journal of Forest Research 35: 1942-1951.

Holmes, R.L. 1983. Computer-assisted quality control in tree-ring dating and measurement. Tree-Ring Bulletin 43: 69-78.

Huggard, D.J. 1999. Static life-table analysis of fall rates of subalpine fir snags. Ecological Applications 9: 1009-1016.

Hunter, M.L.Jr. 1990. Wildlife, forests, and forestry: principles of managing forests for biological diversity. Prentice-Hall, Englewood Cliffs, NJ.

Hutto, R.L. 1995. Composition of bird communities following stand-replacement fires in northern Rocky Mountain (U.S.A.) conifer forests. Conservation Biology 9: 1041-1058.

Hytteborn, H., Liu, Q., Verwijst, T. 1991. Natural disturbance and gap dynamics in a Swedish boreal spruce forest. pp. 93-108 *In:* Nakagoshi, N., Golley, F.B. (Éditeurs). Coniferous forest ecology, from an international perspective. SPB Academic Publishing, La Hague.

Imbeau, L. et Desrochers, A. 2002. Foraging ecology and use of drumming trees by three-toed woodpeckers. Journal of Wildlife Management 66: 222-231.

Jayen, K. 2004. Utilisation des cartes d'impact de feux pour estimer la sévérité des feux et rôle de la sévérité des feux dans le succès de la régénération en forêt boréale dans le nord-ouest du Québec. Mémoire de maîtrise, Université du Québec à Montréal.

Jessome, J.P. 1977. Strength and related properties of woods grown in Canada. Eastern Forest Products Lab., Ottawa, Forestry Technical Report 21.

Johannesson, H. et Stenlid, J. 1999. Molecular identification of wood-inhabiting fungi in an unmanaged *Picea abies* forest in Sweden. Forest Ecology and Management 115: 203-211.

Johnson, E.A. 1992. Fire and vegetation dynamics - Studies from the North American boreal forest. Cambridge Studies in Ecology. Cambridge University Press, Cambridge.

Johnson, E.A. et Greene, D.F. 1991. A method for studying dead bole dynamics in *Pinus contorta* var. *latifolia - Picea engelmannii* forests. Journal of Vegetation Science 2: 523-530.

Jonsson, B.G., Kruys, N. et Ranius, T. 2005. Ecology of species living on dead wood - Lessons for dead wood management. Silva Fennica 39: 289-309.

Jonsson. B.G. et Kruys, N. (Éditeurs) 2001. Ecology of woody debris in boreal forests. Ecological bulletins 49.

Julien, D. et Darveau, M. 2005. Où sont les gros arbres d'intérêt faunique? Répartition des arbres par essences, âge, diamètres, qualité de stations et sous-domaines bioclimatiques dans les peuplements forestiers naturels du Québec. Canards Illimités, rapport technique no Q2005-3.

Kafka, V., Gauthier, S. et Bergeron, Y. 2001. Fire impacts and crowning in the boreal forest: study of a large wildfire in western Quebec. International Journal of Wildland Fire 10: 119-27.

Kaila, L., Martikainen, P., Punttila, P. et Yakovlev, E. 1994. Saproxylic beetles (Coleoptera) on dead birch trunks decayed by different polypore species. Annales Zoologici Fennici 31: 97-107.

Kasischke, E.S. 2000. Processes influencing carbon cycling in the North American boreal forest. *In*: Kasischke, E.S. et Stocks, B.J. (Éditeurs). Fire, climate change and carbon cycling in the boreal forest. Ecological Studies 138:103-110.

Keen, F.P. 1955. The rate of natural falling of beetle-killed ponderosa pine snags. Journal of Forestry 53: 720-723.

Keen, F.P. 1929. How soon do yellow pine snags fall? Journal of Forestry 27: 735-737.

Keyser, T.L., Smith, F.W., Lentile, L.B. et Shepperd, W.D. 2006. Modeling postfire mortality of ponderosa pine following a mixed-severity wildfire in the Black Hills: The role of tree morphology and direct fire effects. Forest Science 52: 530-539.

Kneeshaw, D. et Bergeron, Y. 1998. Canopy gap characteristics and tree replacement in the southeastern boreal forest. Ecology 79: 783-794.

Krankina, O.N. et Harmon, M.E. 1995. Dynamics of the dead wood carbon pool in northwestern Russian boreal forests. Water, Air and Soil Pollution 82: 227-238.

Kruys, N., Jonsson, B.G. et Ståhl, G. 2002. A stage-based matrix model for decay-class dynamics of woody debris. Ecological Applications 12: 773-781.

Kruys, N. et Jonsson, B.G. 1999. Fine woody debris is important for species richness on logs in managed boreal spruce forests of northern Sweden. Canadian Journal of Forest Research 29: 1295-1299.

Kushla, J.D. et Ripple, W.J. 1997. The role of terrain in a fire mosaic of a temperate coniferous forest. Forest Ecology and Management 95: 97-107.

Laiho, R. et Prescott, C.E. 2004. Decay and nutrient dynamics of coarse woody debris in northern coniferous forests: A synthesis. Canadian Journal of Forest Research 34: 763-777.

Lambert, R.L., Lang, G.E. et Reiners, W.A. 1980. Loss of mass and chemical change in decaying boles of a subalpine balsam fir forest. Ecology 61: 1460-1473.

Lecomte, N., Simard, M. et Bergeron, Y. 2006. Effects of fire severity and initial tree composition on stand structural development in the coniferous boreal forest of northwestern Québec, Canada. Ecoscience 13: 152-163.

Lee, P. 1998. Dynamics of snags in aspen-dominated midboreal forests. Forest Ecology and Management 105: 263-272.

Lertzman, K.P. et Krebs, C.J. 1991. Gap-phase structure of a subalpine old-growth forest. Canadian Journal of Forest Research 21: 1730-1741.

Lindenmayer, D.B., Foster, D.R., Franklin, J.F., Hunter, M.L., Noss, R.F., Schmiegelow, F.A. et Perry, D. 2004. Salvage harvesting policies after natural disturbance. Science 303: 1303.

Linder, P. et Östlund, L. 1998. Structural changes in three mid-boreal Swedish forest landscapes, 1885-1996. Biological Conservation 85: 9-19.

Lussier, J.-M., Morin, H. et Gagnon, R. 2002. Mortality in black spruce stands of fire or clear-cut origin. Canadian Journal of Forest Research 32: 539-547.

MacLean, D.A. et Ostaff, D.P. 1989. Patterns of balsam fir mortality caused by an uncontrolled spruce budworm outbreak. Canadian Journal of Forest Research 19: 1087-1095.

Mäkinen, H., Hynynen, J.S.J. et Sievänen, R. 2006. Predicting the decomposition of Scots pine, Norway spruce, and birch stems in Finland. Ecological Applications 16: 1865-1879.

Manion, P.D. 1991. Tree disease concepts, 2nd ed. Prentice Hall, Englewood Cliffs, NJ.

Martikainen, P., Kaila, L. et Haila, Y. 1998. Threatened beetles in white-backed woodpecker habitats. Conservation Biology 12: 293-301.

Martikainen, P., Siitonen, J., Kaila, L. et Punttila, P. 1996. Intensity of forest management and bark beetles in non-epidemic conditions: A comparison between Finnish and Russian Karelia. Journal of Applied Entomology 120: 257-264.

Martin, K., Aitken, K.E.H. et Wiebe, K.L. 2004. Nest sites and nest webs for cavity nesting communities in interior British Columbia, Canada: nest characteristics and niche partitioning. The Condor 106: 5-19.

Martin, K. et Eadie, J.M. 1999. Nest webs: A community-wide approach to the management and conservation of cavity-nesting forest birds. Forest Ecology and Management 115: 243-257.

Mascarúa López, L., Harper, K.A. et Drapeau, P. 2006. Edge influence on forest structure in large forest remnants, cutblock separators, and riparian buffers in managed black spruce forests. Ecoscience 13: 226-233.

Maser, C., Anderson, R., Cromack, K. Jr, William, J.T. et Martin, R.E. 1979. Dead and down woody material. pp. 78-95 *In:* Thomas, J. (ed). Wildlife habitats in managed forests, the Blue mountains of Oregon and Washington. USDA Forest Service, Agriculture Handbook 553.

Mast, J.N. et Veblen, T.T. 1994. A dendrochronological method of studying tree mortality patterns. Physical Geography 15: 529-542.

Mattson, K.G., Swank, W.T. et Waide, J.B. 1987. Decomposition of woody debris in a regenerating, clear-cut forest in the Southern Appalachians. Canadian Journal of Forest Research 17: 712-721.

McComb, W.C. et Muller, R.N. 1983. Snag densities in old-growth and second-growth Appalachian forests. Journal of Wildlife Management 47: 376-382.

McGee, G.G. et Birmingham, J.P. 1997. Decaying logs as germination sites in northern hardwood forests. Northern Journal of Applied Forestry 14: 178-182.

Means, J.E., MacMillan, P.C. et Cromack, K.Jr. 1992. Biomass and nutrient content of Douglas-fir logs and other detrital pools in an old-growth forest, Oregon, U.S.A. Canadian Journal of Forest Research 22: 1536-1546.

Means, J.E., Cromack, K.Jr. et MacMillan, P.C. 1985. Comparison of decomposition models using wood density of Douglas-fir logs. Canadian Journal of Forest Research 15: 1092-1098.

Miller, T.F., Mladenoff, D.J. et Clayton, M.K. 2002. Old-growth northern hardwood forests: spatial autocorrelation and patterns of understory vegetation. Ecological Monographs 72: 487-503.

Ministère des Ressources naturelles, de la Faune et des Parcs (MRNFP). 2005. Objectifs de protection et de mise en valeur des ressources du milieu forestier, Plans généraux d'aménagement forestier 2007-2012 - Document de mise en œuvre, Gouvernement du Québec.

Mitchell, S.J. 1995. The windthrow triangle: A relative windthrow hazard assessment procedure for forest managers. The Forestry Chronicle 71: 446-450.

Morin, H., Laprise, D., Simard, A.-A. et Amouch, S. 2008. Régime des épidémies de la tordeuse des bourgeons de l'épinette dans l'Est de l'Amérique du Nord. pp. 165-192 *In:* Gauthier, S., Vaillancourt, M.-A., Leduc, A., De Grandpré, L., Kneeshaw, D., Morin, H., Drapeau, P. et Bergeron, Y. (Éditeurs). Aménagement écosystémique en forêt boréale. Presses de l'Université du Québec, Montréal.

Morin, H., Laprise, D. et Bergeron, Y. 1993. Chronology of spruce budworm outbreaks near Lake Duparquet, Abitibi region, Quebec. Canadian Journal of Forest Research 23: 1497-1506.

Morrison, M.L. et Raphael, M.G. 1993. Modeling the dynamics of snags. Ecological Applications 3: 322-330.

Naesset, E. 1999. Decomposition rate constants of *Picea abies* logs in southeastern Norway. Canadian Journal of Forest Research 29: 372-381.

Nappi, A. 2009. Sélection d'habitat et démographie du pic à dos noir dans les forêts brûlées de la forêt boréale. Thèse de doctorat, Université du Québec à Montréal.

Nappi, A. 2000. Distribution des pics et utilisation des arbres morts dans les forêts soumises aux perturbations naturelles en pessière à mousse. Mémoire de maîtrise, Université du Québec à Montréal.

Nappi, A., Drapeau, P., Saint-Germain, M. et Angers, V.A. 2010. Effect of fire severity on long-term occupancy of burned boreal conifer forests by saproxylic insects and wood-foraging birds. International Journal of Wildland Fire 19, 500-511.

Nappi, A. et Drapeau, P. 2009. Reproductive success of the black-backed woodpecker (*Picoides arcticus*) in burned boreal forests: Are burns source habitats? Biological Conservation 142: 1381-1391.

Nappi, A., Drapeau. P. et Savard, J.-P.L. 2004. Salvage logging after wildfire in the boreal forest: Is it becoming a hot issue for wildlife? The Forestry Chronicle 80: 67-74.

Niemelä, J. 1997. Invertebrates and boreal forest management. Conservation Biology 11: 601–610.

Newberry, J.E., Lewis, K.J. et Walters, M.B. 2004. Estimating time since death of *Picea glauca* x *P. engelmannii* and *Abies lasiocarpa* in wet cool sub-boreal spruce forest in east-central British Columbia. Canadian Journal of Forest Research 34: 931-938.

Oliveras, I., Gracia, M., Moré, G., Retana, J. 2009. Factors influencing the pattern of fire severities in a large wildfire under extreme meteorological conditions in the Mediterranean basin. International Journal of Wildland Fire 18: 755-764.

Olson, J. S. 1963. Energy storage and the balance of producers and decomposers in ecological systems. Ecology 44: 322-331.

Östlund, L., Zackrisson, O. et Axelsson, A. L. 1997. The history and transformation of a Scandinavian boreal forest landscape since the 19th century. Canadian Journal of Forest Research 27: 1198-1206.

Panshin, A.J. et De Zeeuw, C. 1980. Textbook of Wood Technology, 3*rd* Ed., McGraw-Hill, New York.

Passovoy, M.D. et Fulé, P.Z. 2006. Snag and woody debris dynamics following severe wildfires in northern Arizona ponderosa pine forests. Forest Ecology and Management 223: 237-246.

Payette, S. 1992. Fire as a controlling process in the North American boreal forest. pp. 144-169 *In:* Shugart, H.H., Leemans, R., et Bonan, G.B. (Éditeurs). A system analysis of the global boreal forest. Cambridge University Press, Cambridge.

Peterson, E.B. et Peterson N.M. 1992. Ecology, management, and use of aspen and balsam poplar in the prairie provinces. Forestry Canada, Northwest region, Northern Forestry Centre, Special report 1.

Petranka, J.W., Brannon, M.P., Hopey, M.E. et Smith, C.K. 1994. Effects of timber harvesting on low elevation populations of southern Appalachian salamanders. Forest Ecology and Management 67: 135-147.

Pham, A.T., De Grandpré, L., Gauthier, S. et Bergeron, Y. 2004. Gap dynamics and replacement patterns in gaps of the northeastern forest of Quebec. Canadian Journal of Forest Research 34: 353-364.

Potvin, F. et Bertrand, N. 2004. Leaving forest strips in large clearcut landscapes of boreal forests: A management scenario suitable for wildlife. The Forestry Chronicle 80: 44-53.

Putz, F.E., Coley, P.D., Lu, K., Montalvo, A. et Aiello, A. 1983. Uprooting and snapping of trees: structural determinants and ecological consequences. Canadian Journal of Forest Research 13: 1011-1020.

Raphael, M.G. et Morrison, M.L. 1987. Decay and dynamics of snags in the Sierra Nevada, California. Forest Science 33: 774-783.

Rayner, A. D. M. et Boddy, L. 1988. Fungal decomposition of wood - Its biology and ecology. John Wiley and Sons, Bath, UK.

Renvall, P. 1995. Community structure and dynamics of wood-rotting Basidiomycetes on decomposing conifer trunks in northern Finland. Karstenia 35: 1-51.

Richards, S.A. et Johnson, E.A. 2007. Using decomposition rates to infer how far back tree populations can be reconstructed. Ecology 88: 1582-1586.

Rinn, F. 1996. TSAP (Technology for tree and wood analysis) - Reference manual. - Rinntech.

Roberge, J.M. et Desrochers, A. 2004. Comparaison des caractéristiques des gros chicots entre une sapinière primitive et une sapinière aménagée sur la péninsule gaspésienne, Québec. Canadian Journal of Forest Research 34: 1-5.

Robitaille, A. et Saucier, J.-P. 1998. Paysages régionaux du Québec méridional. Les publications du Québec, Ste-Foy.

Rouvinen, S. et Kouki, J. 2002. Spatiotemporal availability of dead wood in protected old-growth forests: A case study from boreal forests in eastern Finland. Scandinavian Journal of Forest Research 17: 317-329.

Rouvinen, S., Kuuluvainen, T. et Siitonen, J. 2002. Tree mortality in a *Pinus sylvestris* dominated boreal forest landscape in Vienansalo Wilderness, Eastern Fennoscandia. Silva Fennica 36: 127-145.

Rudolph, T.D. et Laidly, P.R. 1990. Jack pine. *In:* Burns, R.M., Honkala, B.H. (Éditeurs.). Silvics of North America: Vol 1 Conifers. USDA Forest Service Agriculture Handbook 654.

Ruel, J.-C. 1995. Understanding windthrow: Silvicultural implications. The Forestry Chronicle 71: 434-445.

Russell, R.E., Saab, V.A., Dudley, J.G. et Rotella, J.J. 2006. Snag longevity in relation to wildfire and postfire salvage logging. Forest Ecology and Management 232: 179-187.

Ryan, K.C., Peterson, D.L. et Reinhardt, E.D. 1988. Modeling long-term fire-caused mortality of Douglas-fir. Forest Science 34: 190-199.

Saint-Germain, M., Drapeau, P. et Buddle, C.M. 2007. Host-use patterns of saproxylic phloeophagous and xylophagous Coleoptera adults and larvae along the decay gradient in standing dead black spruce and aspen. Ecography 30: 737-748.

Saint-Germain, M., Drapeau, P. et Hébert, C. 2004. Xylophagous insect species composition and patterns of substratum use on fire-killed black spruce in central Quebec. Canadian Journal of Forest Research 34: 677-685.

SAS Institute. 2002. Version 9.1. SAS Institute Inc., Cary, NC.

Schaetlz, R.J., Burns, S.F., Johnson, D.L. et Small, T.W. 1989. Tree uprooting: review of impacts on forest ecology. Vegetatio 79: 165-176.

Schmiegelow, F.K.A., Stepnisky, D.P., Stambaugh, C.A. et Koivula, M. 2006. Reconciling salvage logging of boreal forests with a natural-disturbance management model. Conservation Biology 20: 971-983.

Scott, M.L. et Murphy, P.G. 1987. Regeneration patterns of northern white cedar, an old-growth forest dominant. The American Midland Naturalist117: 10-16.

Senecal, D., Kneeshaw, D. et Messier, C. 2004. Temporal, spatial and structural patterns of adult trembling aspen and white spruce mortality in Quebec's boreal forest. Canadian Journal of Forest Research 34: 396-404.

Shigo, A.L. et Marx, H.G. 1977. Compartmentalization of decay in trees. USDA, Forest Service, Agr. Inf. Bull. no 405.

Shorohova, E. V. et Shorohov, A. A. 2001. Coarse woody debris dynamics and stores in a boreal virgin spruce forest. Ecological Bulletins 49: 129-135.

Shorohova, E., Kapitsa, E. et Vanha-Majamaa, I. 2008. Decomposition of stumps 10 years after partial and complete harvesting in a southern boreal forest in Finland. Canadian Journal of Forest Research 38: 2414-2421.

Siitonen, J., Penttilä, R. et Kotiranta, H. 2001. Coarse woody debris, polyporous fungi and saproxylic insects in an old-growth spruce forest in Vodlozero National Park, Russian Karelia. Ecological Bulletins 49: 231-242.

Siitonen, J. et Martikainen, P. 1994. Occurrence of rare and threatened insects living on decaying Populus tremula: A comparison between Finnish and Russian Karelia. Scandinavian Journal of Forest Research 9: 185-191.

Simard, M., Lecomte, N., Bergeron, Y., Bernier, P.-Y. et Paré, D. 2007. Forest productivity decline caused by successional paludification of Boreal soils. Ecological Applications 17: 1619-1637.

Simard, M. et Payette, S. 2001. Black spruce decline triggered by spruce budworm at the southern limit of lichen woodland in eastern Canada. Canadian Journal of Forest Research 31: 2160-2172.

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

Smith, V.G., Watts, M. et James, D.F. 1987. Mechanical stability of black spruce in the clay belt region of northern Ontario. Canadian Journal of Forest Research 17: 1080-1091.

Smirnova, E., Bergeron, Y., Brais, S., et Granström, A. 2008. Postfire root distribution of Scots pine in relation to fire behaviour. Canadian Journal of Forest Research 38: 353-362.

Smith, V.G., Watts, M. et James, D.F. 1987. Mechanical stability of black spruce in the clay belt region of northern Ontario. Canadian Journal of Forest Research 17: 1080-1091.

Söderström, L. 1988. Sequence of bryophytes and lichens in relation to substrate variables of decaying coniferous wood in Northern Sweden. Nordic Journal of Botany 8: 89-97.

Sollins, P., Cline, S.P., Verhoeven, T., Sachs, D. et Spycher, G. 1987. Patterns of log decay in old-growth Douglas-fir forests. Canadian Journal of Forest Research 17: 1585-1595.

Spies, T.A., Franklin, J.F. et Thomas, T.B. 1988. Coarse woody debris in Douglas-fir forests of western Oregon and Washington. Ecology 69: 1689-1702.

Ståhl, G., Kruys, N., Fries, C., Jonsson, B.G. et Lämas, T. 1999. Wood-inhabiting cryptograms on dead Norway spruce (*Picea abies*) trees in managed Swedish boreal forests. Canadian Journal of Forest Research 29: 178-186.

Stocks, B.J. 1987. Fire potential in the spruce budworm-damaged forests of Ontario. Forestry Chronicle 63: 8-14.

Storaunet, K.O. 2004. Models to predict time since death of *Picea abies* snags. Scandinavian Journal of Forest Research 19: 250-260.

Storaunet, K.O. et Rolstad, J. 2004. How long do Norway spruce snags stand? Evaluating four estimation methods. Canadian Journal of Forest Research 34: 376-383.

Storaunet, K.O. et Rolstad, J. 2002. Time since death and fall of Norway spruce logs on old-growth and selectively cut boreal forest. Canadian Journal of Forest Research 32: 1801-1812.

Sturtevant, B.R., Bissonette, J.A., Long, J.N. et Roberts, D.W. 1997. Coarse woody debris as a function of age, stand structure, and disturbance in boreal Newfoundland . Ecological Applications 7: 702-712.

SYSTAT 2004. SYSTAT 12. SYSTAT Software Inc., Richmond, CA.

Tarasov, M.E. et Birdsey, R.A. 2001. Decay rate and potential storage of coarse woody debris in the Leningrad region. Ecological Bulletins 49: 137-147.

Taylor, S.L. et MacLean, D.A. 2007. Dead wood dynamics in declining balsam fir and spruce stands in New Brunswick, Canada. Canadian Journal of Forest Research 37: 750-762.

Thomas, J.W., Anderson, R.G., Maser, C. et Bull, E.L. 1979. Snags. pp. 60-77 *In:* Thomas, J.W. (ed). Wildlife habitats in managed forests: the Blue Mountains of Oregon and Washington. USDA Forest Service, Agriculture Handbook 553.

Tremblay, G. 1974. Géologie du Quaternaire, Région de Rouyn-Noranda et de l'Abitibi, comté Abitibi-est, Québec. Ministère des Richesses naturelles, Rapport intérimaire.

Trofymow, J. A., Moore, T. R., Titus, B., Prescott, C., Morrison, I., Siltanen, M., Smith, S., Fyles, J., Wein, R., Camiré, C., Duschene, L., Kozak, L., Kranabetter, M. et Visser, S. 2002. Rates of litter decomposition over 6 years in Canadian forests: influence of litter quality and climate. Canadian Journal of Forest Research 32: 789-804.

Turner, M.G., Hargrove, W.W., Gardner, R.H. et Romme, W.H. 1994. Effects of fire on landscape heterogeneity in Yellowstone National Park, Wyoming. Journal of Vegetation Science 5: 731-742.

Tyrrell, L.E. et Crow, T.R. 1994. Dynamics of dead wood in old-growth hemlock-hardwood forests of northern Wisconsin and northern Michigan. Canadian Journal of Forest Research 24: 1672-1683.

Vaillancourt, M.-A., Drapeau, P., Gauthier, S. et Robert, M. 2008. Availability of standing trees for large cavity-nesting birds in the eastern boreal forest of Québec, Canada. Forest Ecology and Management 255: 2272-2285.

Vallentgoed, J. 1991. Some important woodborers related to export restrictions. Forestry Canada, Forest Pest Leafl. 74.

Vanderwel, M.C., Caspersen, J.P. et Woods, M.E. 2006. Snag dynamics in partially harvested and unmanaged northern hardwood forests. Canadian Journal of Forest Research 36: 2769-2779.

Vanha-Majamaa, I. et Jalonen, J. 2001. Green tree retention in Fennoscandian forestry. Scandinavian Journal of Forest Research 16: 79-90.

Viereck, L.A. et Johnston, W.F. 1990. Black spruce. *In:* Burns, R.M. et Honkala, B.H. (Éditeurs). Silvics of North America: Vol 1 Conifers. USDA Forest Service Agriculture Handbook 654.

Vincent, J.S. et Hardy, L. 1977. L'évolution et l'extinction des lacs glaciaires Barlow et Ojibway en territoire québécois. Géographie physique et Quaternaire 31: 357-372.

Virkkala, R., Alanko, T., Laine, T. et Tiainen, J. 1993. Population contraction of the white-backed woodpecker *Dendrocopos leucotos* in Finland as a consequence of habitat alteration. Biological Conservation 66: 47-53.

Waskiewicz, J.D., Fulé, P.Z. et Beier, P. 2007. Comparing classification systems for Ponderosa pine snags in Northern Arizona. Western Journal of Applied Forestry 22: 233-240.

Watt, R. et Caceres, M.C. 1999. Managing for snags in the boreal forests of northeastern Ontario. Ontario ministry of natural resources, Northeast Science and Technology Technical Note TN-016.

Whitney, R.D. 1989. Root rot damage in naturally regenerated stands of spruce and balsam fir in Ontario. Canadian Journal of Forest Research 19: 295-308.

Whitney, R.D., Fleming, R.L., Zhou, K. et Mossa, D.S. 2002. Relationship of root rot to black spruce windfall and mortality following strip clear-cutting. Canadian Journal of Forest Research 32: 283-294.

Whittaker, R.H. 1957. Recent evolution of ecological concepts in relation to the eastern forests of North America. American Journal of Botany 44: 197-206.

Woodall, C.W., Grambsch, P.L., Thomas, W. et Moser, W.K. 2005. Survival analysis for a large-scale forest health issue: Missouri oak decline. Environmental Monitoring and Assessment 108: 295-307.

Worrall, J.J., Lee, T.D. et Harrington, T.C. 2005. Forest dynamics and agents that initiate and expand canopy gaps in *Picea-Abies* forests of Crawford Notch, New Hampshire, USA. Journal of Ecology 93: 178-190.

Yatskov, M., Harmon, M.E. et Krankina, O.N. 2003. A chronosequence of wood decomposition in the boreal forests of Russia. Canadian Journal of Forest Research 33: 1211-1226.

Zhong, H. et Schowalter, T. D. 1989. Conifer bole utilization by wood-boring beetles in western Oregon. Canadian Journal of Forest Research 19: 943-947.

APPENDICE A

AIC$_C$ PARAMETERS OF THE MULTIPLE LINEAR REGRESSION MODELS OF DENSITY LOSS IN SNAGS BY SPECIES PRESENTED IN CHAPTER 2

Model[*]	Model ID	Log-likelihood	K[†]	AIC$_c$	Δ AIC$_c$	w_i[‡]
Trembling aspen (*n* = 50)						
NULL (intercept only)	1	122.60	2	-240.94	27.14	0.00
[§]TSD	2	136.32	3	-266.13	1.96	0.11
TSD + DBH	3	136.44	4	-263.99	4.10	0.04
TSD + AGE	4	136.53	4	-264.16	3.92	0.04
TSD + GROWTH	5	137.42	4	-265.94	2.14	0.10
TSD + SCOL	6	136.96	4	-265.03	3.06	0.06
[‖]TSD + CER	7	138.49	4	-268.09	0.00	0.28
[§]TSD + SCOL + CER	8	139.02	5	-266.67	1.42	0.14
[§]TSD + AGE + SCOL	9	139.29	5	-267.22	0.87	0.18
FULL GROWTH (TSD + GROWTH + SCOL + CER)	10	139.39	6	-264.83	3.26	0.06
FULL AGE (TSD + DBH + AGE + SCOL + CER)	11	127.60	7	-238.53	29.55	0.00
Jack pine (*n* = 37)						
NULL (intercept only)	1	95.24	2	-186.13	21.64	0.00
TSD	2	105.83	3	-204.94	2.83	0.08
TSD + DBH	3	107.02	4	-204.79	2.98	0.07
TSD + GROWTH	4	107.00	4	-204.75	3.02	0.07
TSD + SCOL	5	106.66	4	-204.07	3.69	0.05
[‖]TSD + CER	6	108.51	4	-207.77	0.00	0.33
[§]TSD + SCOL + CER	7	109.46	5	-206.98	0.78	0.22
FULL GROWTH (TSD + GROWTH + SCOL + CER)	8	109.90	6	-205.00	2.76	0.08
FULL without AGE (TSD + DBH + SCOL + CER)	9	110.04	6	-205.27	2.49	0.09
Balsam fir (*n* = 57)						
NULL (intercept only)	1	173.66	2	-343.10	9.00	0.00
TSD	2	177.12	3	-347.79	4.30	0.03
TSD + DBH	3	177.18	4	-345.59	6.50	0.01
TSD + AGE	4	176.25	3	-346.04	6.05	0.01
TSD + GROWTH	5	178.30	4	-347.83	4.27	0.04
TSD + SCOL	6	177.19	4	-345.61	6.48	0.01
§TSD + CER	7	180.31	4	-351.85	0.25	0.27
§TSD + SCOL + CER	8	180.88	5	-350.58	1.52	0.14
‖TSD + AGE + CER	9	181.64	5	-352.09	0.00	0.30
§FULL GROWTH (TSD + GROWTH + SCOL + CER)	10	181.96	6	-350.24	1.86	0.12
FULL AGE (TSD + DBH + AGE + SCOL + CER)	11	182.65	7	-349.01	3.09	0.06

Model	Model ID	Log-likelihood	K	AIC$_c$	Δ AIC$_c$	w_i
Black spruce (*n* = 63)						
NULL (intercept only)	1	148.72	2	-293.25	5.20	0.02
TSD	2	150.54	3	-294.68	3.77	0.03
[§]TSD + DBH	3	153.01	4	-297.33	1.12	0.13
TSD + AGE	4	150.64	4	-292.58	5.87	0.01
[§]TSD + GROWTH	5	152.94	4	-297.20	1.25	0.12
TSD + SCOL	6	151.87	4	-295.05	3.39	0.04
TSD + CER	7	150.81	4	-292.92	5.52	0.01
TSD + SCOL + CER	8	152.23	5	-293.42	5.03	0.02
[§]DBH + SCOL	9	153.07	4	-297.44	1.00	0.13
[‖]TSD + DBH + SCOL	10	154.75	5	-298.45	0.00	0.22
[§]TSD + DBH + AGE + SCOL	11	155.66	6	-297.81	0.63	0.16
FULL GROWTH (TSD + GROWTH + SCOL + CER)	12	154.54	6	-295.57	2.87	0.05
FULL AGE (TSD + DBH + AGE + SCOL + CER)	13	155.66	7	-295.28	3.17	0.05

[*] TSD: Time since death; DBH: Diameter at breast height; AGE: Age of stem; GROWTH: Average growth; SCOL: Scolytinae activity; CER: Cerambycidae activity.

[†] Number of parameters including intercept and variance.

[‡] Akaike weight.

[§] Models competing for best model according to Akaike model selection approach (Δ AIC$_c$ < 2).

[‖] Best model according to Akaike model selection approach.

APPENDICE B

AIC$_C$ PARAMETERS OF THE MULTIPLE LINEAR REGRESSION MODELS OF SNAG FALL BY SPECIES PRESENTED IN CHAPTER 3

Model[A]	Model ID	Log-likelihood	K[B]	AIC[C]	Δ AIC[D]	w_i[E]
Trembling aspen (*n* = 453)						
NULL (intercept only)	1	-367.75	3	741.49	110.32	0.00
DBH	2	-350.11	4	708.22	77.05	0.00
COMP	3	-367.35	4	742.70	111.53	0.00
SEV	4	-330.65	5	671.31	40.13	0.00
BA	5	-367.73	4	743.46	112.28	0.00
SEV+BA	6	-315.12	6	642.25	11.08	0.00
COMP+SEV+BA	7	-315.03	7	644.05	12.88	0.00
SALVG	8	-353.84	5	717.68	86.51	0.00
DBH+SEV	9	-327.57	6	667.13	35.96	0.00
DBH+SALVG	10	-343.71	6	699.41	68.24	0.00
SEV+SALVG	11	-330.07	7	674.14	42.97	0.00
DBH+SEV+SALVG	12	-327.05	8	670.10	38.93	0.00
[F]FULL:DBH+COMP+SEV+ BA+SALVG	13	-305.59	10	631.17	0.00	0.99
Jack pine (*n* = 244)						
NULL (intercept only)	1	-187.47	3	381.04	29.87	0.00
DBH	2	-186.91	4	381.99	30.82	0.00
[F]SEV	4	-170.46	5	351.17	0.00	0.49
BA	5	-186.55	4	381.26	30.10	0.00
[G]SEV+BA	6	-170.37	6	353.09	1.92	0.19
SALVG	8	-182.44	5	375.14	23.97	0.00
DBH+SEV	9	-170.44	6	353.24	2.07	0.17
DBH+SALVG	10	-181.60	6	375.55	24.38	0.00
SEV+SALVG	11	-169.97	7	354.42	3.25	0.10
DBH+SEV+SALVG	12	-169.96	8	356.54	5.37	0.03
FULL:DBH+COMP+SEV+ BA+SALVG	13	-169.09	9	356.94	5.77	0.03

Model[A]	Model ID	Log-likelihood	K[B]	AIC[C]	∆ AIC[D]	w_i[E]
Black spruce (n = 1039)						
NULL (intercept only)	1	-1184.40	3	2374.81	72.27	0.00
DBH	2	-1183.66	4	2375.32	72.77	0.00
COMP	3	-1176.68	5	2363.36	60.82	0.00
SEV	4	-1180.50	5	2371.01	68.47	0.00
BA	5	-1183.29	4	2374.58	72.03	0.00
SEV+BA	6	-1179.87	6	2371.74	69.20	0.00
COMP+SEV+BA	7	-1165.86	8	2347.72	45.18	0.00
GSALVG	8	-1147.03	5	2304.06	1.52	0.19
DBH+SEV	9	-1179.82	6	2371.63	69.09	0.00
DBH+SALVG	10	-1146.41	6	2304.82	2.27	0.13
FSEV+SALVG	11	-1144.27	7	2302.54	0.00	0.40
GDBH+SEV+SALVG	12	-1143.67	8	2303.34	0.80	0.27
FULL:DBH+COMP+SEV+ BA+SALVG	13	-1143.44	11	2308.89	6.34	0.02

[A] DBH: Diameter at breast height; COMP: Stand composition; SEV: Fire severity; BA: Stand basal area; SALVG: Proportion of salvage-logged area in a 100 m radius.

[B] Number of parameters including intercept and variance.

[C] AIC_c in the case of jack pine

[D] ∆ AIC_c in the case of jack pine

[E] Akaike weight.

[F] Best model according to Akaike model selection approach.

[G] Models competing for best model according to Akaike model selection approach (∆ $AIC_c < 2$).