UNIVERSITÉ DU QUÉBEC À RIMOUSKI

SUCCESSION SAPROXYLIQUE ET CYCLAGE DU BOIS APRÈS FEU DANS LE NORD DE LA FORÊT BORÉALE DU QUÉBEC

MÉMOIRE
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RÉSUMÉ

Dans cette étude, nous évaluons différents éléments du cyclage des débris ligneux ainsi que de la succession après feu des arthropodes saproxyliques en milieu subarctique québécois le long d'une chronoséquence de sites brûlés sur une période de 29 ans. Le stockage des débris ligneux après feu ainsi que la décomposition et le cyclage du carbone et de l'azote provenant des débris ligneux grossiers (DLG) d'épinette noire furent estimés. La succession des communautés saproxyliques fut évaluée à l'aide de deux techniques de capture soit des pièges à fenêtre disposés sur les chicots et l'encagement de sections troncales de débris au sol et de chicots produits après feu. Le stockage des débris ligneux après feu (21,88-76,39 $m^3.ha^{-1}$) est comparable à celui observé à l'intérieur de peuplements similaires ailleurs au Canada. Toutefois, la décomposition des DLG d'épinette noire dans cette région est excessivement faible (k=0,0041-0,0101) et demeure l'un des plus faibles à avoir été enregistré en milieu boréal. Ceci pourrait s'expliquer par le faible taux d'humidité des chicots associé à une décortication rapide des troncs, ainsi qu'à une faible colonisation par les perceurs de xylème. L'assèchement rapide des chicots pourrait s'expliquer par la chute rapide de l'écorce laquelle serait conséquente à la calcination sévère lors du feu. Étant donné les faibles taux de décomposition et de stockage des DLG, les pertes de C demeurent relativement peu importantes et varient entre 0,0355 and 0,1288 $MgC.ha^{-1}.yr^{-1}$ à l'intérieur des différents peuplements. La concentration et le contenu réel en azote des DLG diminuent rapidement suite au feu pour augmenter de nouveau en fin de chronoséquence lorsque le débris se retrouve au sol. Vingt-neuf ans après feu néanmoins, les DLG constituent une source d'azote (28,4%) comparativement aux arbres vivants. La perte rapide de l'azote serait associée à la décomposition rapide des tissus subcorticaux, au lessivage de même qu'en raison de la fragmentation par certains insectes xylophages. L'augmentation de l'azote en fin de

chronoséquence serait conséquente à la translocation fongique une fois le débris ligneux au sol et les conditions d'humidité propices à la croissance fongique.

Un total de 37 312 arthropodes appartenant à au moins 220 taxons furent capturés à l'aide des deux méthodes de capture. La diversité des coléoptères saproxyliques demeure faible (88 spp.) lorsque comparée à celle observée peu de temps après feu en forêt boréale méridionale du Québec ainsi qu'à l'entomofaune associée aux débris ligneux d'épinette en Europe nordique. La succession après feu de la faune saproxylique à l'intérieur des DLG se déroule par étapes distinctes. La colonisation initiale débute immédiatement après feu alors qu'une deuxième colonisation se produit lorsque le débris chute au sol. La plupart des espèces colonisatrices incluent des prédateurs et des xylophages subcorticaux ainsi que certaines espèces s'alimentant d'ascomycètes. Les longicornes ainsi que les coléoptères cucujoides sont plus abondants l'année même du feu et diminuent par la suite à l'instar de la majorité des colonisateurs initiaux. L'absence de succession réelle à l'intérieur des chicots serait conséquente aux faibles taux de décomposition puisque le substrat demeure inapproprié pour les espèces associées à des stades de décomposition plus avancés. La chute des chicots et leur colonisation subséquente par les basidiomycètes saproxyliques s'accompagne de la colonisation par certaines espèces de coléoptères de diptères micro- et saprophages. Qui plus est, ce phénomène augmente l'accessibilité du substrat ligneux pour plusieurs espèces épigées notamment d'acariens et de collemboles. Par conséquent, la chute du débris ligneux est un mécanisme déclencheur déterminant dans la succession de la faune saproxylique après feu en milieu subarctique.

AVANT-PROPOS

Ce mémoire aborde deux chapitres distincts énoncés dans le titre. Le premier chapitre intitulé "*Postfire black spruce coarse woody debris cycling in the lichen woodland of northern Québec.* " concerne la décomposition et le cyclage du carbone et de l'azote chez les débris ligneux grossiers d'épinette noire après feu en forêt boréale nordique. Ce manuscrit sera soumis au *Canadian Journal of Forest Research.*

Le deuxième chapitre intitulé « *Post-fire succession of saproxylic arthropods in black spruce coarse woody debris in northern Quebec* » vise à caractériser la succession des communautés d'arthropodes saproxyliques associées à la décomposition du mort après feu dans la pessière à lichen de l'est du Canada. Ce manuscrit sera soumis à *Biodiversity and Conservation.*

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RÉSUMÉ

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Un total de 37 312 arthropodes appartenant à au moins 220 taxons furent capturés à l'aide des deux méthodes de capture. La diversité des coléoptères saproxyliques demeure faible (88 spp.) lorsque comparée à celle observée peu de temps après feu en forêt boréale méridionale du Québec ainsi qu'à l'entomofaune associée aux débris ligneux d'épinette en Europe nordique. La succession après feu de la faune saproxylique à l'intérieur des DLG se déroule par étapes distinctes. La colonisation initiale débute immédiatement après feu alors qu'une deuxième colonisation se produit lorsque le débris chute au sol. La plupart des espèces colonisatrices incluent des prédateurs et des xylophages subcorticaux ainsi que certaines espèces s'alimentant d'ascomycètes. Les longicornes ainsi que les coléoptères cucujoides sont plus abondants l'année même du feu et diminuent par la suite à l'instar de la majorité des colonisateurs initiaux. L'absence de succession réelle à l'intérieur des chicots serait conséquente aux faibles taux de décomposition puisque le substrat demeure inapproprié pour les espèces associées à des stades de décomposition plus avancés. La chute des chicots et leur colonisation subséquente par les basidiomycètes saproxyliques s'accompagne de la colonisation par certaines espèces de coléoptères de diptères micro- et

saprophages. Qui plus est, ce phénomène augmente l'accessibilité du substrat ligneux pour plusieurs espèces épigées notamment d'acariens et de collemboles. Par conséquent, la chute du débris ligneux est un mécanisme déclencheur déterminant dans la succession de la faune saproxylique après feu en milieu subarctique.

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1. Introduction générale

Les débris ligneux grossiers (DLG), i.e. tous débris ligneux (souche, chicots, débris ligneux au sol) dont le diamètre dépasse 10 cm (Harmon et al., 1986), constituent un élément ostensible des écosystèmes forestiers où ils remplissent d'importants rôles fonctionnels et structuraux (Swift, 1977a). En effet, la présence de débris ligneux au sol favorise l'établissement de nombreuses plantes vasculaires tandis que maintes formes de DLG contribuent aux processus géomorphologiques en influençant la stabilité des sols et le transport des sédiments en milieux fluviaux (Harmon et al., 1986). De plus, les DLG représentent un habitat critique pour de nombreux taxons auto- et hétérotrophes incluant bryophytes (ex. : Òdor et Standovar, 2001), champignons (ex. : Renvall, 1995), oiseaux nichant cavicoles (ex. : Drapeau et al., 2002; Torgensen et Bull, 1995), amphibiens, reptiles, petits mammifères (ex. : Ecke et al., 2001) et insectes particulièrement (ex. : Hammond, 1996). Ces organismes qualifiés de saproxyliques, concernent toute espèce qui dépend de la présence d'arbres morts ou moribonds ou encore de l'activité de champignons ou d'autres organismes hétérotrophes saproxyliques à au moins un moment de son cycle vital (Speight, 1989). En milieu boréal, la nécromasse ligneuse constitue un important réservoir de carbone et de nutriments compte tenu du long temps de résidence de ce matériau à l'intérieur de l'écosystème. La stabilité à long terme des cycles du carbone et de certains nutriments en milieu forestier est donc inhérente à un apport constant de nécromasse ligneuse (Ausmus, 1977; Swift, 1977b).

De récentes estimations suggèrent que près de 113-157 Pg[1] de carbone serait stocké sous forme de débris ligneux à l'échelle mondiale (Harmon et al., 2000). Pour cette raison, on observe un intérêt de recherche grandissant ainsi qu'une plus grande reconnaissance des DLG comme une composante essentielle au maintien de la biodiversité mondiale et du cyclage du C dans les écosystèmes forestiers (Wang et al., 2003; Krankina et al., 2002; Harmon et al., 2000; Kasischke et Stocks, 2000; Chambers et al., 2000). Dès lors, plusieurs études nord-américaines et européennes se sont penchées sur la distribution, la qualité et le stockage des DLG (voir Harmon et al., 1986). Néanmoins, les investigations concernant l'entomofaune saproxylique (ex. : Hammond et al. 2001; Hammond, 1997, 1996; Saint-Germain 2004a,b,c) ainsi que le stockage et le cyclage des DLG en forêt boréale canadienne (ex. : Laiho et Prescott, 2004; Bond-Lamberty et al., 2002; Wang et al., 2002) demeurent rares.

1.1 La forêt boréale, le feu et le carbone

Occupant 17 % des surfaces émergées mondiales (Kasischke, 2000a), la forêt boréale demeure le second biome forestier en importance sur Terre. Une proportion considérable (~30 %) de ces forêts se trouve en sol canadien où les feux constituent la principale forme de perturbation (Rowe et Scotter, 1973). Ceux-ci jouent donc un rôle prépondérant dans dans la dynamique forestière (Bergeron et al. 2001, 2004 ; Johnson 1992; Payette 1992), la détermination des patrons de diversité végétale (Heinselman, 1981; Rowe et Scotter, 1973) et sur la distribution du carbone à l'intérieur de l'écosystème (Kasischke et al., 2000).

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[1] Pg = x 10^{15} g

Il n'y a pas unanimité à savoir si le biome boréal constitue une source ou un puits de carbone atmosphérique notamment dans l'expectative des récents changements climatiques (Goulden et al., 1998). En effet, ces forêts possèdent à la fois un très grand potentiel de séquestration ou d'émission d'importantes quantités de carbone (Alexyev et al., 2000). En dépit d'une faible productivité primaire, les faibles taux de décomposition de la matière organique en milieu boréal entraînent une forte accumulation de carbone (Richter et al., 2000). Ainsi, les forêts boréales mondiales contiendraient environ 703 PgC ce qui demeure supérieur aux forêts tropicales et tempérées combinées (Kasischke, 2000a). Malgré que la plus grande proportion du carbone en forêt boréale soit stockée dans la fraction humique du sol (Kasischke, 2000b), une portion appréciable est accumulée sous forme de débris ligneux (Wang et al., 2003). En fait, le passage récurrent des feux de forêts occasionne une production considérable de nécromasse ligneuse. Puisque ces feux consument une part importante de la litière et de la fraction organique du sol, les débris ligneux peuvent constituer le plus grand réservoir de carbone à l'intérieur de l'écosystème incendié (Krankina et Harmon, 1995). D'un autre côté, en considérant la consommation des tissus organiques par le feu ainsi que la décomposition subséquente de la nécromasse, notamment celle des débris ligneux, des portions distinctes de la forêt boréale peuvent émettre d'importantes quantités de carbone (Shvidenko et Nilsson, 2000). De ce fait, la décomposition du substrat ligneux après feu peut contribuer fortement aux flux de CO_2 totaux en surface du sol (Bond-Lamberty et al., 2002; Wang et al., 2002). Étant donné l'importance mondiale de la forêt boréale canadienne, il devient impératif d'acquérir davantage de connaissances sur la dynamique après feu du carbone ligneux, et ce d'autant plus dans la perspective des bouleversements écologiques appréhendés par les changements climatiques.

1.2 La décomposition des débris ligneux

La décomposition de la matière ligneuse comprend à la fois le catabolisme fongique, le lessivage des éléments organiques et minéraux de même que la fragmentation du substrat (Swift, 1977b). Cependant, c'est essentiellement par la dégradation fongique des composantes organiques complexes impliquées dans la constitution des parois cellulaires végétales (lignine, cellulose et hémicellulose) qu'est perdue la majorité de la masse ligneuse (Boddy et Watkinson, 1995). Cette perte se traduit éventuellement par un dégagement de CO_2 ainsi qu'une réduction concomitante de la densité du bois (Harmon et al., 1986). Par conséquent, la décomposition du bois mort est inhérente à la croissance fongique laquelle dépend principalement de la qualité du substrat ainsi que de l'environnement immédiat (humidité, température, aération) (Laiho et Prescott, 2004; Harmon et al., 1986). D'une façon générale, on observe une tendance vers de faibles taux de décomposition aux hautes latitudes (Chambers et al., 2000) et altitudes (Brown et al., 1998) ou encore à l'intérieur d'environnements trop secs (Erickson et al., 1985) ou trop humides (Progar et al., 2000). Ainsi, les taux de décomposition les plus élevés furent enregistrés en milieu tropical où les conditions d'humidité et de température favorisent la croissance fongique et la diversité hétérotrophique tout au long de l'année (Chambers et al., 2000). En forêt boréale, une faible température moyenne annuelle ainsi qu'une courte saison de croissance réduisent d'autant les activités des espèces hétérotrophes à quelques mois par année, menant à de faibles taux de décomposition. Qui plus est, le type de perturbation peut fortement influencer les taux de décomposition de la nécromasse ligneuse en affectant simultanément la colonisation fongique et le patron de succession des espèces hétérotrophes (Renvall, 1995). De ce fait, les chicots nouvellement créés suite à un incendie de forêt peuvent demeurer sur pied pendant plusieurs décennies (Tinker et Knight, 2000) dans un état de dessiccation empêchant la colonisation fongique et la dégradation de la matrice ligneuse (Johnson et Greene, 1991). Une grande portion de la nécromasse organique aérienne demeure alors séquestrée durant une période relativement longue suite à un feu de forêt, à plus forte raison lorsque celui-ci survient en milieu subarctique où les taux de décomposition sont déjà faibles.

1.3 Le cyclage de l'azote chez les débris ligneux

De récentes investigations ont montré que le rôle des DLG dans le cyclage des nutriments en forêt coniférienne demeurait relativement faible en raison de la concentration négligeable du bois en éléments nutritifs (Laiho et Prescott, 1999, 2004; Swift, 1977a). Néanmoins, le taux de décomposition de la matrice ligneuse influence directement le cyclage des nutriments qui y sont présents. En effet, on remarque des changements de concentration chez plusieurs nutriments, notamment l'azote, à mesure que la nécromasse ligneuse se décompose (Creed et al., 2004a, 2004b). La concentration en azote à l'intérieur du substrat ligneux peut soit augmenter, diminuer ou demeurer stable, en raison d'activités biotiques (ex. : colonisation fongique, fixation bactérienne) ou abiotiques (ex. : lessivage, nitrification), lesquelles fluctuent en fonction du stade de décomposition du substrat.

1.4 Diversité et succession des arthropodes saproxyliques en forêt boréale

La contribution de l'entomofaune saproxylique à la biodiversité boréale est substantielle (Olberg et al., 2001; Kaila et al., 1997). Hammond (1996) estime qu'environ 2000 espèces d'arthropodes saproxyliques sont associées à la nécromasse ligneuse de *Populus* dans le nord de l'Alberta alors que près de 1300 espèces de coléoptères sont répertoriées comme étant saproxyliques en Fennoscandie (Kaila et al., 1997). La grande hétérogénéité du substrat ligneux serait à l'origine du maintien de la biodiversité saproxylique, plusieurs espèces étant intimement associées à certaines propriétés physiques de la matrice ligneuse et du biotope immédiat (Jonsell et al., 1999; Økland et al., 1996; Kaila et al., 1994).

La majorité des efforts de recherche sur la diversité saproxylique furent dirigés en Scandinavie (ex. : Nilsson et al., 2001; Olberg et al., 2001; Bakke, 1999; Økland et al., 1996) où plusieurs siècles de supressions effective des feux et de pratiques sylvicoles intensives ont considérablement réduit le volume et la répartition de la nécromasse ligneuse (Siitonen, 2001; Økland et al., 1996). Selon ces auteurs, il appert que la colonisation par l'entomofaune saproxylique s'effectue selon un patron successionnel distinct en raison d'une différentiation spatio-temporelle des niches écologiques (Simandl, 1993). Par conséquent, les espèces associées aux différents états de décomposition de la matrice ligneuse se succèdent à mesure que la colonisation fongique dégrade le substrat (Esseen et al., 1992, 1997). La phase initiale de colonisation débute habituellement très peu de temps après la mort de l'arbre par les coléoptères subcorticaux et les perceurs de xylème auxquels suivent les prédateurs et les parasitoïdes associés ainsi que certaines espèces mycétophages s'alimentant sur les ascomycètes qui dégrade les tissus subcorticaux. En consommant la matrice ligneuse et en favorisant l'inoculation par les champignons saproxyliques, les espèces xylophages initiales peuvent influencer les patrons de décomposition des DLG ainsi que le cyclage subséquent des nutriments (Schowalter et al., 1992; Edmonds et Eglitis, 1989; Zhong et Schowalter, 1989; Ausmus, 1977). Les espèces phléophages secondaires, détritivores et mycétophages se nourrissant de mycélium en croissance succèdent aux colonisateurs initiaux. La croissance subséquente des sporocarpes attire une entomofaune mycétophage, prédatrice et parasite spécifique à mesure que l'habitat subcortical disparaît. À ce point, la succession saproxylique peut varier sensiblement en fonction de la colonisation fongique en raison des associations très spécifiques des communautés colonisant les sporocarpes (Jonsell et Weslien, 2003; Rukke, 2002; Kaila et al., 1997). Éventuellement, l'entomofaune saproxylique inclut graduellement davantage d'espèces épigées en raison de la décomposition extensive de l'aubier et du duramen et de leur incorporation à la couche humique du sol (Irmler et al., 1996).

1.5 Cas particulier des arbres incendiés

Le patron de colonisation des arbres tués par le feu constitue un cas particulier de la succession saproxylique. En effet, à l'inverse de la mort isolée d'un arbre les feux transforment soudainement une quantité considérable de biomasse ligneuse en nécromasse, créant du même coup un substrat de colonisation abondant, spatialement défini, et dépourvu de compétition pour nombre d'espèces hétérotrophes. Malgré que le feu puisse réduire substantiellement l'abondance de l'entomofaune en tuant directement les individus ou en altérant les propriétés physico-chimiques de l'habitat (McCullough et al., 1998; Puntilla et Haila, 1996), maints taxons présentent des adaptations morphologiques et comportementales afin de détecter et coloniser le bois calciné (Wikars et Schimmel, 2001; Lundberg, 1984; Evans, 1966). Bien que le patron de colonisation saproxylique du substrat ligneux calciné soit particulièrement bien documenté (St-Germain et al., 2004; Wikars et Schimmel, 2001; Dajoz, 1998; Muona et Rutanen, 1994), très peu d'études à ce jour ont évalué les changements à long terme des communautés saproxyliques après feu (Werner, 2002; Howden et Vogt, 1951). Sachant que la décomposition et la colonisation fongique diffèrent fortement selon le type de perturbation, la succession saproxylique à long terme des arbres incendiés devrait présenter un patron de colonisation distinct de celui des arbres sénescents et morts en forêts surmatures en fonction des changements de propriétés du substrat ligneux.

1.6 Objectifs

Le premier volet de cette étude concerne la décomposition ainsi que le cyclage du carbone et de l'azote des débris ligneux grossiers d'épinette noire après feu en milieu subarctique. Les objectifs spécifiques de ce volet portent sur i) une évaluation du volume total de débris ligneux dans les pessières brûlées, ii) une estimation des taux de décomposition, de stockage et des pertes de carbone ligneux ainsi que iii) sur la mesure des changements de concentration en azote et en carbone en relation avec le stade de décomposition des débris ligneux grossiers d'épinette noire dans une chronoséquence de sites brûlés pour une période de 29 ans.

Le deuxième volet de ce mémoire s'articule autour de l'étude de la succession des arthropodes saproxyliques le long de la même chronoséquence. Les objectifs spécifiques consistent à i) décrire la diversité totale des coléoptères saproxyliques après feu et ii) de déterminer la succession des assemblages d'arthropodes saproxyliques en relation avec diverses caractéristiques physiques des DLG d'épinette noire après feu.

CHAPITRE PREMIER

POSTFIRE BLACK SPRUCE COARSE WOODY DEBRIS CYCLING IN THE LICHEN WOODLAND OF NORTHERN QUÉBEC

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Abstract

In this study, we investigate woody debris cycling in northern Quebec using a 29-year post-fire chronosequence. Post-fire woody debris storage along with decomposition rates, and variation of N and C content of coarse woody debris (CWD) of black spruce (*Picea mariana* [Mill.]) are estimated. Post-fire woody debris storage (21.88-76.39 $m^3.ha^{-1}$) is within the range previously estimated for northern black spruce stand. Decomposition of post-fire black spruce CWD in northern Quebec is excessively slow (k=0.0041-0.0101) and one of the slowest ever recorded in boreal forest. Low decomposition rate could be related to low moisture content in snags, fast bark shedding and low initial larval colonisation by xylem borer. Quick drying of snags may be associated with fast bark shedding as barked trunk retain moisture content for a longer time period. Fast bark shedding could be related to severe scorching during fire. Given the low decomposition rate and CWD storage, C losses are relatively low and vary between 0.0355 and 0.1288 $MgC.ha^{-1}.yr^{-1}$ in study sites. Nitrogen concentration and content clearly show a U-shaped pattern with time since fire. Nevertheless, post-fire black spruce CWD are still a N source (28.4%) 29 years after fire relative to living trees. Initial quick loss of N is associated with rapid decomposition of subcortical tissus, leaching and insect communition. Increase in N content in late chronosequence may be related to fungal translocation once CWD is on the ground and moisture content is propitious for fungal growth. Nitrogen content is not related to decomposition stage of dead wood since N can be relocated outside of debris as fungal spores are dispersed after sporocarp fruiting.

Keywords: CWD, boreal forest, C cycling, fire, black spruce

Introduction

Coarse woody debris (CWD) are a conspicuous feature of forest ecosystems. Structural and functional roles of CWD in forest ecosystems have been recognized at both the local and global scales (Kasischke and Stocks 2000; Swift 1977a). Dead woody material decomposes rather slowly (Harmon et al. 1986) and may form important carbon and nutrient pools that may have long term significance in C and nutrient cycling in woodland ecosystem (Ausmus 1977; Swift 1977b). Furthermore, rotting logs on forest floor are known to favour the establishment of various vascular plants while many forms of CWD are greatly involved in geomorphic processes by influencing soil and sediment transport and storage (Harmon et al. 1986). Decaying wood represents also a critical habitat for several auto- and heterotroph taxa including bryophytes (e.g. Òdor and Standovar 2001), fungi (e.g. Renvall 1995), cavity-nesting birds (e.g. Drapeau et al. 2002; Torgensen and Bull 1995), amphibians, reptiles, mammals (e.g. Ecke et al. 2001) and particularly insects (e.g. Hammond 1996).

At the global scale, there has been increasing research attention and growing appreciation of CWD as an essential component of ecosystems in the last decades notably to address C budget assessments with the prospect of global climate change (Wang et al. 2003; Krankina et al. 2002; Harmon et al. 2000; Kasischke and Stocks 2000; Chambers et al. 2000). Coarse woody debris storage and decomposition rates have been estimated for numerous forest ecosystems, particularly in temperate North America and in boreal Eurasia. Hence, recent estimates suggest that nearly 113-157 PgC is stored as woody detritus (WD) globally (Harmon et al. 2000). Despite a growing accuracy of global CWD storage data, a significant portion of global forest area has been neglected. For instance, very few studies (e.g. Bond-Lamberty et al. 2002; Wang et al. 2002; Laiho and Prescott 1999) have investigated CWD assessments in boreal North America which a large fraction is located in Canada.

Boreal forests have a great potential to sequester or emit large amount of carbon over short periods of time (Alexeyev et al. 2000). In fact, despite a low net primary productivity (NPP), low decomposition rates of the organic matter in boreal forest lead to a great accumulation of C (Richter et al. 2000). For instance, global boreal forests contain *ca.* 703 PgC which is more than tropical and temperate forests combined (Kasischke 2000b). Though the greatest C fraction in boreal forest is stored in the soil organic layer (Kasischke 2000a), a fairly large amount is accumulated as WD (Wang et al. 2003). In fact, lethal wildfires, which are one of the main disturbances occurring in boreal forest (Rowe and Scotter 1973), produce large bulk of WD annually. When a severe fire consumes much of the litter and organic soil, woody detritus can become the dominant detrital C store in the ecosystem (Krankina and Harmon 1995). On the other hand, considering duff combustion and subsequent decomposition of the post-fire detrital mass, discrete patches of boreal forest can temporarily become a carbon source. Hence, respiration of post-fire WD as a result of the decomposition process contributes to a rather large fraction of total soil surface CO_2 efflux (Bond-Lamberty et al. 2002; Wang et al. 2002). Giving the importance of Canada's boreal forest, it becomes clear that a better knowledge of post-fire CWD dynamic and decomposition rates is essential in order to develop more accurate national and global carbon budget models. Since an increase in temperature and change in fire frequency in the boreal forest is forecasted with the global climate changes (Flannigan and van Wagner 1991, Bergeron et al. 2001, 2004), CWD dynamic and CO_2 emission should be directly affected by these changes.

Large scale assessment of CWD decomposition and subsequent carbon loss require a closer look to local factors affecting this process. Decomposition of CWD highly depends on substrate quality and environment (moisture, temperature and aeration). (Laiho and Prescott 2004; Harmon et al. 1986). In a general way, there is a trend toward decreasing CWD decomposition rates with latitude (Chambers et al. 2000), elevation (Brown et al. 1998) and in too dry (Erickson et al. 1985) or in too wet environments (Progar et al. 2000). Highest decomposition rates have been measured under tropical environments where temperature and moisture conditions lead to high heterotrophic activities all year round (Chambers et al. 2000). In boreal forest, low mean annual temperature and short growing season reduce heterotrophic activity to few months per year which lead to low WD decomposition rates. Furthermore, the cause of death in tree can strongly influences the decomposition rate by affecting fungi colonisation and heterotrophic succession pathways (Renvall 1995). Fire-killed trees may take several decades to fall on the ground (Tinker and Knight 2000) and desiccate very quickly which leads to low CWD decomposition rates (Johnson and Greene 1991). Hence, a great fraction of aboveground carbon detrital mass may remain sequestrated for a long time period in fire-killed trees, particularly in subarctic environment where decomposition rates are slow.

In coniferous forest, the role of CWD in nutrient cycling is thought to be relatively low since nutrient concentration in wood is very poor compared to other litter components (Laiho and Prescott 2004, 1999; Swift 1977a). Nevertheless, decomposition rates of CWD have a direct influence on nitrogen cycling from wood (Creed et al. 2004a,b). Nitrogen is viewed as one of the main limiting factor in wood decomposition as C/N ratio of this substrate is frequently over 350 (Cowling and Merrill 1966). Following either biotic (e.g. fungi colonisation, anaerobic bacterial fixation) or abiotic processes (e.g. leaching, nitrification), nitrogen content in wood can either increases, decreases or stabilizes (Creed et al. 2004a,b) with time since tree death. Consequently, assessing nitrogen dynamic in dead wood can give additional information on the decomposition process of woody detritus.

The objectives of this study are to i) evaluate total WD volume in post-fire black spruce (*Picea mariana* [Mill.]) stands ; ii) estimate the decomposition rates, C storage and C losses and iii) estimate changes in N and C contents with time since fire and decay stage of post-fire black spruce CWD in northern Quebec using a chronosequence approach.

Material and Methods

Study area

Sampling was held within a range of 100 km of the town of Radisson (53°79' N, 77°62 W) in north central Québec, Canada (Fig. 1). This area belongs to the lichen woodland ecosystem and is located at only 150 km of the southern border of the subarctic forest tundra. The sampling area is located in the precambrian geological formation of the canadian shield which is mainly composed of granitic and gnessic rocks (Stockwell et al. 1968). Topography consists in a mainly low altitude (100-200m) plateau dissected by lowlands. Surface deposits are mainly from fluvioglacial origin (Stockwell et al. 1968). The climate is typical of the lower-subarctic region with a mean annual air temperature (MAT) of –3.6 °C and January and July averages of –25 and 13°C respectively. Annual precipitation averages 637 mm, 40 % of which falling as snow (Environment Canada 1993). Forest occupies every non-edaphically limited site and is mainly composed of even-aged stands of jack pine (*Pinus banksiana* Lamb.) and black spruce (*Picea mariana* [Mill.] BSP.). Open, uneven-aged stands dominated by black spruce are found on paludified sites of the lowlands, intermingled with extended bogs and fens. Wildfire constitutes the most important natural disturbance and its recurrence cycle is approximately 100 years (Parisien and Sirois 2003; Payette et al. 1989).

Sites

Sites were located along a chronosequence of five different fires that occurred in the vicinity of Radisson in either 1973, 1988, 1989, 1996 or 1998. Sites were located using fire maps provided by the *Société de Protection des Forêts contre le Feu* (SOPFEU) for the 1972-2002 time period and from fire scar analysis in this area (Sirois and Arseneault, unpublished data). Considering the relatively high fire frequency in this region, pure stands of black spruces are mainly located on sites with poor drainage conditions and various depth of organic forest floor. Sampling was conducted in June and July 2002 except for the stand burned in 1988 which was sampled in June 2003. Within each fire, one 60 x 60 m site was settled according to the following criteria : 1) no slope, 2) mature black spruce dominated stands, i.e. aged from 60 to 250 yr when fire occurred and 3) 100 % tree mortality following fire.

Methods

Four square plots of 100 m^2 located 40 m apart were settled in one site within each burned area. Within each plot, all woody debris that were at least 1m long were measured for maximum and minimum diameter and length. With these data, we estimated woody debris volume as a cone. When the main axis was broken, total volume was estimated as a truncated cone. Only woody debris with the base inside the plots were considered. Distinction between woody debris present before fire and those produced at the time of fire was made; the latter exhibit burned small branches combined with a lack of charcoal on main trunk whereas woody debris produced before fire showed large area of scorched wood. Apices breakage when present was noted as for position (fallen : log ; standing : snag) of the debris. Additional data coming from two others recently burned stands (2002, 2001) sampled in 2002 in a parallel study were included in the analysis for total WD volume and snag fall rate. Woody debris were identified to species level in field following general appearance, remaining cones, bark and twigs or in laboratory by wood anatomy criteria (Hoadley 1990) when necessary.

Further sampling was performed on coarse woody debris with base diameter between 10 and 15 cm which is the dominant diameter class of mature spruce in that area. Bark cover was noticed and then peeled off. Fraction of bark cover remaining on main trunk was assessed as low (ca. < 33%), medium (ca. 33-65%) or high (ca. >65%). All entrance holes created by xylem borer larvae were counted from the base of CWD until a diameter of 4 cm was reached on the debris. After examination, it appears that these holes were mainly done by *Monochamus scutellatus* (L.) (Coleoptera : Cerambycidae) since this species is the main spruce deep-boring xylophagous Coleoptera encountered in this area (chapter two). No hole performed by other wood borers (e.g. Scolytinae, Buprestidae) was noticed. Two cross-sections of approximately 5 cm thick were sampled on every snag and log. On snags, cross-sections were taken 50 cm and 150 cm above ground whereas those sampled on logs were selected at 50 cm and 150 cm from breakage point of woody debris, i.e. from the largest end. Eight mature living spruces with maximum diameter between 10-15 cm were selected from random location in a residual old-growth stand (>200 years old). Cross-sections were sampled at 50 and 150 cm of height in order to estimate pre-fire condition of trees (basic density, moisture, carbon and nitrogen contents).

Samples were put in hermetic bags to prevent moisture loss and put in a freezer to stop further fungal or bacterial degradation until laboratory analyses. Remaining bark on samples was removed. Cross-sections were weighted for green mass and then oven-dried at 70°C until a constant weight was reached. Dry mass was determined from the last weighting. Moisture content was estimated from mass loss after drying and was expressed as proportion of dry mass. Fragmented or highly irregular cross-sections (16.6% of all samples) were put in vacuum-sealed bag and volume was determined by water displacement. Remaining cross-sections (83.4%) were considered as a cylinder and volume was estimated by approximating the mean diameter and thickness of cross sections to the nearest millimetre.

Wood density ($g.cm^{-3}$) was expressed as dry weight on dry volume. Samples with high amount of lignin corresponding to compression wood or branch knots were discarded (Erickson et al. 1985). Oven-dried cross-sections were ground to pass a 35-mesh filter. Concentration ($mg.g^{-1}$ of dry weight) of C, H and N were determined on one 3-mg subsample of ground material using a Perkin Elmer 2400 CHN Elemental analyser. Nutrient concentration alone is not an accurate measure of nutrient dynamic (Holub et al. 2001). In fact, the concentration of N may change if the rate of N loss differs from the rate of C loss (Creed et al. 2004b; Boddy and Watkinson 1995). In order to consider mass loss during decomposition, C and N content ($mg.cm^{-3}$) were determined by multiplying concentration of either N or C by density of cross sections (Creed et al. 2004b). Values of density, moisture content, N and C concentrations and contents coming from cross-sections of the same CWD were averaged.

Total CWD mass and C storage in each burned site was estimated from mean density and carbon content in cross sections and calculated CWD volumes respectively. Total C loss from CWD was estimated from the difference between mean carbon content in living trees and mean carbon content in CWD volume at t post-fire years, in each sampled site. Carbon loss and CWD mass were extrapolated to all CWD (>10 cm of max. diameter). Dead trees larger than sampled (>15 cm of diameter) represent less than 20 % of CWD abundance in burned stand.

Data analyses

Decomposition process of dead wood implies that wood lose mass with time as complex organic compounds (lignin, cellulose, hemicellulose) are degraded mainly from fungal activity (Harmon et al. 1986). Coarse woody debris decomposition was modelled independently on snags and logs with density data ($g.cm^{-3}$) from cross sections with two different functions depending on time :

$$(1) \qquad Y_t = Y_0.e^{-kt}$$

$$(2) \qquad Y_t = Y_0.(1-(1-e^{-kt})^n)$$

where Y_t is wood density at t post-fire years, Y_0 is initial wood density, *k* is a decomposition constant and *n* represents a lag-period (yr) where decomposition delays in early chronosequence. Those models imply that CWD retains its structural integrity thus keeping a constant volume during the decomposition process (Harmon et al. 1986). This assumption is not always met in highly decayed woody material where structural matrix is too weak which lead to shrinkage of WD. Nevertheless, initial density of CWD was assessed as density of living spruces. The single exponential (1) or lag-time (2) function that resulted in best R^2 was selected for either snags and logs decomposition modelling.

Fall rate of snags assessed as the fraction of fire-killed trees that remains standing in site was estimated with simple linear regression. Variation in bark cover along the chronosequence was evaluated by likelihood ratio chi-square test. Since snags and logs do not occur simultaneously in either the 1998 or the 1973 burned sites, position of debris was not considered as a factor in analyses. Instead, snags and logs were considerated as different groups along the chronosequence (e.g. living trees: group 1; 1998 snags: group 2, 1996 logs: group 3). Differences in mean moisture, carbon and nitrogen contents as well as nitrogen concentration between groups were assessed by Kruskal-Wallis tests. Levene tests on mean residual wood density and moisture content values were used to evaluate the differences in the variability of data along chronosequence. Tukey's honestly significant difference test (α=0.05) was used in both cases for post-hoc multiple comparison tests. Effect of bark cover and position of debris on both moisture content and wood density in the 1989 burned site was assessed with Sheirer-Ray-Hare tests. Variations of N concentration and content as well as C/N ratio with wood density for both snags and logs were evaluated with simple linear regressions. All statistical analyses were performed using SYSTAT 9.01.

Results

Vegetation structure of burned stand

Sites vegetation structure is summarized in Table 1. Black spruce stem density before fire varied between 525 and 2400 ind.ha^{-1} (mean=1882) whereas other species are negligeable. Post-fire regeneration stem density (> 1m high), mainly of *P. mariana*, is almost exclusively assessable in the oldest burned site (1973) and equals 3575 ind.ha^{-1} Burned organic matter is the dominant substrate in study sites except in the two oldest burned sites (1988 and 1973) where *Sphagnum* sp. becomes more abundant. Ground vegetation is mostly dominated by *Ledum groenlandicum* Oeder and *Cassandra calyculata* (L.) except in the most recent burned site where no ground vegetation is observed. Arbustive vegetation only appears in two burned sites (1989 and 1973) and is made of either *Betula glandulosa* Michaux or *Salix* sp.. No arboreal cover (> 3 m high) is noticed in any burned sites. Mean *Monochamus* sp. larval entrance hole density on CWD vary from 0.46 to 26.9 per square meter (mean=9.36) in burned sites.

Total volume of WD

Total WD volume in sites averages 46.4 ± 21.4 $m^3.ha^{-1}$ (mean ± SD) and varies between 21.9 and 76.4 $m^3.ha^{-1}$ (Table 2). Volume of post-fire WD in study sites is always greater than pre-fire WD volume. Between 21.3 $m^3.ha^{-1}$ and 66.8 $m^3.ha^{-1}$ of post-fire WD are noticed along chronosequence which represent 83.1-100% of total spruce WD volume in corresponding site. Woody debris produced before fire and still present in burned stands are relatively scarce, averaging 3.62 $m^3.ha^{-1}$. Apparent prefire WD (i.e. not burried in forest floor) are virtually absent from the stands burned in 2002 and 2001.

A total of 230 cross sections coming from 107 CWD (56 snags and 51 logs) and 8 living black spruces were sampled in this study. Coarse fraction (CWD) of total post-fire WD volume is particularly important and vary from 48.7% in the stand burned in 1996 to 84.9% in the 1989 burned site (Table 2). Total mass of post-fire *Picea* CWD estimated from mean density of sampled cross sections and total volume in sampled plots varies between 6.0 and 28.8 $Mg.ha^{-1}$.

Snag fall rate

Fall rate of coarse snags throughout chronosequence follows a regular linear trend ($R^2 = 0.992$; $p<0.001$; Fig. 3). The onset of breakage is noticed in the 1998 burned stand and is sustained at 3.37% of initial volume falling per year. According to this model, 50% (T_{50}) of snags would be on the ground after 16.2 years while all of them would be fallen after 31.0 years.

Decomposition rate

Single exponential models better explain the variation of CWD wood density with time since fire for both snags and logs (Fig. 4). Both models however exhibit low R^2 (snags: 0.045; logs: 0.154) since a great variation in densities is noticed in older sites. Moreover, snag data failed normality test. Decay rate expressed as the k constant is much faster for logs (k=0.0101) than snags (k=0.0041). According to the models, half-time of snags is 169.0 years while logs lose 50 % of their mass in 68.6 years. Hypothetical complete degradation (T_{95}) of snags would be effective 730 years after fire while logs would be cycled after 296 years.

Bark cover

Bark cover on CWD significantly differs along chronosequence ($G_{[8,0.05]}=80.83$; $p<0.001$; Fig. 5). All snags and logs from the 1998 burned stand exhibit high bark cover ; bark cover decreases with time since fire to become low for all CWD from the oldest burned site. Bark shedding does not seem to be homogenous from an individual to another with time since fire. While there is not a great variation in bark cover in early or late chronosequence, both CWD exhibiting high and low bark cover occur simultaneously in either 1988 or 1989 burned stands.

Moisture content

Moisture content in CWD differs significantly ($H_{[8,0.05]}=41.82$; $p<0.001$) among groups along chronosequence (Fig. 6a). For snags, the moisture content decreases from an initial value of 65.1% in living trees to 23.5% four years after fire. The mean moisture content is maintained under 27 % in standing snags in all sites and is lowest for the oldest snags at 14.7%. Logs are always significantly more humid by 10.6 % to 17.8 % than snags in concurrent sites. Moreover, mean moisture content of logs is always above the value of 32% and is highest in the older sites with a value of 77.3%.

Variation in moisture content and wood density in late chronosequence

Wood density (Fig.4), as for moisture content (Fig. 6a), is greatly variable in CWD from burned sites of late chronosequence. Post-hoc multiple comparison Tukey test assessed on moisture residual values shows that variance in logs from the oldest site is significantly higher ($p<0.01$) than moisture variance values elsewhere in chronosequence. However, although wood density residual values are higher in late chronosequence, post-hoc Tukey test does not reveal any significant differences ($p>0.05$) between mean wood density residual values throughout chronosequence. In the 1989 burned stand, these variations could be related to bark cover since wood density is highest on both snags and logs with low bark cover while logs with high bark cover are the most decayed (Fig.7b). Nevertheless, effect of bark cover on wood density is not significant ($H_{[0.05,2]}=5.24$; $p=0.0728$) as for position of debris ($H_{[0.05,1]}=0.87$; $p=0.350$) and their interaction ($H_{[0.05,2]}=0.536$; $p=0.764$) in this site. In the same stand, remaining bark cover has a significant effect ($H_{[0.05,2]}=12.48$; $p<0.01$) on moisture content (Fig. 7a) as opposed to position ($H_{[0.05,1]}=1.05$; $p=0.306$) and their interaction ($H_{[0.05,2]}=0.375$; $p=0.829$). Highest moisture content is noticed on woody debris which have high remaining bark cover on both snags and logs with 34.2 and 76.8% respectively. Mean moisture contents of CWD (snags and logs) with low and moderate bark cover vary between 16.7 to 29.7%.

Carbon and nitrogen fluctuations

The mean C concentration is rather similar between groups along chronosequence and leans between 47.71 to 50.08% (Fig.6b) and this, even if Kruskal-Wallis test indicate significant differences ($H_{[0.05,8]}=25.62$; $p<0.01$). Carbon concentration expressed as fraction of dry weight does not vary significantly with wood density ($R^2=0.0023$; $p=0.644$). Carbon storage in sites estimated from mean carbon content in woody samples varies from 2.85 to 13.84 $MgC.ha^{-1}$. Considering post-fire CWD volume in each burned site and mean carbon content in samples, carbon losses average between 35.5 and 128.8 $kgC.ha^{-1}.yr^{-1}$ along chronosequence.

Nitrogen concentrations differ significantly ($H_{[0.05,8]}=26.98$; $p<0.001$) along the chronosequence (Fig. 6c). Nitrogen concentration clearly shows a U-shaped pattern with time since fire. Mean nitrogen concentration decreases quickly from 11.74 $g.kg^{-1}$ in living trees to 7.36 $g.kg^{-1}$ four years after fire and is maintained between 6.58 and 7.61 $g.kg^{-1}$ on snags thereafter. Mean nitrogen concentration of logs increases from 6.92 $mg.g^{-1}$ six years after fire to 12.01 $g.kg^{-1}$ 29 years after fire. Nitrogen concentration increases significantly with decreasing wood density (Fig. 8a) for logs (R^2=0.306 ; p<0.001) whereas no significant relation is noticed in snags (R^2=0.002 ; p=0.740). As a result, C/N ratio decreases significantly with decreasing wood density (Fig. 8c) in logs (R^2=0.125 ; p<0.05) as opposed to snags (R^2=0.020 ; p=0.332) though normality tests failed in both cases.

Results are quite different with nitrogen content that consider mass loss through decomposition of CWD (Fig. 6d). When considering mass loss, N content does not show any significant relationship with wood density (Fig. 8b) in logs (R^2=0.003 ; p=0.724) and snags (R^2=0.064 ; p=0.075). Mean N content differs significantly in groups with time since fire ($H_{[0.05,8]}$=23.34 ; p<0.01). From 0.67 $kg.m^{-3}$ in living trees, there is a net loss of 37% to 0.42 $kg.m^{-3}$ of nitrogen in snags four years after fire and net amount of nitrogen is lowest in the 1989 burned stand at 0.33 $kg.m^{-3}$. On the other hand, logs gain N with time since fire to reach 0.48 $kg.m^{-3}$ in the oldest site. These estimates suggest that woody debris would be a N source representing 28.4% of initial N content in living trees 29 years after fire.

Discussion

The chronosequence approach has been used extensively in the past for coarse woody debris assessments (cf. Harmon et al. 1986). According to Krankina et al. (2002) this approach allows valid approximations of temporal dynamics of WD decomposition processes. Nevertheless, comparisons of results with other studies concerning CWD storage are rather difficult since methods of field measurements and calculations vary widely among studies (Krankina et al. 2002). Furthermore, much of the studies are biased toward results concerning CWD storage in old-growth forests rather than post-disturbance recruitment and decomposition of CWD.

CWD storage after fire

The volume of woody detritus storage observed in this study (21.88 – 76.39 $m^3.ha^{-1}$) is rather low compared to volumes (145 – 450 $m^3.ha^{-1}$) reported in post-disturbed natural stands of southern to mid boreal zones in northern Europe (Krankina et al. 2002; Siitonen 2001). Nevertheless, total CWD dry mass (6.00-28.79 $Mg.ha^{-1}$) are within values reported from other black spruce post-fire stands in Canada (1.4 – 177.6 $Mg.ha^{-1}$, Bond-Lamberty et al. 2002). Total post-fire WD storage comes mainly from two sources i.e. woody detritus in stand existing in pre-disturbance conditions as well as woody debris produced by the disturbance itself. Woody necromass in pre-disturbed natural stands mostly depends on 1) site productivity, 2) stand successionnal stage, both affecting the input rate of dead wood and 3) decomposition rate of woody necromass (Krankina and Harmon 1995; Harmon et al. 1986). On the other hand, the potential volume of post-fire woody debris is mostly correlated to the volume of living trees present when fire occurred. Assuming a 100% mortality of living stems following intense crown fires, post-fire woody necromass will roughly equal the volume of living spruces since fire hardly consumes any bole-wood of living trees (Siitonen 2001). In study sites, both pre- and post-fire woody necromass are particularly low. Whereas the reduced pre-fire woody detritus volume (0 – 9.61 $m^3.ha^{-1}$) could be partly related to fire consumption, conversion to charcoal (Siitonen 2001; Tinker and Knight 2000) and to burial through the process of forest-floor build-up, both low pre-fire and post-fire woody detritus volumes are related to the reduced productivity in pre-fire stand (Krankina and Harmon 1995) resulting from low tree density at northern latitudes (Payette 1989).

Decomposition rates of CWD

Estimated decomposition rates for fire-killed black spruce CWD in the present study (k=0.0041 – 0.0101) are particularly low and are among the lowest ever recorded in boreal forest. Estimated decay rates for spruce species in northern Europe range between 0.005-0.059 (e.g. Tarasov and Birdsey 2001; Shorohova and Shorohov 2001; Harmon et al. 2000, Naesset 1999; Krankina and Harmon 1995) while rates ranging between 0.0025-0.071 have been reported in boreal North America (Laiho and Prescott 1999; Alban and Pastor 1993; Johnson and Greene 1991; Graham and Cromarck 1982; Foster and Lang 1982). Slow decomposition rates could be related to low mean annual temperature (-3.6 °C) as microbial activity and the decomposition of organic matter is mainly expected to be temperature-dependant (Wang et al. 2002; Chambers et al. 2000) although studies vary in this respect (Harmon et al. 2000). Nevertheless, Bond-Lamberty et al. (2002) estimates of black spruce decay rates in Thomson, Manitoba (MAT=-3.4°C, precipitation=537mm), which has a similar climate to Radisson, are higher (0.016-0.045) than those assessed in the present study. Higher decay rates could be attributable to higher snag fragmentation rate and the inclusion of smaller size class and pre-fire woody debris in sampling.

Estimated decomposition rate of logs is nearly 2.5 fold higher than snag. Several studies have already pointed out that decomposition of standing woody debris can be very slow (Shorohova and Shorohov 2001; Kasischke 2000a; Johnson and Greene 1991; Krankina and Harmon 1995; Fahey 1983). Naesset (1999) and Mattson et al. (1987) have found that woody sections with direct contact with the forest floor had faster decomposition rate than those held in the air. Sampling shows that mean moisture content in snags quickly drops with time since fire and remains under 30 % throughout the chronosequence. Similar low moisture content have already been noticed elsewhere (Johnson and Greene 1991). Bond-Lamberty et al. (2002) noticed that respiration of CWD was moisture-limited below 43.1 %. It has been shown in previous studies that moisture is frequently limiting WD decomposition (Wang et al. 2002; Laiho and Prescott 1999) since fungi, mainly basidiomycetes, cannot reach water below the fiber saturation point which is commonly fixed at 30 % in dead wood (Harmon et al. 1986; Erickson et al. 1985). Limited moisture content in snags probably delays or strongly reduces fungi respiration and other heterotrophic activities which directly influences the decomposition rate of WD. Higher moisture content maintained in logs presumably favours fungi growth which increases the decomposition rate of wood. Since their decomposition rate is very low, post-fire snags should constitute a major carbon reservoir in boreal forest (Kasischke 2000b).

Although logs generally displayed a greater decomposition rate compared to snags from concurrent sites, heterogeneity between individuals in wood density and in moisture content is very important, especially in late chronosequence. Both environmental and structural microsite conditions of CWD probably play an important role in decay rates. High variation in density and moisture content in logs from the oldest sites could reflect the amount of time the fire-killed tree have stood before falling (Brown et al. 1998) as fragmentation of snags noticed along chronosequence is very gradual, though consistent, with rates estimated from many fire-killed species in boreal forest (Harmon et al. 1986). Past studies (Tinker and Knight 1998; Harmon et al. 1986) have shown that post-fire snags can remain standing for few years to several decades. Therefore, considering higher decomposition rates once fire-killed trees fall to the ground, logs that have been on the ground only since few years may exhibit lower mass losses than even-aged logs that fell sooner.

Likewise, moisture content and decomposition rate of wood seem related to a certain extent to post-fire bark shedding which is particularly fast in this case compared to other studies (Harmon et al. 2000). Large variation in bark cover between trees only few years following disturbance may be related to fire intensity since highly scorched bark shed faster than lightly or unburned bark (Wikars 2002). Dead trees that retain an important bark cover for a longer time period could maintain a higher moisture content in detrital tissues which could in turn facilitate the colonisation of saproxylic fungi. Although fungi diversity was not estimated from sampling, some preliminary observations show that primary coloniser inhabiting fire-killed spruces are mainly *Gleophyllum*, *Fomes* and *Trichaptum* species. Whereas the latter is classified as white-rot fungi, *Gleophyllum* and *Fomes* spp. cause a cubic brown-rot in various coniferous trees, making them ineffective to degrade the lignin component as oppose to white-rot fungi (Boulet 2003; Renvall 1995; Niemelä 1985; Swift 1977a). *Trichaptum* species are rapid invaders that aggressively occupy large volume of dead spruce or pine trunks which results in quick mass loss (Temnuhin 1996; Renvall 1995). As brown-rot fungi are mainly found in dry environments (Renvall 1995) they are most likely to inhabit fire-killed spruce that quickly loose their bark cover since they contain a lower moisture content. Dead fire-killed trees colonized by these species are susceptible to exhibit slower decomposition rates as only a fraction of the whole complex organic matrix can be degraded.

Low decomposition rates could partly result from poor initial colonisation by wood-borers. Recent investigations in the study area (chapter 2) have shown that *Monochamus scutellatus* (L.) is the main wood-borer encountered in fresh post-fire black spruce CWD. This species is thought to play a significant role in wood decomposition (Edmonds and Eglitis 1989). Past larval density of this species, as revealed from larval entrance hole abundance on fire-killed spruces, averages between 0.46 and 26.88.m^{-2} at each burned site (mean all CWD = 9.35 m^{-2}). Density of *M. scutellatus* in burned black spruce have been found to be much higher in the southern part of the boreal forest in Québec, varying between 20 and 65 holes.m^{-2} (Nappi et al. 2003) to 92.78 holes.m^{-2} (Saint-Germain. Xylophagous insects, particularly wood-borers (Cerambycidae, Buprestidae and Scolytinae) are known to favour the establishment of wood-rotting fungi by providing access to the xylem through larval galleries and/or by active or passive spore inoculation by ovipositing adults (Six and Bentz 2003; Zhong and Schowalter 1989). Moreover, channelizing invertebrates in woody material could trigger bacterial nitrogen fixation resulting in a higher nitrogen concentration and decomposability of the woody substrate (Ausmus 1977). Low wood-borer density could therefore reduces the colonisation and growth potential for certain species of saproxylic fungi and in turn reduces mass loss.

It is likely that decomposition rates of post-fire woody debris may be higher in stands older than those sampled due to high solar exposure and hence evaporation throughout the studied chronosequence. Sites subjected to limited solar exposure due to slope aspect have shown to exhibit higher soil moisture content and faster woody debris decomposition rate (Naesset 1999; Mattson et al. 1987). In fact, moisture content in wood should increase with the canopy closing as woody debris would experience less direct solar radiation and evaporative demand (Bond-Lamberty et al. 2002; Erickson et al. 1985). Even in the oldest site (29-yr after fire), regeneration cover was relatively scarce whereas arboreal cover was completely lacking. Estimated decomposition rates of post-fire black spruce WD is probably underestimated as gradual canopy closure with time since fire could increase ambient moisture level.

Contribution of CWD decomposition to carbon emission

Given the relatively slow decomposition rate and low volume of CWD in sites, carbon losses mainly through fungi respiration are particularly low compare to more southern studies. Obviously, C losses from CWD in forest ecosystems are related to CWD mass and its decomposition rate. Whereas C losses from post-fire black spruce CWD average between 0.0355 and 0.1288 $MgC.ha^{-1}.yr^{-1}$ in the study sites, values as high as 0.11 – 1.92 $Mg.ha^{-1}.yr^{-1}$ were estimated in post-fire black spruce stands in northern Manitoba

(Bond-Lamberty et al. 2002). Higher C losses in northern Manitoba could be explained by higher estimated decomposition rates and woody detrital mass in few sites.

Carbon and nitrogen concentration

Nitrogen content that reflected changes in density showed that CWD is a net N source 29 years after fire since 28.4 % of original N content was lost over the chronosequence. Nitrogen in CWD can have one of several fates i.e. 1) net retention by bacteria and/or fungi; 2) net gain from a) bacterial conversion of atmospheric N_2 to organically bound N or b) fungal translocation from atmosphere, forest floor or soil; 3) net loss by a) leaching of dissolved N, b) denitrification or volatilization to gaseous N or c) from CWD fragmentation (cf. Creed et al. 2004a). When considering changes through mass loss, nitrogen content in post-fire CWD of the present study follows a sequence of three distinct phases. In fact, abrupt net loss of N is noticed shortly after tree death then N content is rather stable for at least a decade while CWD in late chronosequence exhibit a net gain of N. Initial release of N was already reported in spruce (Laiho and Prescott 1999) whereas Idol et al. (2001) noticed the immobilization of N in early decay stages. Initial nitrogen loss can be attributable to either the rapid decomposition of cambium and phloem by ascomycetes, leaching (Harmon et al. 1986) or comminution and frass production by subcortical insects (Schowalter et al. 1998). Degradation of these woody fractions could represent a great loss of N as the concentration of many nutrients, including N, is highest in phloem and cambial tissues (Cowling and Merrill 1966). Frass produced by Douglas-fir beetles does not contribute greatly to nutrient cycling although nitrogen content in frass was three to fourfold higher than logs (Edmonds and Eglitis 1989). Investigations held in the study area (chapter 2) have shown that xylophagous subcortical feeding activities, mostly by Lepturinae (Coleoptera : Cerambycidae), was mainly restricted to the two first postfire years. Low heterotrophic activities and degradation of the woody necromass between year 4 and 15 after fire could explain the relative stability at low-nitrogen content in both snags and logs. Potential retention by bacteria and fungi during this time-period is possible in woody samples where decomposition process of woody tissue has been initialized.

A critical C/N ratio has been suggested as a controlling factor in the immobilization and release of N in decomposing substrate (Edmonds and Eglitis 1989). The critical ratio would be related to the decomposition rates of the substrate and should be estimated as follow :

$$\text{Critical C/N} = [\ln(k/0.49)]/-0.01$$

where the critical C/N ratio is the C/N where N loss can occur and k is the decomposition constant. Following this assumption, critical C/N ratio should be higher for substrate that decomposes slowly. Considering a separate k constant for snags (0.0041) and logs (0.0101), critical C/N ratio would be 478 and 388 respectively which is consistent with previous studies (Creed et al. 2004a; Edmonds and Eglitis 1989). Giving these thresholds, N loss can mostly occur in early chronosequence as C/N ratio in living spruce which is though to be the same at time of tree death, averages 424. Mineralization of N may have occurred in some samples throughout chronosequence, mostly in logs from late chronosequence (Fig. 9). These data are consistent with the initial net loss of N noticed right after fire in post-fire snags and may explain its immobilization in the following decade.

One should expect that the net gain of nitrogen in the oldest site results from translocation by growing fungal hyphae as wood become more decayed with time since fire. In many cases, nitrogen content have been shown to increase with decreasing wood density (cf. Laiho and Prescott 2004). Although N content is higher in late chronosequence, nitrogen does not show any relationship with decreasing density of woody samples in both snags and logs. Nitrogen content could be more related to fungal colonisation rather than decomposition stage of CWD. In fact, net gain of nitrogen is possible through translocation via fungal hyphae as fungi grows and consumes woody necromass (Boddy and Watkinson 1995; Schowalter et al. 1998; Edmonds and Eglitis 1989; Ausmus 1977). However, translocated nitrogen can be relocated outside CWD as fruiting bodies and spores are produced and dispersed (Boddy and Watkinson 1995). Spatial relocation in spores can represent a considerable drain of nutrients including nitrogen (Cowling and Merrill 1966) although recent investigations have shown that N export in sporocarps was very small in some cases (Edmonds and Lebo 1998). Hence, CWD colonized by fungi producing fruiting bodies can exhibit lower nitrogen content than debris that are colonized by growing hyphae of a not yet fruiting fungi.

Considerations for future studies

The elaboration of complete C budgets from post-fire CWD in northern Quebec requires further specifications on the variation in CWD storage affected by NPP, fire history and decomposition rates. Spatial heterogeneity of CWD and decomposition over large areas can be considerable according to several biotic and abiotic factors (Rouvinen et al. 2002). Throughout northern Quebec, fire frequency is greatly variable, decreasing with latitude (Payette et al. 1989) and at the proximity of marine influence from the Atlantic (Foster 1985) and the Hudson and James Bays (Parisien and Sirois 2003) whereas decomposition rates as NPP should decrease with latitude as climate becomes harsher. The inclusion of these models with data on CWD production in regenerated stands should give a more precise look on C storage and cycling in the Canadian boreal forest and how they can represent a net sink or source of atmospheric carbon.

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Table 1. Stand structure of burned sites

Sites	**Time since fire (year)**	**Pre-fire stem density[1] (ha^{-1})**		**Post-fire stem density[2] (ha^{-1})**		**Dominant substrate**	**Dominant ground vegetation (< 1m)**	**Dominant arbustive vegetation (height : 1-3m)**	**Dominant arboreal tree species (height > 3 m)**	**Monochamus larval entrance holes density[3] ± 1 SD (m^{-2})**
		Picea	Other[4]	*Picea*	Other[4]					
2002	0.17	2250	25	0	0	Burnt organic matter	-	-	-	No data
2001	1	525	150	0	0	Burnt organic matter	*Cassandra calyculata* (L.)	-	-	No data
1998	4	2400	75	0	0	Burnt organic matter	*Ledum groenlandicum* Oeder	-	-	9.73 ± 8.98
1996	6	2250	0	0	0	Burnt organic matter	*Ledum groenlandicum* Oeder	-	-	26.9 ± 22.64
1989	13	2275	0	75	50	Burnt organic matter	*Ledum groenlandicum* Oeder	*Betula glandulosa* Michaux	-	0.99 ± 1.26
1988	15[a]	1625	0	0	0	*Sphagnum* sp.	*Ledum groenlandicum* Oeder	-	-	16.46 ± 15.71
1973	29	1850	100	3425	150	*Sphagnum* sp.	*Ledum groenlandicum* Oeder	*Salix* sp.	-	0.46 ± 1.23

[1] Estimated from post-fire CWD of > 5 cm of maximum diameter

[2] All tree species individual of >1 cm of base diameter and >1 m long

[3] Counted on CWD of 10-15 cm of maximum diameter

[4] Include *Pinus banksiana*, *Larix laricina* and *Populus tremuloides*

[a] Site was sampled 1 year later (2003) than other sites

Table 2. Volume, mass, mass of C and C loss in WD of each burned stand.

Site	**Time since fire yr**	**Vol. WD $m^3.ha^{-1}$**	**Vol. pre-fire WD $m^3.ha^{-1}$**	**Vol. post-fire *Picea* WD $m^3.ha^{-1}$**	**Vol. post-fire *Picea* WD standing $m^3.ha^{-1}$ (%)**	**CWD fraction of total post-fire WD (%)**	**Mass post-fire CWD[1] $Mg.ha^{-1}$**	**C Mass from post-fire CWD[1] $Mg\ C.ha^{-1}$**	**C losses from post-fire CWD[1] $kg\ C.ha^{-1}.yr^{-1}$**
2002	0.17	65.08	0	61.69	61.69 (100)	82.9	-	-	-
2001	1	30.33	0	8.44	8.44 (100)	78.8	-	-	-
1998	4	44.24	7.48	35.24	32.97 (93.6)	59.7	11.42 (6.15)	5.48 (2.95)	70.6 (38.0)
1996	6	25.94	2.89	23.05	17.21 (74.7)	48.7	6.00 (6.00)	2.85 (2.85)	37.0 (37.0)
1989	13	76.39	9.61	66.78	46.36 (69.4)	84.9	28.79 (16.26)	13.84 (7.82)	128.8 (72.7)
1988	15[a]	21.88	0.29	21.29	10.53 (49.5)	68.7	7.11 (6.33)	3.47 (3.09)	35.5 (31.6)
1973	29	60.90	5.11	45.07	8.35 (18.5)	73.2	13.53 (8.93)	6.57 (4.34)	84.6 (55.9)

[1] Values in parentheses are for post-fire CWD of 10-15 cm diameter class

[a] Site was sampled 1 year later (2003) than other sites

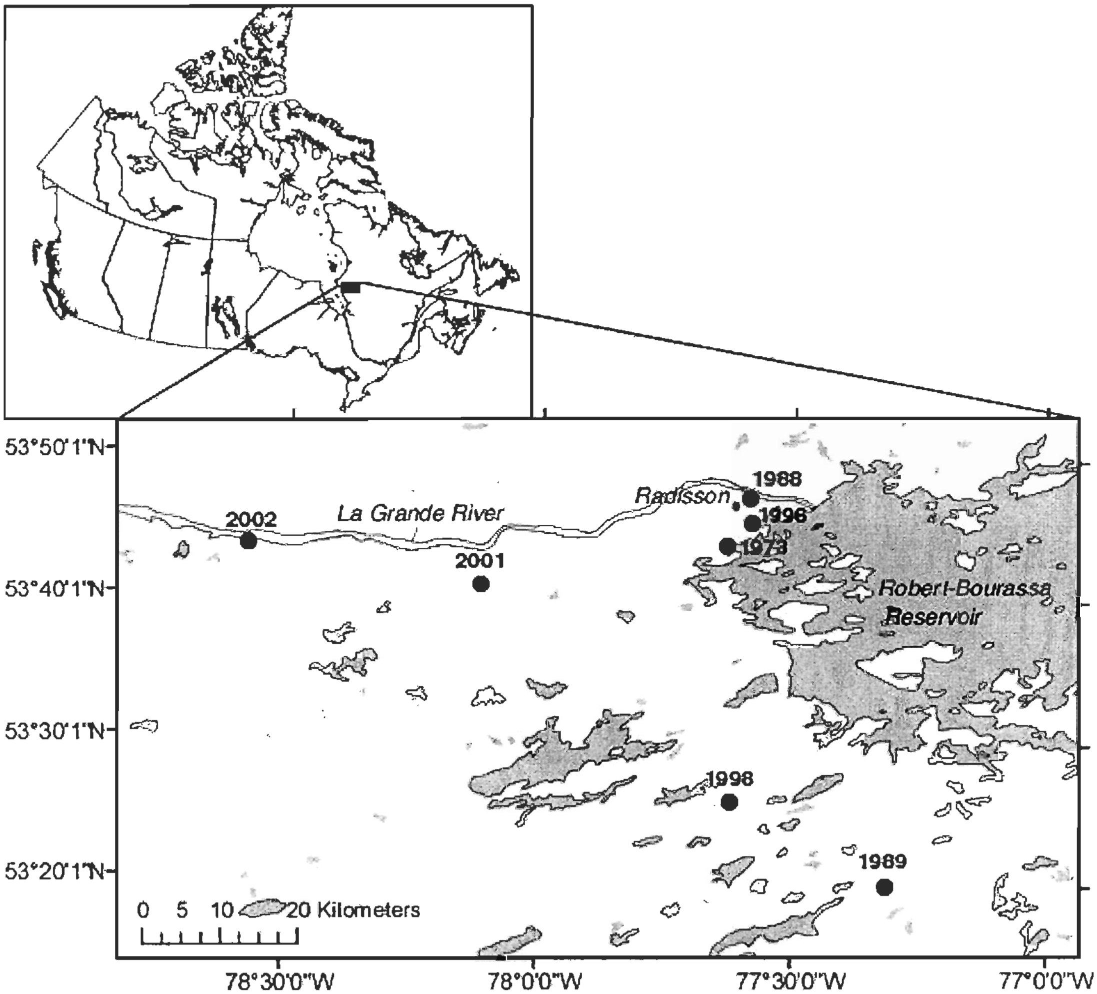

Figure1. Location of the study area.

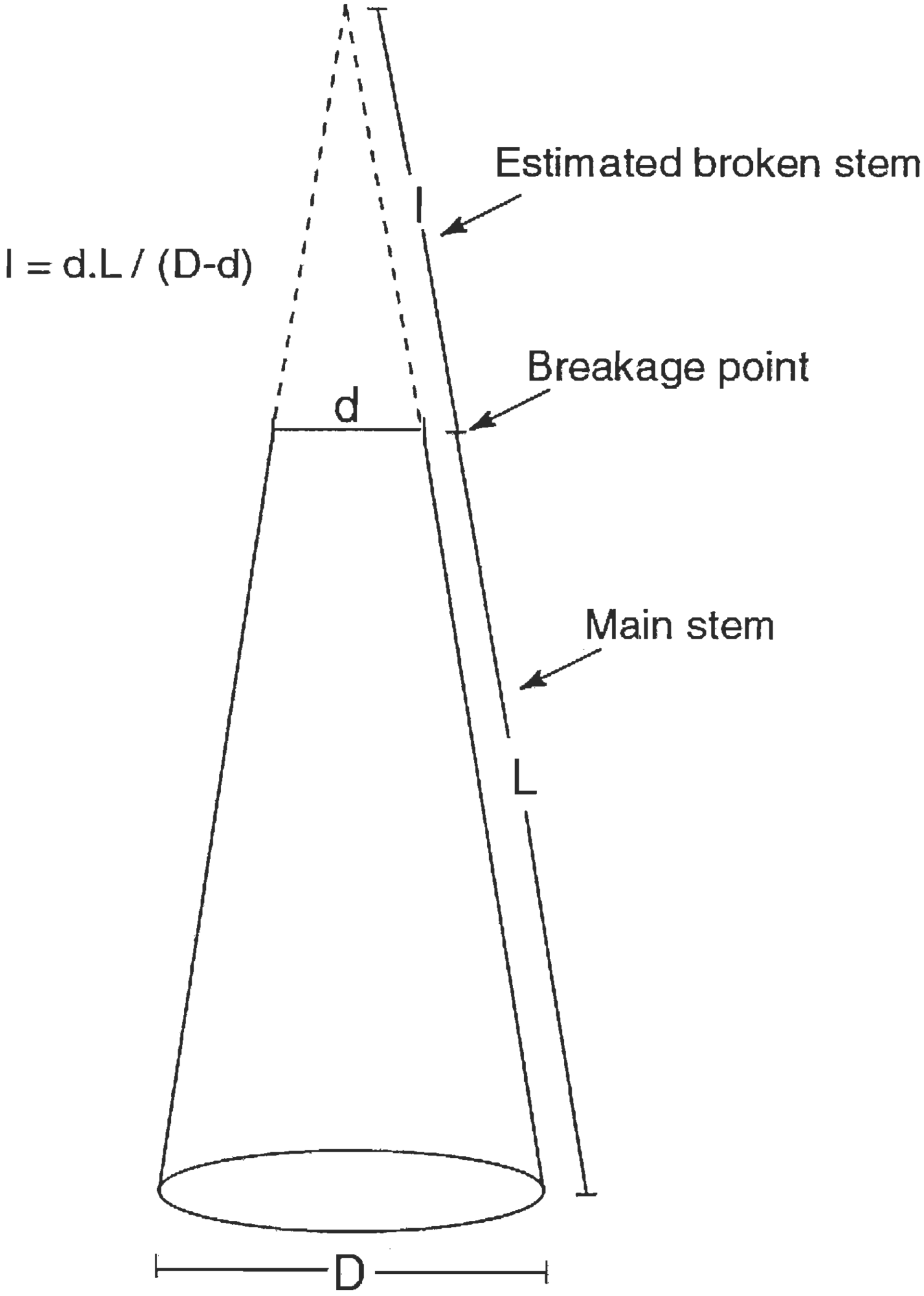

Figure 2. Schematic representation of broken CWD volume estimation. Main stem is considered as a truncated cone whereas the estimated broken stem volume is considered as the remaining volume of the truncated cone. D = Diameter at the largest end ; d = diameter at the smallest end ; L = length of main stem ; l = estimated length of broken stem.

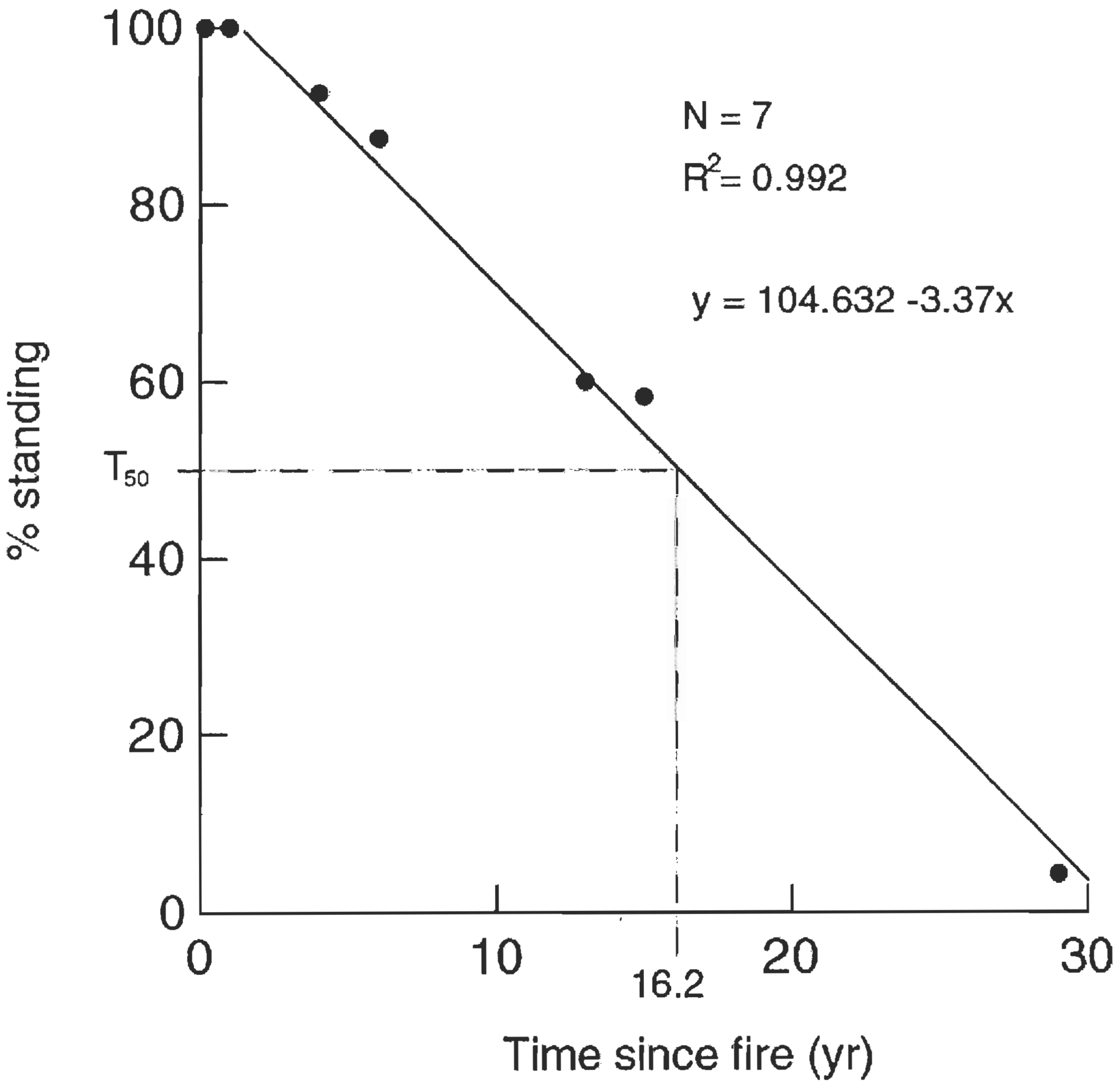

Figure 3. Proportion of snags (maximum diameter=10-15cm) still standing in each burned stand. Half-time (T_{50}) of snag is 16.2 years.

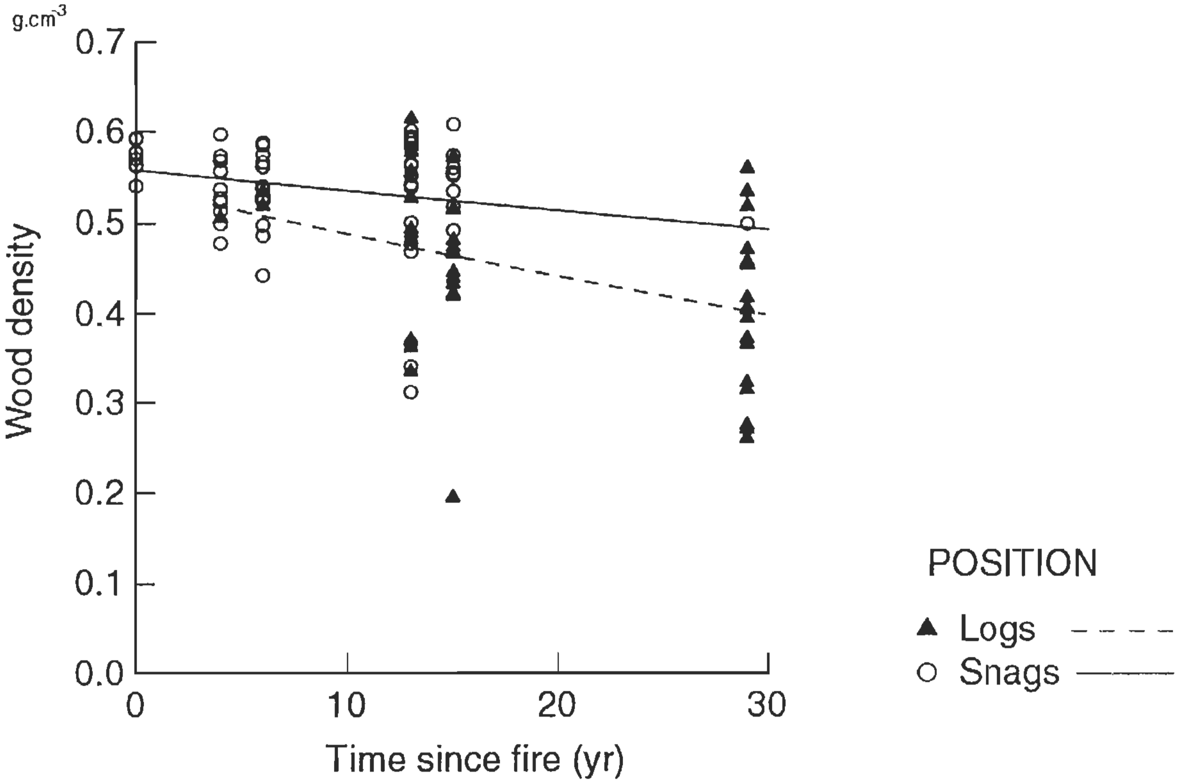

Figure 4. Exponential decomposition models for snags and logs. Logs: $Y_t=0.540e^{-0.0101t}$, $R^2=0.154$; Snags: $Y_t=0.558e^{-0.0041t}$, $R^2=0.045$ where t is time since fire (yr) and Y_t wood density at time t.

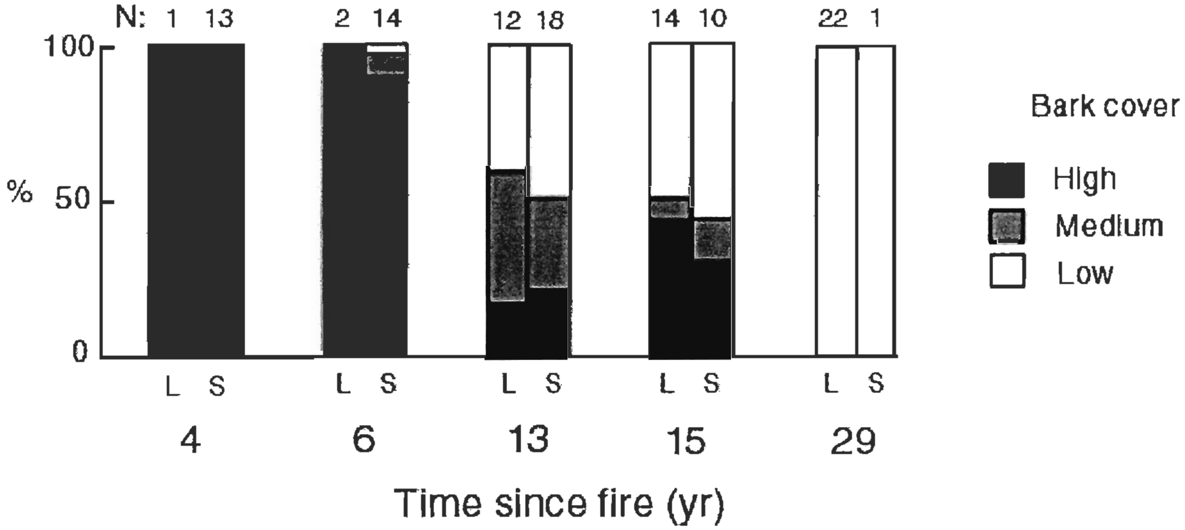

Figure 5. Proportion of snags (S) and logs (L) exhibiting low (<33%), medium (33-65 %) and high (>65%) bark cover remaining on trunk along chronosequence.

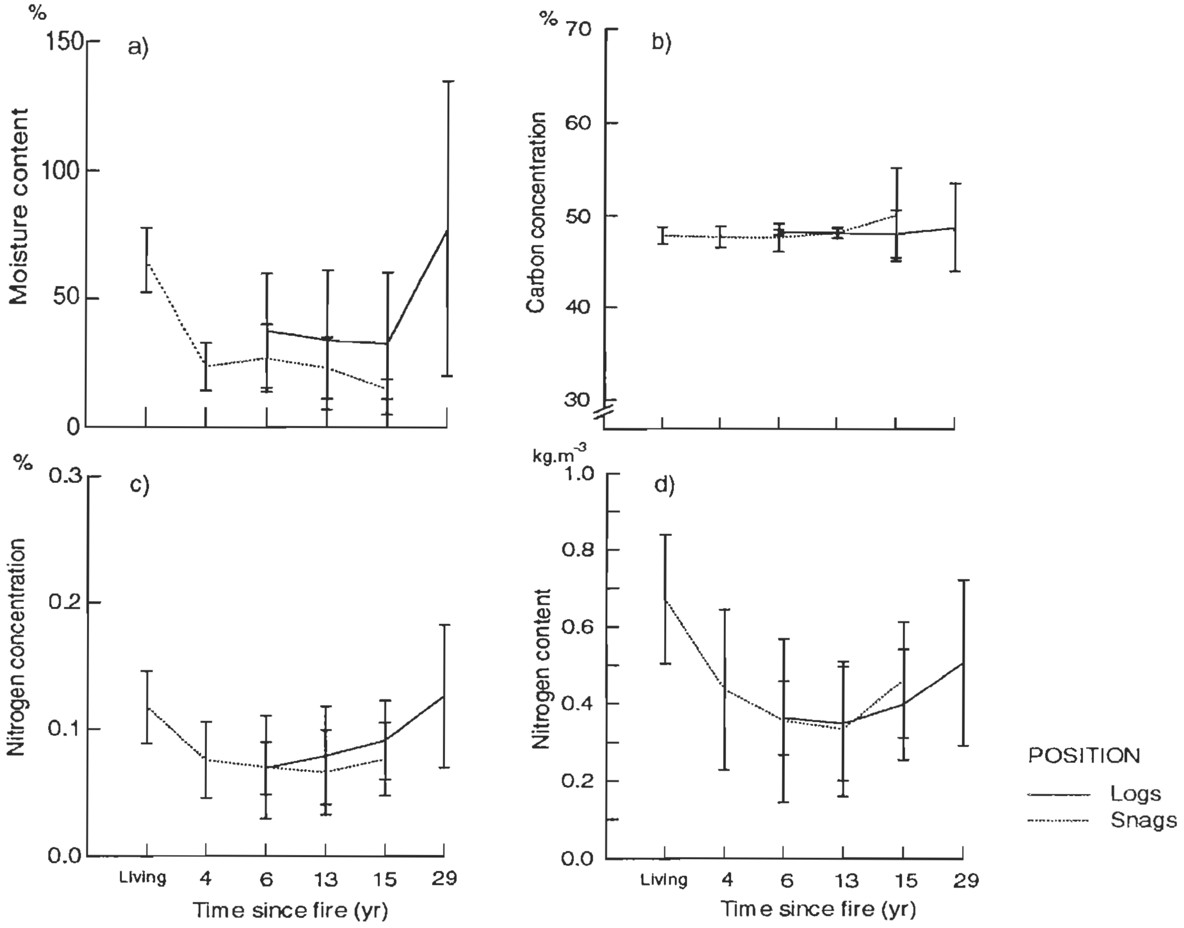

Figure 6. Moisture content (% of dry weight), carbon and nitrogen concentration (%) as well as nitrogen content (kg.m^{-3}) in snags (dashed line) and logs (plain line) along chronosequence. Error bars represent 1 SD.

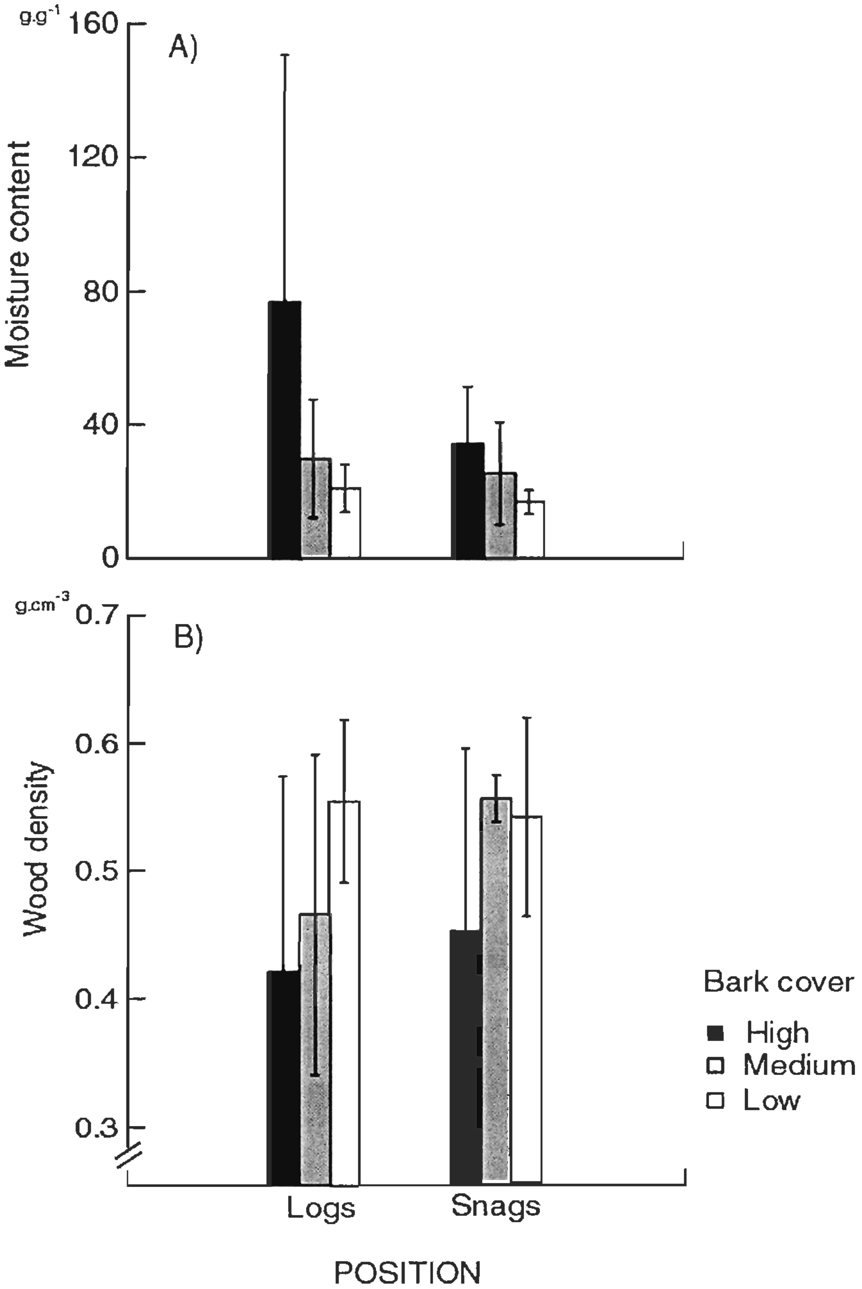

Figure 7. Moisture content and wood density in relation with bark cover for logs and snags coming from the stand burned in 1989 (13 years after fire). Error bars represent 1 SD.

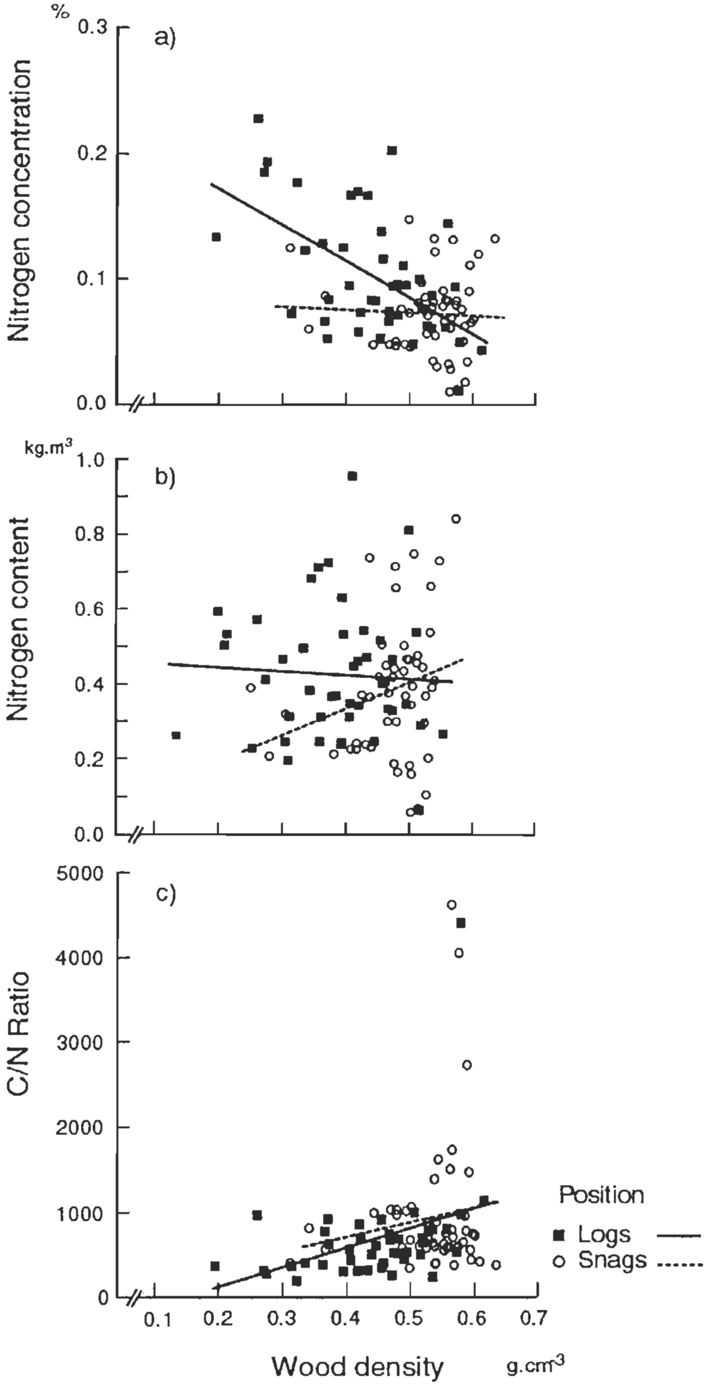

Figure 8. Nitrogen concentration (%) and content (kg.m^{-3}) as well as C/N ratio in relation with wood density (g.cm^{-3}) for both snags and logs.

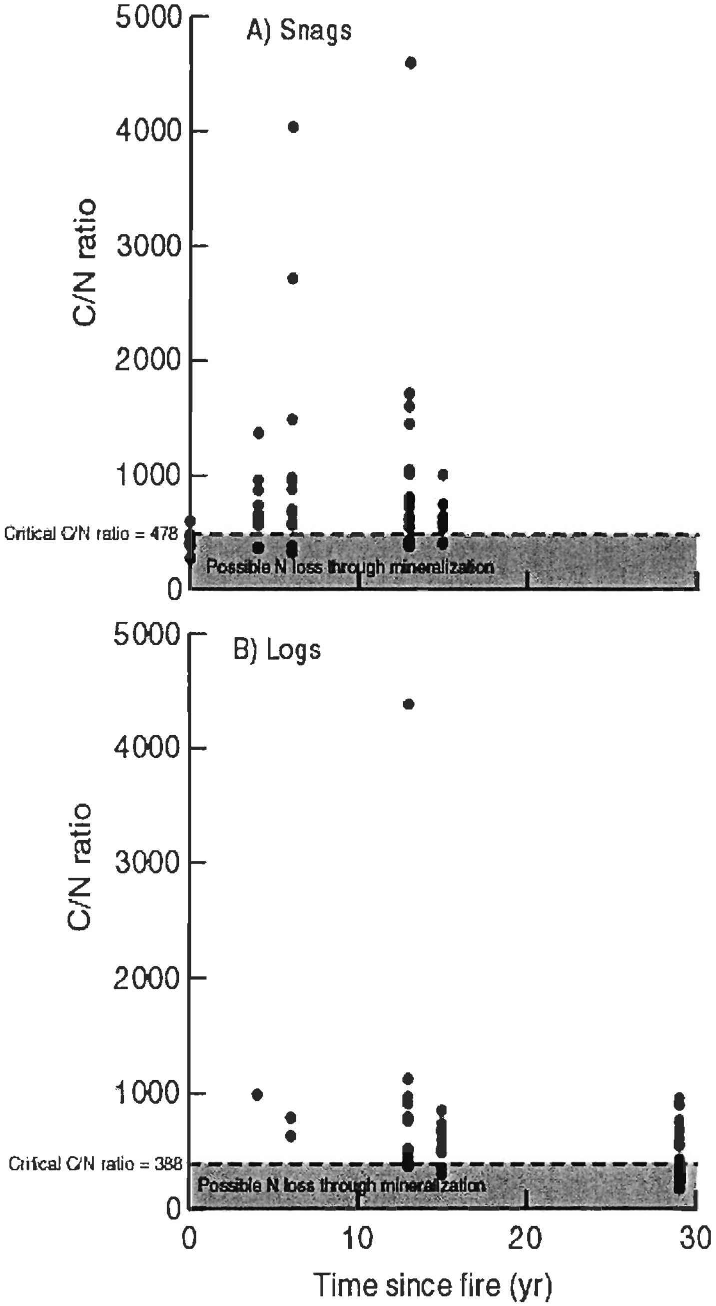

Figure 9. C/N ratio of woody samples along chronosequence for snags and logs. Samples below the dashed line, i.e. critical C/N ratio, could possibly exhibit N loss through mineralization. Critical C/N ratio is 478 for snags and 388 for logs.

CHAPITRE 2

POST-FIRE SUCCESSION OF SAPROXYLIC ARTHROPODS IN BLACK SPRUCE COARSE WOODY DEBRIS IN NORTHERN QUÉBEC

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Abstract

Saproxylic arthropod diversity and succession in black spruce (*Picea mariana* [Mill.]) coarse woody debris (CWD) in northern Quebec are estimated in this study using a 29-yr post-fire chronosequence. Sampling was performed using both trunk-window traps on snags and rearing of snag and log sections. A total of 37 312 arthropods belonging to at least 220 taxa were collected using both sampling method. Saproxylic beetle diversity shortly after fire is lower and distinct from the saproxylic communities observed in the southern part of the Québec's boreal forest. Overall post-fire saproxylic coleopteran diversity (88 spp.) is lower compared to the one associated with spruce woody debris in northern Europe. Saproxylic succession in post-fire black spruce CWD clearly shows a stepwise pattern as the onset of initial colonisation occurs the year of fire while the second colonisation phase begins only once the debris falls on the ground. Initial colonisation is mostly influenced by pyrophilous species which include subcortical predators and xylophagous species as well as ascomycetes feeders. Cerambycidae and cucujoid beetles are mostly abundant the very year of fire and decrease thereafter. Abundance and diversity of most initial colonisator species decline with time since fire and very few species colonize snag before it falls on the ground. Lack of succession in snags may be related to low decomposition rate as substrate is unsuitable for species associated with highly decayed wood. Fragmentation of snags triggers fungal growth and concomitant saproxylic succession toward micro- and saprophagous Coleoptera and Diptera. Moreover, falling of CWD increases accessibility for soil-dwelling organisms as seen from high abundance of Acari and Collembola in late chronosequence. Since position of woody debris greatly influence overall physical properties of dead wood, falling of burned CWD plays a major role in saproxylic community shift at least in the first decades after disturbance.

Keywords: CWD, boreal forest, saproxylic insects, fire, black spruce

Introduction

Recurrent wildfires constitute the most important natural disturbance in Canada's northern forests where they contribute to both structure and floristic diversities (Johnson 1992, Payette 1992, Rowe and Scotter 1973) and influence the carbone distribution inside the ecosystems (Kasischke et al. 2000). Even if fire destroys most of original biotic components of the ecosystem (McCullough et al. 1998), several fire-adapted animal species have evolved to take advantage of this newly created and competition-free environment (Schütz et al. 1999, Wikars 1994, Evans 1966), including burned and mineral soil substrates as well as dead wood (Wikars 1994, 1997, Muona and Rutanen 1994, Danks 1998, Paquin and Coderre 1997).

Stand-replacing wildfires can transform most of the living trees into woody necromass at once (Tinker and Knight 2000). In fact, Penttilä and Kotiranta (1996) reported that fire increased woody debris by 2-3 folds in a small coniferous stand of central Finland. This newly created substrate will play major structural and functional roles in the ecosystem (Swift 1977a). Dead woody material decomposes rather slowly (Harmon et al. 1986) and may form an important carbon and nutrient pool which may have long term significance in C and nutrient cycling in the woodland environment (Ausmus 1977, Swift 1977b). Moreover, rotting logs are known to favour the establishment of various vascular plants while many forms of woody debris are greatly involved in geomorphic processes by influencing soil and sediment transport and storage (Harmon et al. 1986). Decaying wood represent also a critical habitat for several heterotroph taxa including fungi (Renvall 1995), cavity-nesting birds (Nappi et al. 2003, Torgensen and Bull 1995), amphibians, reptiles, mammals and particularly insects (Harmon et al. 1986).

Several authors (e.g. Nilsson et al. 2001, Olberg et al. 2001, Bakke 1999, Kaila et al. 1997, Hammond 1996, Økland et al. 1996) have already pointed out that coarse woody debris, i.e. woody debris with a minimum diameter of 10 cm (Harmon et al. 1986), host a tremendous diversity of insects. These species called "saproxylic" are 'species that depend for at least part of their life cycle upon dead or dying wood of moribund or dead trees, or upon wood-inhabiting fungi, or upon the presence of other saproxylic species' (Speight 1989). This functional group may form one of the largest assemblage contributing to the species richness in boreal forests (Olberg et al. 2001, Kaila et al. 1997). For instance, Hammond (1996) estimated that *ca.* 2000 species of saproxylic arthropods occur in *Populus* decaying wood in northern Alberta while 1300 beetle species are classified saproxylic in Fennoscandia (Kaila et al. 1997). High heterogeneity of woody substrate probably maintains the large diversity of saproxylic entomofauna since many species are associated with particular physical properties of decaying wood and structure of the surrounding biotope (Jonsell et al. 1999, Økland et al. 1996, Kaila et al. 1994). By feeding on woody substrate and providing access to carbohydrate reserves to symbiotic saproxylic fungi (Six and Bentz 2003, Haberkern et al. 2002, Paine et al. 1997, Stillwell 1964), several saproxylic insects may influence decomposition patterns of CWD and subsequent nutrient cycling (Schowalter et al. 1992, Edmonds and Eglitis 1989, Zhong and Schowalter 1989, Ausmus 1977).

There has been a growing appreciation of CWD as an essential component of ecosystem's biodiversity (e.g. Nilsson et al. 2001, Olberg et al. 2001, Bakke 1999, Økland et al. 1996) as well as carbon and nutrient cycling (e.g. Krankina et al. 2002, Kasischke 2000) in the last decade. Although several investigations have assessed the distribution, quality and quantification of CWD in North America (cf. Harmon et al. 1986), studies on saproxylic entomofauna are sparse and were mostly conducted on economically important pest species (Cerezke 1977, Gardiner 1957, Richmond and Lejeune 1945) with few notable exceptions (cf. Hammond 1996, 1997, Hammon et al. 2001).

Studies adressing saproxylic insect succession have most exclusively focused on saproxylic communities inhabiting senescent or wind-thrown trees in old-growth forests (e.g. Jonsell et al. 2004, Jonsell and Weslien 2003, Sippola et al. 2002, Esseen 1997, Økland et al. 1996) while fire-killed trees have been extensively overlooked. Furthermore, studies addressing fire and saproxylic insect relationship have mainly focused on short-term fire effects (Saint-Germain et al. 2004a,b, Wikars and Schimmel 2001, Dajoz 1998, Muona and Rutanen 1994) while very few have assessed long-term changes in post-fire saproxylic communities (Werner 2002, Howden and Vogt 1951). Saproxylic insect succession in fire-killed trees should display a discrete colonisation pattern according to distinct woody substrate changes since decomposition pathway and fungi colonisation in fire-killed trees greatly differ from those that die from other causes (Siitonen 2001, Renvall 1995).

Most research investigations on overall saproxylic community succession were completed in Scandinavia (e.g. Nilsson et al. 2001, Olberg et al. 2001, Bakke 1999, Økland et al. 1996) where several centuries of utilisation and intensive forest management have considerably reduced the amount of dead wood (Siitonen 2001) and changed the quality and the spatial distribution of the saproxylic habitats (Økland et al. 1996). According to these studies, saproxylic insect fauna displays a distinct successionnal pattern corresponding to a spatio-temporal differentiation of ecological niches (Simandl 1993). Saproxylic species adapted to different decay stages successively colonise dead wood as time since tree death brings woody substrate to appropriate properties (Esseen et al. 1992, 1997). Initial phase of colonisation generally occurs shortly after tree death by subcortical-feeders and xylem borers along with associated predators, parasitoids, scavengers and fungivores. Secondary phloem-feeding and detritivorous species as well as fungivores feeding on subcortical mycelia quickly follow initial saproxylic species whereas subsequent development of sporocarps attracts specific insect communities as subcortical habitat disappears with bark shedding. Association can be very straightforward for specialist insects living in sporocarps, so saproxylic succession may differ greatly between trees colonised by different saproxylic fungi (Jonsell and Weslien 2003, Rukke 2002, Kaila et al. 1997). Eventually, saproxylic entomofauna gradually include more epigeic species when extensive decomposition of sapwood and heartwood and consequent incorporation of highly degraded wood to the ground layer progress (Irmler et al. 1996).

In this paper, we investigate the post-fire saproxylic communities of Québec's northern boreal forest using a post-fire chronosequence ranging from the moment of fire occurrence to 29 years of post-fire wood decay. Our specific objectives are to describe i) the overall post-fire coleopteran saproxylic fauna and ii) the long term succession of saproxylic arthropods assemblages associated with post-fire black spruce CWD.

Material and methods

Study area

Sampling was held within a range of 100 km of Radisson, Québec (53°79' N, 77°62 W) in north central Québec, Canada (Fig. 1). This area belongs to the lichen woodland ecoregion and is located at only 150 km of the southern border of the forest-tundra transition zone (Payette 1983). Sampling area is located in the precambrian geological formation of the Canadian shield which is mainly composed of acidic granitic and gnessic rocks (Stockwell et al. 1968). Topography consists in a mainly low altitude (100-200m) plateau dissected by lowlands. Surface deposits are mainly from fluvioglacial origin. Climate is typical of lower-subarctic with a mean annual temperature of –3.6 °C while January and July average –25 and 13°C respectively. Mean annual precipitation averages 637 mm, 40 % falling as snow (Environment Canada 1993). Forest occupies every non-edaphically limited site and is mainly composed of even-aged stands of jack pines (*Pinus banksiana* Lamb.) and black spruces (*Picea mariana* [Mill.] BSP.). Open uneven-aged stands dominated by black spruces are found on paludified sites of the lowlands. Bogs and fen with herbaceous and shrubby vegetation are located in sites with very poor drainage conditions. Fire constitutes the most important natural disturbance with a mean interval of approximately 100 years on mesic sites (Parisien and Sirois 2003, Payette et al. 1989).

Sites

This study area was selected since i) several stands burned at different time periods are accessible within a limited range and ii) that these wildfires lack any major anthropogenic disturbance. A chronosequence of five different fires that occurred in either 1973, 1989, 1998, 2001 or 2002 in the vicinity of Radisson was used in the present study. According to Krankina et al. (2000), the chronosequence approach provides valid approximations of temporal dynamic concerning ecological processes of woody debris. Fire location was derived from maps provided by the *Société de Protection des Forêts contre le Feu* (SOPFEU) for the 1972-2002 time period and from fire scar analysis in this area (Sirois and Arseneault, unpublished data). Within each burned area, one 60 x 60 m site was selected according to the following criteria: 1) no slope, 2) stand of mature, i.e. > 60 yr black spruces before fire and 3) 100 % tree mortality following fire.

Methods

Measurements of CWD were compiled within four 100 m^2 plots distant of 40 m from each other in each sampled site. Along with position of debris (standing vs fallen), total volume of fire-killed spruce and volume of scorched CWD already dead at the time of fire was estimated in each plots.

Sampling of insect fauna was limited to coarse woody debris of black spruce with a diameter of 10 to 15 cm. Only woody debris originating from the last fire were considered. Those are distinct of woody debris existing before fire by exhibiting burned small branches combined with a lack of charcoal on main trunk. To obtain a representative sample of regional saproxylic fauna, two sampling methods were used. Trunk-window-traps (TWT) modified from Kaila (1993) were used to characterise saproxylic entomofauna related to snags. This kind of trap allows sufficient number of specimens for statistical analyses and keeps insect habitat intact (Økland 1996). The traps consisted of a 10 x 20 cm Lexan™ translucent plate, attached perpendicularly to the stem surface along the axe of the snag with screws and braces at 1.30 m of height on trunk. Plate was oriented to minimise interstices with snag surface. A funnel was placed under the plate to collect the specimens in a jar filled with ethylene glycol used as a killing and preservative agent. Forty-eight trunk-window traps (n=12 per site) were located randomly in sites burned in 1989, 1998, 2001 and 2002. The 1973 burned stand did not contained enough snags for sampling. Because repeated bear attacks resulted in lost samples on two traps in 1998 and 1989 sites, ten traps were randomly selected in the remaining sites to keep sampling effort constant along the chronosequence. Traps were operated from early June to late August 2002 with the exception of those installed in the stand that burned in 2002. In this site, traps were fixed on July 5th, i.e. 48 hours after fire. Traps were emptied twice during the sampling period.

In order to document the diversity of species developing exclusively in woody debris, trunk sections from snags and logs of black spruces were sampled and put in rearing conditions. Combination of both trapping method has previously proved to better sample the heterogeneity of habitat associated with dead wood since several species are frequently collected from only one sampling method (Hammond 1997, Økland 1996, Kaila 1993). Two 50-cm long sections located at the tree base and at 1 m high were sampled on 18 randomly selected snags (n=6 per site) in sites burned in 1989, 1998 and 2001. Additionally, 12 logs (n=6 per site) were selected in sites burned in 1973 and 1989. In this case, two 50-cm long trunk sections were sampled at the breakage point and from 1 m of it. Bark cover percentage and presence/absence of sporocarps were noticed on trunk sections. Decomposition state of woody debris was noticed according to four decomposition classes established in function of transversal proportion of section showing fungal deterioration or coloration (1=no apparent degradation; 2=1-33% ; 3=34-65% ; 4=66-100% of transversal section showing fungal degradation). Trunk sections were enfolded with a fine tissue in field and carried in a non-heated building where they and screwed below a rack shelf. A killing jar placed under a funnel attached at the bottom of the woody debris collected emerging specimens. Ethylene glycol was used as a killing and preservative agent. Trunk sections were sampled at the beginning of June 2002 and were maintained in rearing conditions until the end of October 2002. Ecological and entomological data coming from the trunk sections of the same log or snag were pooled for statistical analyses.

Specimens were sorted and identification was completed to the most precise taxonomic level with the exception of larvae and some other difficult taxa because of the lack of entomological expertise. Further ecological analyses of specimens coming from TWT were restricted to saproxylic Coleoptera since the ecological information concerning this group is more abundant in the literature. Trophic levels (e.g. xylophagous, mycophagous, predators, saprophagous) of each coleopteran species was identified according to the available literature (cf. appendix 2 and 3) and from expert advice. Efforts were made to have a more precise identification of specimens coming from rearing in order to have further information on ecological preferences of overall arthropod diversity developing in CWD. Voucher specimens are kept at the Université du Québec à Rimouski.

Statistical analyses

Saproxylic Coleoptera from TWT

In order to consider the disparities between the numbers of trapping-days in each site, Coleoptera abundance from TWT was standardized on a 100 trapping-days basis. Differences in abundance of each trophic group between sites, with the exception of predators, was assessed by one-way analyses of variance on logarithmic (x+1) transformed data to meet normality and homogeneity of variance. Non-parametric Kruskal-Wallis test was used to assess differences in mean predator abundance between sites since no data transformation could met the homoscedasticity condition. Separate analyses of variance on cerambycid beetles abundance between sites were done since this abundant xylophagous group is known to have an impact in the decomposition process of the woody necromass (Edmonds and Eglitis 1989). Either parametric or non-parametric Tukey's honestly significant difference tests ($\alpha=0.05$) were used for post-hoc multiple comparison. Statistical analyses were performed using SYSTAT 9.01.

Sørensen's (1948) indices were computed for each pair of sites as a measure of similarity of saproxylic coleopteran species assemblage. Shannon-Wiener indices calculated from standardised abundance of saproxylic beetles were used as a diversity index in each site.

Arthropod communities from rearing

Trunk-window traps measure the activity of insects around the trunk, which to some extent reflects the fauna that may reproduce in dead wood but they can also include transient visitors (Jonsell and Weslien 2003). Data from rearing are thought to reflect more reliably association of species and physical properties of dead wood. As a result, detrended correspondence ordination analysis (DCA) was used to explore variation in the species composition of saproxylic arthropods among reared samples. Since coleopteran diversity and abundance was relatively limited in samples, other arthropod taxa were included in the analysis. Analysis performed on Acari, Collembola as well to Hemiptera, Diptera, Hymenoptera and Coleoptera taxa that were present in at least four woody debris and have an overall abundance of at least ten individuals. Equal weight was applied to each taxa while taxa abundance was log(x+1)-transformed. Detrending was performed by second order polynomials instead of segments since the number of samples (n=30) was low (Sippola et al. 2002). CANOCO 4.5 (ter Braak and Smilauer 2002) was used to compute DCA-ordination. Six taxa (Coleoptera : Lepturinae larvae, *Pteryx* sp.; Diptera : Lestremiinae; Hymenoptera : *Leptothorax canadensis* ; Acari and Collembola) had enough number of individuals to test their preferences to site and position of woody debris. Differences were assessed by one-way ANOVA on log+1 transformed abundance data or with Kruskal-Wallis tests where homoscedasticity of variance was not met. Analyses of variance and Kruskal-Wallis test were performed using SYSTAT 9.01.

Results

Sites structure

Sites structure is summarized in Table 1. Volume of post-fire woody debris in sites averages 42.76 ± 19.46 $m^3.ha^{-1}$ (mean ± SD) and vary between 21.58 and 66.78 $m^3.ha^{-1}$. Woody debris produced before fire and still present when sampling are scarce with a mean of 3.89 ± 3.63 $m^3.ha^{-1}$ (mean ± SD) and are virtually absent from the 2002 and 2001 sites. Post-fire CWD fraction of total woody detritus produced by fire lies between 59.7 and 84.9 %. Fragmentation of post-fire snags begin in the 1998 burned site and continue progressively in oldest site (1973) where only 18.5% of CWD remain standing. Burned organic matter is the dominant substrate in study sites except in the 1973 burned site where *Sphagnum* sp. becomes more abundant. Ground vegetation is mostly dominated by *Ledum groenlandicum* Oeder and *Cassandra calyculata* (L.) except in the most recent burned stand where no ground vegetation is observed. Arbustive vegetation only appears in the two oldest burned stands and is made of either *Betula glandulosa* Michaux or *Salix* sp..

Total arthropod and insect diversities

A total of 37 312 arthropods were collected from both sampling methods. Trunk-window-traps collected 28 486 arthropods while 8826 were collected from rearing. Diptera (33.9%), Coleoptera (28.7%) and Acari (27.0%) were the most abundant taxa collected in trunk-window-traps whereas Acari (68.1%), Collembola (16.2%) and Coleoptera (4.7 %)

were dominants in rearing. Both methods collected at least 220 insect taxa. Overall, at least 115 different coleopteran species (cf. appendix 1), approximately 88 being considered as saproxylic (cf. appendix 2 and 3), were recorded from either TWT or rearing. Twenty-one species were collected from both methods but this number could be higher since some specimens (mostly larvae) in rearing were not identified to the species level.

Coleopteran saproxylic diversity from trunk window traps

A total of 8177 beetles from at least 109 species belonging to 34 families were collected from trunk-window traps (cf. appendix 2). Staphylinidae ($\geq$ 21 spp.), Curculionidae (15 spp.), Elateridae (11 spp.) and Cerambycidae (7 spp.) are the most diversified families represented in samples. Among species collected from this sampling method, 83 can be classified as saproxylic. Families with the most diversified saproxylic fauna are Staphylinidae ($\geq$18 spp.), Curculionidae (12 spp.), especially Scolytinae (10 spp.) and Cerambycidae (7 spp.).

Only 9 species made up 92 % of total catches, *Corticaria* spp. being the most abundant taxa with 72.2 % of the total saproxylic beetle abundance. More than half species (48 spp.) are considered uncommon (less than 5 ind.100days^{-1}) whereas 20 species were collected only once. Out of the 21 species having more than 20 ind.100days^{-1}, 18 are most commonly encountered in the 0-1 post-fire year while none are more numerous in the older site (cf. appendix 2). According to the Sørensen index, species communities are quite similar between sites with values always over 0.750 (Table 2). Similarity is greatest among sites which are closer in the chronosequence. Lowest similarity is noticed between sites 2002-1998 and sites 2002-1989 while sites 1998-1989 have the highest Sørensen value.

Thirty-nine saproxylic species were recorded the year of the fire while saproxylic diversity along chronosequence is highest in the 2001 site with 54 spp. Total number of saproxylic species is still high (50 spp.) in the 1998 site but decreases to 32 in the oldest site. Diversity expressed as Shannon-Wiener indices (Table 3) is highest in the 2001 site (S=2.666) while site 2002 as the lowest value (S=0.888). Low Shannon-Wiener value in the 2002 site partly resulted from the presence of some very abundant species (*Corticaria* sp, *Thanasimus undatulus*, *Gnathacmaeops pratensis*) noticed at this site.

Xylophagous (28 spp.), predator (22 spp.), mycetophagous (21 spp.) and saprophagous beetles (5 spp.) are the most common feeding habit documented. Richness of xylophagous species (Fig. 2) is highest the year following fire (20 spp.) while lowest xylophagous diversity is noticed in the oldest site (6 spp.). Overall xylophagous diversity is particularly important considering high number of Cerambycidae (7 spp.) and Scolytinae (10 spp.) species (appendix 2). Abundance of xylophagous beetles differs between sites ($F_{[3,36]}=60.46$; $p<0.001$) and is highest during the year of fire and decreases thereafter. High abundance of this trophic group during the year of fire mainly results from the high number of cerambycid beetles (Fig. 3a). Subcortical borers such as *Gnathacmaeops pratensis*, *Arhopalus foveicollis*, *Acmaeops proteus* and *Pachyta lamed* are most common in the 2002 site, the three latter becoming very scarce afterward (appendix 2). Cerambycid beetles almost disappear in the two older sites with the exception of *G. pratensis* which still have 3.33 ind.trap^{-1}.100days^{-1} in the 1998 site. Other common xylophagous species including *Hylobius congener, Oxypteris acuminata* and melandryids of the *Serropalpus* genus are most numerous the very year of fire while *Rhagium inquisitor* and *Xylita* spp. are most abundant in the 2001 site. The latter is the only xylophagous taxa with more than 2.5 ind.trap^{-1}.100days^{-1} in the older site (appendix 2).

Similar number of mycetophagous species (13 spp.) is noticed along chronosequence except in the oldest site where mycetophagous diversity decreases to 10 species (Fig. 2). Effect of site on abundance of mycetophagous beetles is significant ($F_{[3,36]}$=80.36 ; p<0.001, Fig. 3b). Abundance is particularly high the very year of fire with 862.5 ind.trap^{-1}.100days^{-1}. Abrupt and significant decrease of mycetophagous abundance is noticed in the 2001 burned site and abundance remains low thereafter (Fig. 3b). Trends in mycetophagous abundance along chronosequence is mostly influenced by *Corticaria* spp. which made up to 66.7 to 97.8 % of total mycetophagous catches in each site (appendix 2). Moreover, high mycetophagous abundance during the year of fire results from considerable number of individuals belonging to this taxa with 81.6 % of overall catches in the 2002 site. Abundance of microphagous, ascomycetes and myxomycetes spore feeder *Cartodere constrictus* and most cryptophagids as well decline with time since fire. On the other hand, spore feeder *Sacium fuscum* and polypore feeder *Cis* cf. *striolatus* are most abundant in the 2001 burned site and become sparser in older sites (appendix 2). Other mycetophagous species are seldom encountered throughout chronosequence.

Predator diversity along chronosequence vary between 11 to 15 species and is highest the year following fire (Fig. 2). Most predator species belongs to Staphylinidae (10 spp.) and Carabidae (5 spp.) families. Mean relative standardized abundance of predator beetles is significantly different between sites ($H_{[3,0.05]}=35.92$; $p<0.001$) and decreases with time since fire (fig. 3c). Few species, i.e. *Thanasimus undatulus, Sphaeriestes virescens,* and carabids of the *Sericoda* genus made up 94.0 % of predator catches in the 2002 site. Moreover, *S. quadripunctata* is occurring only during the year of fire. Most predator species occurring during the year of fire decline thereafter with the exception of *S. virescens* and *Phloenomus lapponicus* which become most numerous in the 2001 site. Furthermore, species noticed in recent fires (2002 and 2001) become very scarce in older sites except for *T. undatulus* which is still common in the 1998 burned site. Likewise, nearly all predator species in oldest site are represented by less than 0.3 ind. $trap^{-1}.100days^{-1}$ except for *Pediacus fuscus* which is still occasionally encountered (0.83 ind. $trap^{-1}100days^{-1}$, appendix 2).

Abundance of saprophagous beetles significantly differs along chronosequence ($F_{[3,36]}=5.80$; $p=0.002$). Those are virtually absent during the year of fire and become most numerous in the two older sites (fig. 3d). Nevertheless, abundance averages only 2.7 and 1.7 $ind.trap^{-1}.100days^{-1}$ in the 1998 and 1989 sites respectively. Increase in the two older sites is mainly associate with the increase in *Ampedus* spp. abundance (appendix 2).

Arthropod communities in rearing

Physical characteristics of rearing samples greatly vary with time since fire and position of debris (Table 4). While all snags from the most recent burned stand do not show any sign of decay, few snags of older sites (1998 and 1989) are more decayed although a great proportion (66.7% in 1998 and 50 % in 1989) lacks fungal deterioration in transversal section. Logs are generally more decomposed than snags of concurrent sites and are most deteriorated in oldest site. Bark cover remains high on samples from the two most recent sites whereas most snags and logs from the 1989 and 1973 burned stands exhibit low bark cover. No sporocarps were observed on samples coming from the 2001 and 1998 sites lack any sporocarps while snag and log samples from older sites host more fruiting bodies with time since fire.

Ordination space set by the first and second axes of detrended correspondence analysis (DCA) explain respectively 30.7% and 12.4% of the variation of saproxylic species data. A clear gradient of most recently killed and slightly decayed snags toward oldest, more decomposed logs can be outlined from bottom-right to top-left (Fig. 4). Both most recent and oldest samples are distinctly grouped in the ordination space while various low to moderately decomposed snags and logs samples from the 1998 and 1989 burned sites are clumped together in the transition area. Fungivorous taxa Aradidae, *Corticaria* sp, and *Sacium fuscum* as well as Lepturinae and Cleridae larvae are mainly associated with recently scorched wood. Highly decomposed fallen logs host various Diptera (Chironomidae, Empididae, Lestremiinae, *Neophyllomyza* sp.), microphagous and saprophagous beetles and *Myrmica alaskensis* ants. Few taxa are closely associated with transition samples.

Abundance of Acari (Ac) and Collembola (Co) in woody debris differs among sites (Ac : $H_{[4,0.05]}=19.58$; $p<0.001$, Co : $F_{[4,25]}=17.43$; $p<0.001$) and increases with time since fire (fig. 5a,b). Effect of site on collembolan abundance is significant ($F_{[4,25]}=17.43$; $p<0.001$) while debris in most recent fire are virtually out of individuals. Abundance of

Lepturinae larvae is significantly different ($H_{[4,0.05]}$ = 26.20 ; $p < 0.001$) along chronosequence and is highest in most recently killed wood (fig. 5c). No lepturine larvae were noticed in either standing or fallen CWD from the 1989 and 1973 sites. The ant *Leptothorax canadensis* is more numerous with time since fire (fig. 5d) but differences between sites are not significant ($F_{[4,25]}$=1.40 ; p=0.2613). Aggregation of *Leptothorax canadensis* is important considering the high coefficient of variation (230.8%). Abundance of Lestremiinae ($H_{[4,0.05]}$=10.36 ; p=0.0347) and *Pteryx* sp. ($H_{[4,0.05]}$=25.78 ; $p<0.001$) differs between sites and is highest in the 1973 site (fig. 5e,f). Both taxa are absent from snags of the 2001 and 1998 fires. Aggregation of both *Pteryx* (C.V. = 242.3%) and Lestremiinae (C.V. = 468.5%) is very high especially for the latter where 85.8 % (97/113) of total individuals comes from a single log section in the 1973 site.

Discussion

Coleopteran diversity in fire-killed black spruce

Comparison of coleopteran diversity with other boreal studies is quite difficult since this study seems to be the first to document the long-term saproxylic succession in fire-killed spruce. Overall coleopteran diversity noticed in post-fire black spruce CWD displays similar trends regarding main trophic groups collected from dead woody material in previous studies (Sippola et al. 2002, Olberg et al. 2001, Hammond 1996, Økland 1996, Kaila 1993). Several saproxylic fire-associated taxa collected in our study are closely related to those noticed in other parts of the boreal forest, especially for numerous xylophagous (e.g. Cerambycidae, Scolytidae and Buprestidae) and mycophagous species (e.g. Cryptophagidae, Lathridiidae) (Muona and Rutanen 1994, Wikars 1992, 1994, Saint-Germain 2004a,b). Although 88 saproxylic beetle species were collected from both sampling methods, very few species are dominant while remaining species are relatively scarce. This support earlier observations that in harsh and species-poor environments, the species distribution follows geometric or logarithmic series (Sippola 2001, Whittaker 1972).

Total saproxylic diversity remains higher than the one derived from the studies of Saint-Germain et al. (2004a,b) (68 spp.) which were held in similar fire-killed black spruce stands in the Grands-Jardins Provincial Park (47°41'N; 70°43'W). However, these authors covered only the first two years after fire and did not considered the Staphylinidae family in sampling. Considering similar parameter data from our study, species number is rather lower (52 spp.) than in the previously cited studies. Differences mostly result from higher numbers of Cerambycidae (16 spp.) and Scolytinae species (16 spp.) noticed in the latter studies. We can speculate that several species noticed by these authors do not reach the Radisson area (53°79'N; 77°62'W) since coleoptera diversity clearly decreases with increasing latitudes (Danks 1993). Only 26 spp. are common to both studies suggesting that different saproxylic communities use freshly fire-killed black spruce in either the northern or southern part of the boreal forest. Moreover, although several species of Scolytinae are frequently abundant after fire in other boreal burned stands (Saint-Germain et al. 2004a, Werner 2001, Muona and Rutanen 1994), these beetles though diversified, are particularly uncommon in sampling (appendix 2). Low Scolytinae abundance could resulted from low tree diameter in the northern part of the boreal forest since several species clearly show trends to inhabit large diameter tree (Saint-Germain et al. 2004a) which provide thicker subcortical feeding substrate and fire-insulating capacities through thicker bark cover (Gardiner 1957).

As no long-term study on post-fire saproxylic community has been undergone, comparison of overall post-fire saproxylic diversity can solely be based on studies related to senescent or wind-thrown spruce which were mainly conducted in northern Scandinavia. Post-fire saproxylic beetle diversity in northern Québec remains lower than the saproxylic diversity reported in timberline forests of Finnish Lapland (107 spp.; Sippola et al. 2002) and in northern Norwegian boreal forests (189 spp.; Olberg et al. 2001). However, saproxylic entomofauna restricted to highly decomposed CWD (e.g. mostly saprophagous and mycophagous species) is likely underestimated in the present study as the time period covered by the chronosequence (29 years) leads to a limited number of highly decayed woody samples. Furthermore, an important proportion of total beetle diversity in late chronosequence is likely overlooked as sampling was based solely on rearing in the oldest site. Even if this method has the advantage of sampling directly from the microhabitat (Økland 1996) thus giving a good estimation of variation between wood bolts (Hammond 1997), only species present at time of sampling can be collected. Moreover, coleopteran diversity in sampling is probably greater than reported since few abundant taxa including Staphylinidae (especially Aleocharinae), some Cryptophagidae, Lathridiidae and various larvae were only identified at the above-species level.

Successional patterns of saproxylic arthropods

Few studies have assessed long-term patterns of saproxylic diversity in boreal forests, particularly in North America (Hammond 1997). To our knowledge, this study is the first to document long-term patterns of post-fire saproxylic succession in Canada's northern boreal forest. Our results suggest that two saproxylic colonisation events occur. First saproxylic organisms settle shortly after tree death (0-1 years), then these initial populations decline with no substantial species replacement on snags for several years. A second colonisation event is prompted by the fall of the snag on the ground and its continuing decomposition.

Saproxylic coleopteran diversity shortly after fire (0-1 year) is mostly influenced by fire-associated species which quickly become less abundant with time since fire. Fire specialists include predators living under bark, species developing in dead wood as well as those attracted to wood-rotting fungi (Muona and Rutanen 1994). Among wood- and subcortical-borers, cerambycid beetles are the most common xylophagous taxa caught by both sampling methods. Cerambycid are mostly abundant the year of fire and the following year whereas individuals are seldom encountered in older sites. Similar results were obtained by St-Germain et al. (2004a,b) and Werner (2002) who noticed that abundance of most cerambycid beetles is highest the first year after fire whereas few individuals are collected thereafter. Some of these taxa (*Monochamus* sp., *A. proteus, P. lamed*) are well-known pyrophilous species that are mainly attracted to, or found in, recently scorched wood (Wikars 2002, Werner 2002, McCullough et al. 1998, Lundberg 1984, Gardiner 1957, Richmond and Lejeune 1945). These species mostly feed at larval stages in the nutrientrich cambial and phloem zones of trees (Hanks 1999, Haack and Slansky 1986) which decay very rapidly compared to sapwood and heartwood (Schowalter et al. 1992). Substrate probably become quickly unsuitable for larval development as nutrients and moisture content of dead woody material decrease (Howdie and Vogt 1951). This probably explain why no Lepturinae larvae were detected in snags and logs of the two oldest burned sites although sapwood and heartwood was apparently undecayed in some cases (Table 5).

High densities of *Corticaria* sp. shortly after fire were already noticed in few earlier studies, particularly in northern Europe (e.g. Wikars and Schimmel 2001, Muona and Rutanen 1994, Winter et al. 1980). This species, along with other common cucujoid beetles in sampling (*C. constrictus*, *Atomaria* spp., *C. ferruginea*, *Henoticus serratus*) feed on moulds and other ascomycete fungi growing under bark of recently fire-killed trees (Wikars 2002, Dajoz 1998, Muona and Rutanen 1994). Association of *Corticaria* sp. with freshly killed spruce is also displayed in rearing of snags from the most recent burned site along with flat bugs (Aradidae) which are known to feed on similar substrate (Dajoz 1998). Muona and Rutanen (1994) suggest that cucujoid beetles probably bring fungal spores with them as response to fire and massive colonisation of burned stands can take place the very day of fire (Wikars and Schimmel 2001). As smoke and heat probably attracted insects from several kilometres away (Wikars and Schimmel 2001), sampling of the 2002 site only few hours after fire allowed unusually high number of *Corticaria* sp. that would have been otherwise overlooked. Overall decrease of cucujoid beetles and flat bugs in late chronosequence likely results from rapid degradation of phloem on which ascomycete fungi grow.

Massive colonisation of burned trees by xylophagous beetles and various ascomycete feeders in recently scorched spruces favours concurrent arrival of associated predators mostly *T. undatulus*, *S. virescens*, carabids of the *Sericoda* genus and *P. fuscus*. The two latter Holarctic taxa are known as fire-specialists in northern Scandinavia (Muona and Rutanen 1994). It is likely that these predators feed mostly on cucujoid beetles under bark of fire-killed spruce (Muona and Rutanen 1994) as scolytid, on which they also prey, seems uncommon in study sites. Positive reproductive responses to increased prey density within trees have been demonstrated particularly for *Thanasimus* spp. preying on various scolytids (Schroeder 1999). *S. quadripunctata*, which was collect only from the 2002 burned stand, is thought to be truly pyrophilous (Wikars 1995) being commonly and almost exclusively found in burned forests the year of fire (Moretti et al. 2004, Dajoz 1998, Wikars 1995, Muona and Rutanen 1994, Lundberg 1984). Reduced competition by other carabids inhabiting open-habitat presumably favours colonisation of pyrophilous *Sericoda* in post-fire coniferous stands (Wikars 1995).

Increase in saproxylic richness one year after the fire mostly results from increase in xylophagous diversity although much of newly arrived species are uncommon (cf. appendix 2). High xylophagous larval densities in snags one year after fire, as revealed from rearing, could also have triggered or maintained high predator densities, mostly clerids, salpingids and staphylinids, which contribute to overall increase in diversity of saproxylic beetles. Most wood-feeding species collected the year of fire are still encountered the year following disturbance along with new arrivals, mostly from Scolytinae and Melandryidae (*Xylita* spp.). Several bark-beetles in sampling, such as

Hylurgops spp, *Orthotomicus* spp. and *Trypodendron* spp. infest timbers the first and second summers following disturbance (Jonsell and Weslien 2003, Schroeder et al. 1999, Schroeder and Eidmann 1993) whereas *Dryocoetes* spp. is mostly found in moist phloem in the second year (Jonsell and Weslien 2003) although studies vary in this respect. Scolytids are known to respond to volatile constituents of damaged, dying or recently killed trees (Lindgren and Miller 2002a,b) which strongly vary with time since disturbance (Flechtmann et al. 1999). Different time of arrival in scolytid species could reflect changes in concentration and nature of volatile organic compounds through ageing of inner-bark of post-fire spruce woody debris.

To this point in the chronosequence, saproxylic beetle diversity and abundance on snags quickly drop with time since fire. One would expect that saproxylic community should change with time since fire as a response of changes in overall wood properties. Esseen et al. (1997) stated that distinct saproxylic communities associated with mycelial growing under bark and in surface wood as well as those attracted to polypores appears the second year after tree-fall. Likewise, Hammond (1997, 1996) noticed that succession toward species associated with advance decay classes in *Populus* CWD, begin as soon as two years after tree death as revealed from increase of 50 % in fungivorous diversity. Even though most subcortical borers and ascomycete feeders decrease or even disappear in late chronosequence, our results suggest however that succession toward new beetle communities in spruce snags is particularly slow, as revealed from high Sørensen indices among all stands burned between 1989 and 2002. For instance, out of the 32 saproxylic beetle species recorded in TWT in the 1989 site, 29 were already recorded in more recent burned stands, the three remaining species being collected only as single individual (appendix 2). Decomposition of black spruce post-fire snags is notably slow in that area and is one of the slowest ever recorded in boreal forest (chapter 1). In fact, most of woody necromass still remains 13 years after fire as fungal colonisation and subsequent decomposition of heartwood and sapwood has not already begun in several cases (Table 5). Rapid post-fire shedding of bark strongly decreases moisture content of snags which in turn inhibits fungi growth, mostly basidiomycetes (Renvall 1995). Slow decomposition process could therefore delay the establishment of particular saproxylic species by limiting the colonisation of standing CWD by beetles associated with more decayed woody material such as basidiomycete feeders and their predators.

As seen from rearing data, the second wave of post-fire saproxylic colonisation really begins with increasing decomposition of CWD which is prompted by the fall of CWD on the ground. Earlier studies have shown that several species show preferences for either standing or fallen woody debris (Jonsell and Weslien 2003, Sverdrup-Thygeson and Ims 2002). Difference in species composition would be largely related to increasing moisture content of logs that are in close contact with the ground. Moisture content have been found to increase the abundance of wood-dwelling insects (Dajoz 1980), presumably by affecting water availability and temperature of substrate (Jonsell and Weslien 2003). Furthermore, increasing moisture content favours both the growth and the diversity of wood-decaying fungi and the following decomposition of sapwood and heartwood (Lindblad 1998, Edmonds and Eglitis 1989, Erickson et al. 1985) which in turn greatly influence the insect fauna (Jonsell and Weslien 2003). In fact, several insects species are known to depend on specific wood-decaying fungi, as their activity is intimately related to hyphae growth and physical characteristic of the substrate (Rukke 2002, Irmler et al. 1996). In the present study, mycelial and sporocarp development presumably attracted mostly microphagous and saprophagous Coleoptera (Atomariinae, *Pteryx* sp., *Ampedus* spp.) and Diptera (e.g. Cecidomyiidae, Chironomidae, *Bradysia* sp.) which become more abundant as wood become more decayed. Species of Cecidomyiidae (Jonsell and Nordlander 2002, Økland and Mamaev 1997) and Sciaridae (Irmler et al. 1996) were previously recorded in decaying wood and/or sporocarps of wood-decaying fungi as larvae mostly feed on fungi, on decay-producing organisms or the products of decay (Teskey 1976).

Furthermore, falling of CWD increases accessibility for soil-dwelling organisms (Hammond et al. 2001, Irmler et al. 1996) as seen from high abundance of Acari and Collembola in fallen spruces of the 1989 and 1973 burned sites. Saproxylic arthropod fauna should therefore become more similar to the litter dwelling fauna as abundance and diversity of epigeic and hibernating species should increase with incorporation of highly decomposed logs to the ground (Irmler et al. 1996). This process is probably hastered in poorly drained spruce stands where rapid paludification tend to accelerate the incorporation of woody debris to the ground layer through rapid sphagnum growth.

Simandl (1993) have stated that successional patterns of colonisation by saproxylic entomofauna is influenced by spatiotemporal differentiation of ecological niches. In this regard, succession of arthropod communities in post-fire dead woody material in northern Québec mostly follows a marked stepwise pattern instead of being gradual. Paquin (2001) noticed a similar successionnal trend in Carabidae of post-fire stands of black spruce where community assemblages where strongly related to distinct successionnal vegetation patterns. Several authors (e.g. Kaila et al. 1997, Økland 1996, Howden and Vogt 1951) have shown that physical properties of wood such as decay stages, fungal colonisation and position of debris which all vary with time since tree death are the main factors influencing insect communities developing in dead wood. The successional pattern noticed in this study differs somewhat from that described by Esseen et al. (1997) for decaying wind-thrown logs of boreal Fennoscandia. Renvall (1995) noticed that successionnal pathway of dead standing trees differs clearly from wind-thrown pines. Differences could be related to type of disturbance as wind-thrown trees were probably subjected to higher moisture conditions throughout decomposition process. Since position of woody debris greatly influence overall physical properties of dead wood, falling of burned CWD plays a major role in saproxylic community succession, at least in the first decades after disturbance.

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Table 1. Structural variables concerning woody debris and vegetation in sampled sites.

Site	**Time since fire yr**	**Vol. WD $m^3.ha^{-1}$**	**Vol. pre-fire WD $m^3.ha^{-1}$**	**Vol. post-fire *Picea* WD $m^3.ha^{-1}$**	**Vol. post-fire *Picea* WD standing $m^3.ha^{-1}$ (%)**	**CWD fraction of total post-fire WD (%)**	**Dominant substrate**	**Dominant ground vegetation**	**Dominant arbustive vegetation**
2002	0.17	65.08	0	61.69	61.69 (100)	82.9	Burnt organic matter	-	-
2001	1	30.33	0	8.44	8.44 (100)	78.8	Burnt organic matter	*Cassandra calyculata*	-
1998	4	44.24	7.48	35.24	32.97 (93.6)	59.7	Burnt organic matter	*Ledum groenlandicum*	-
1989	13	76.39	9.61	66.78	46.36 (69.4)	84.9	Burnt organic matter	*Ledum groenlandicum*	*Betula glandulosa*
1973	29	60.90	5.11	45.07	8.35 (18.5)	73.2	*Sphagnum* sp.	*Ledum groenlandicum*	*Salix* sp.

[1] Values in parentheses are for post-fire CWD of 10-15 cm diameter class

Table 2. Sørensen's similarity indices computed between each paired site from saproxylic coleopteran species collected in TWT

	2002	**2001**	**1998**	**1989**
2002	1			
2001	0.763	1		
1998	0.750	0.762	1	
1989	0.750	0.767	0.800	1

Table 3. Shannon-Wiener's diversity of saproxylic beetles from TWT in each sampled sites

Sites	**Shannon-Wiener value**
2002	0,888
2001	2,666
1998	1,838
1989	2,100

Table 4. Physical characteristics of CWD sampled for arthropod rearing

Site	Woody debris position	Decay class per sample[a]				Bark cover[b]			Sporocarp presence
		1	2	3	4	High	Moderate	Low	
2001	Snag	6	0	0	0	6	0	0	0/6
1998	Snag	4	1	1	0	6	0	0	0/6
1989	Snag	3	2	1	0	0	2	4	2/6
1989	Log	1	1	2	2	1	0	5	4/6
1973	Log	0	0	2	4	0	0	6	6/6

[a] 1 = no apparent degradation ; 2 = 1-33% ; 3 = 33-65% ; 4 = >65% of transversal section showing fungal deterioration.
[b] High = > 65 % ; Moderate = 33-65% ; Low = < 33% of bark cover remaining on trunk.

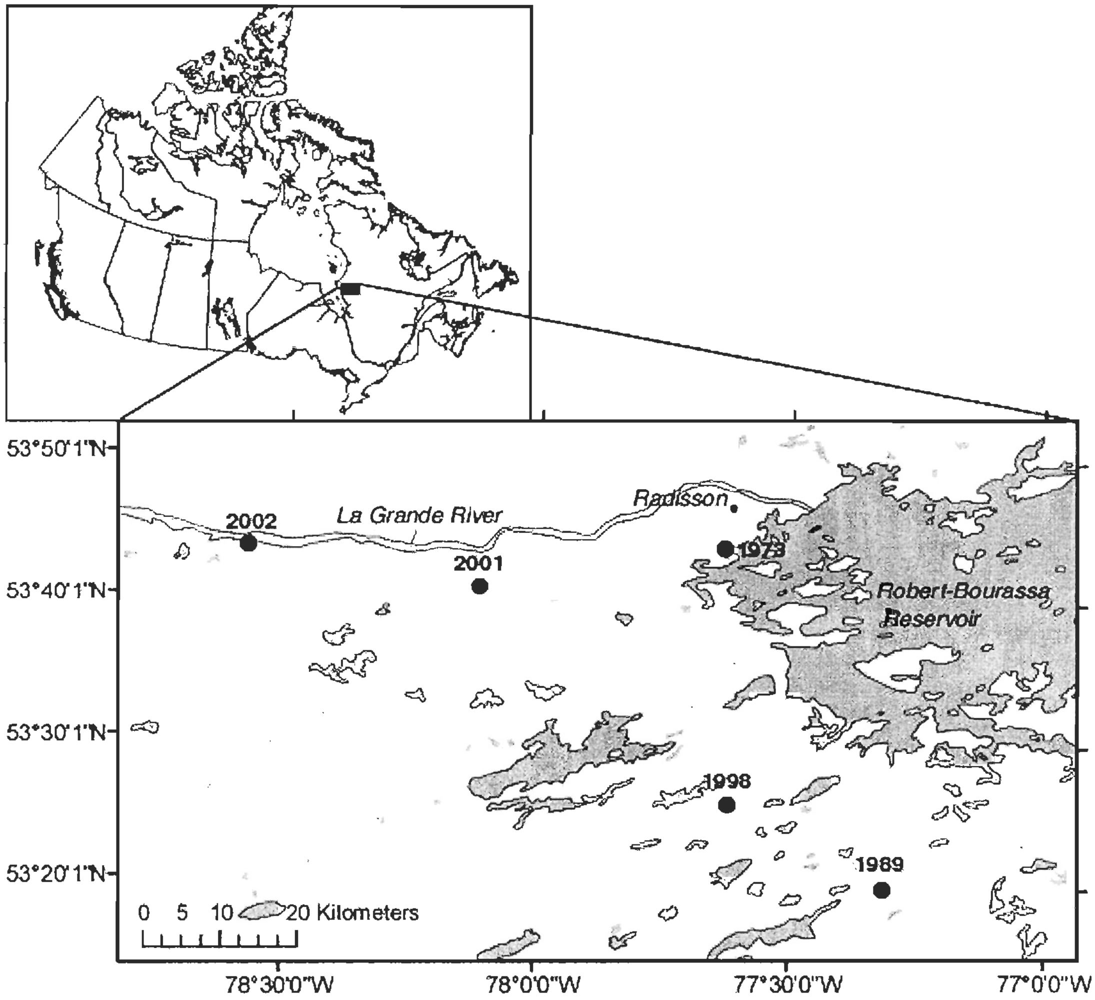

Figure 1. Location of the study area.

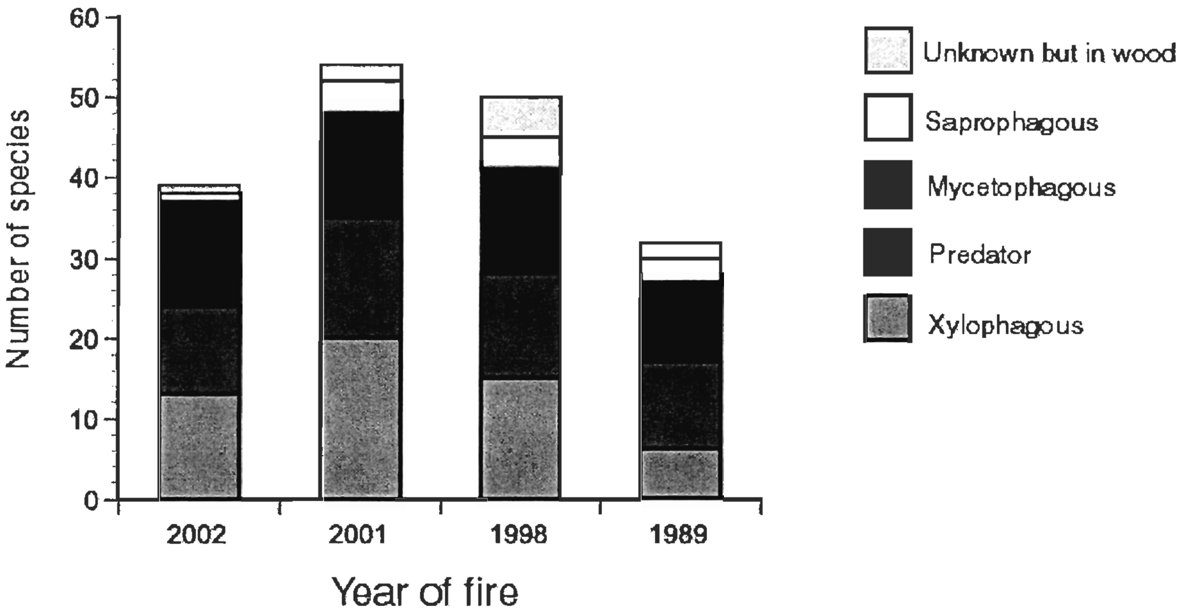

Figure 2. Total number of species of each trophic level captured by means of trunk-window-traps along the chronosequence.

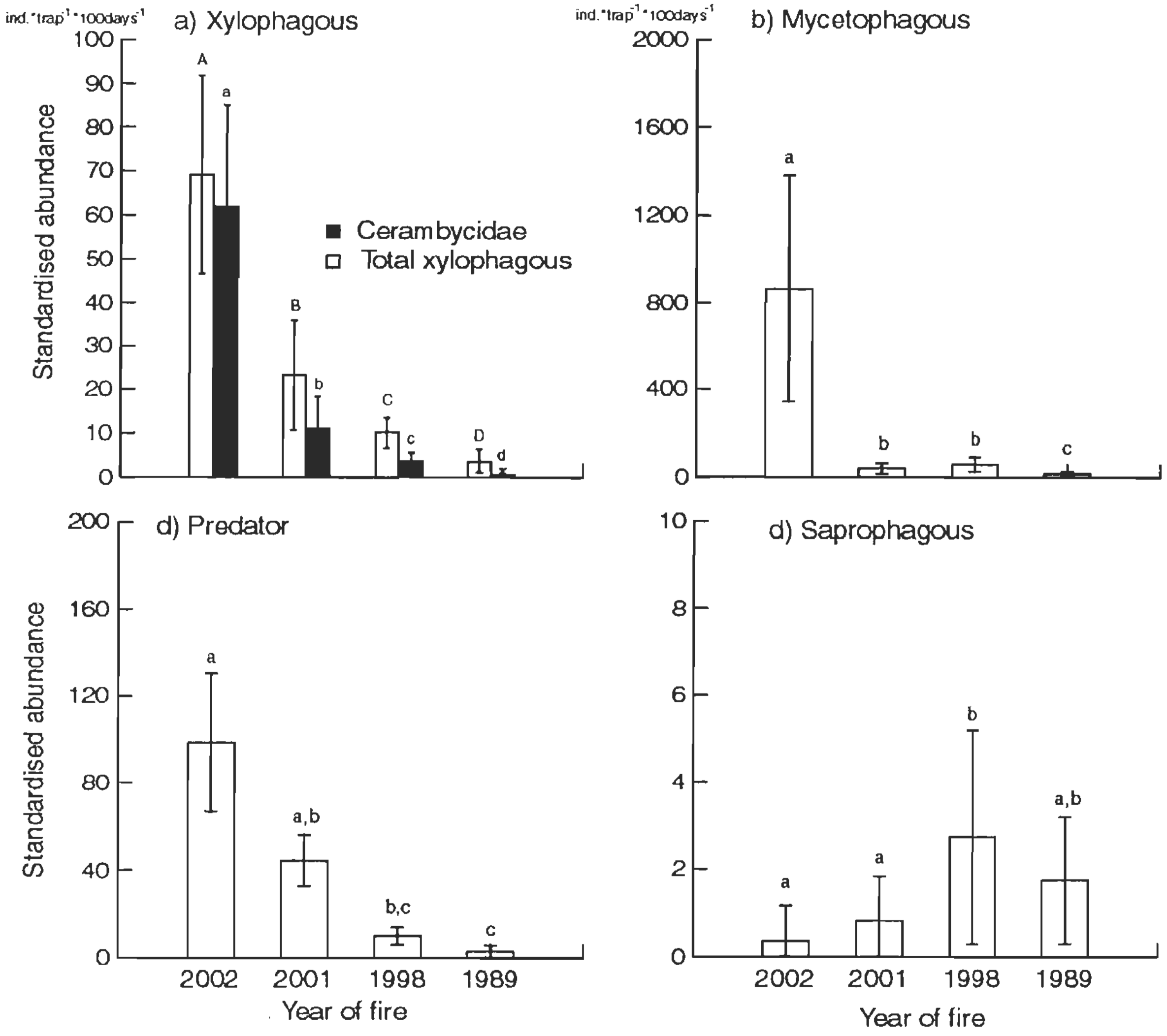

Figure 3. Mean and ± 1 SD standardised abundance of total xylophagous (white bars) and Cerambycidae (black bars) abundance as well as mycetophagous, predators and saprophagous beetles captured per trunk-window-traps in each burned stands. Significant differences in post-hoc multiple comparison test ($\alpha = 0.05$) are represented by letters.

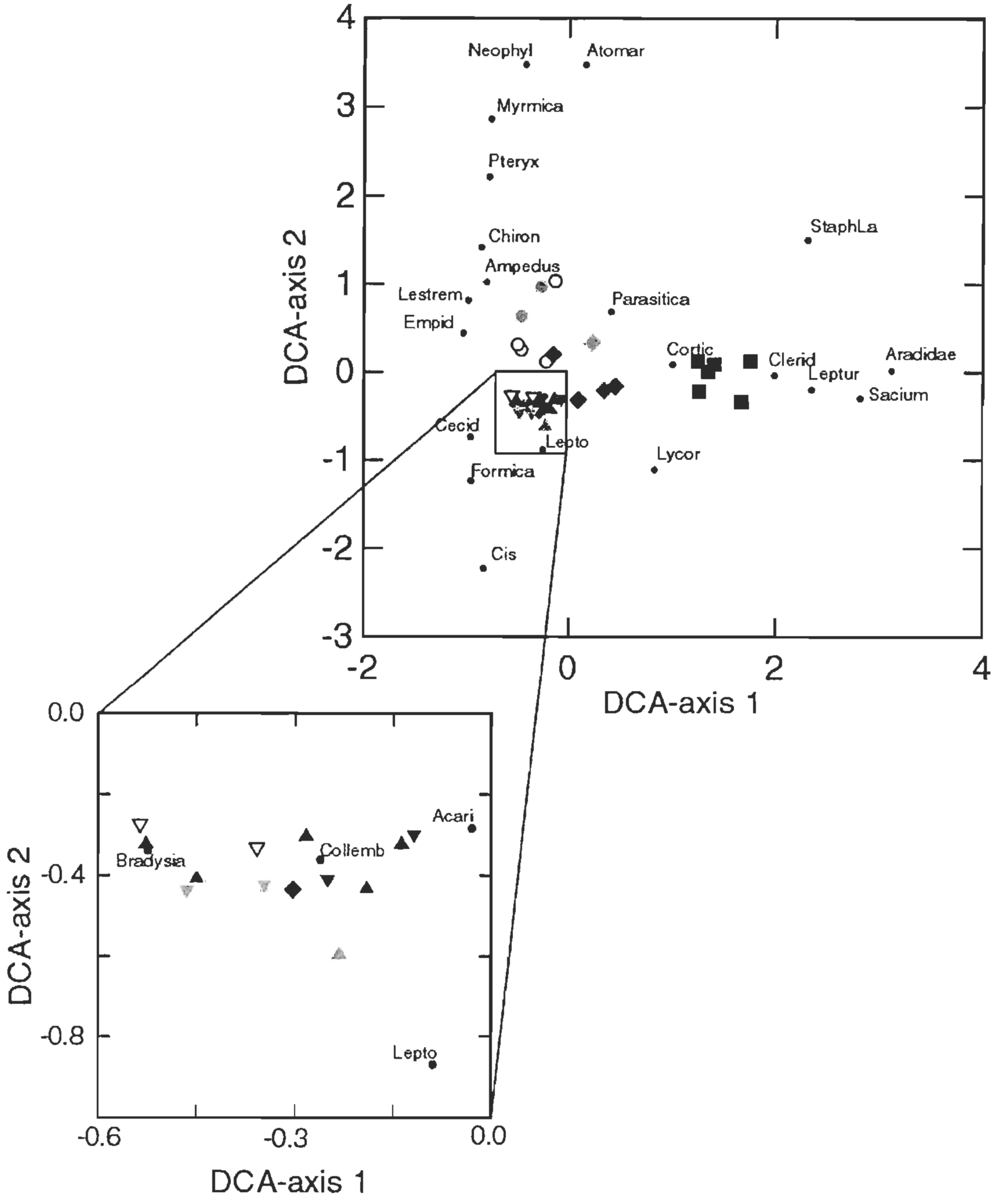

Figure 4. DCA-ordination of saproxylic arthropods emerged from rearing CWD samples of post-fire black spruce. Shape of symbol refers to fire year and position of debris (□ = 2001 snag ; ◊=1998 snag ; Δ = 1989 snag ; ∇ = 1989 log ; o = 1973 log) while colour refers to decay classes as defined in the methods (black = 1 ; dark gray = 2 ; pale gray = 3 ; white = 4).

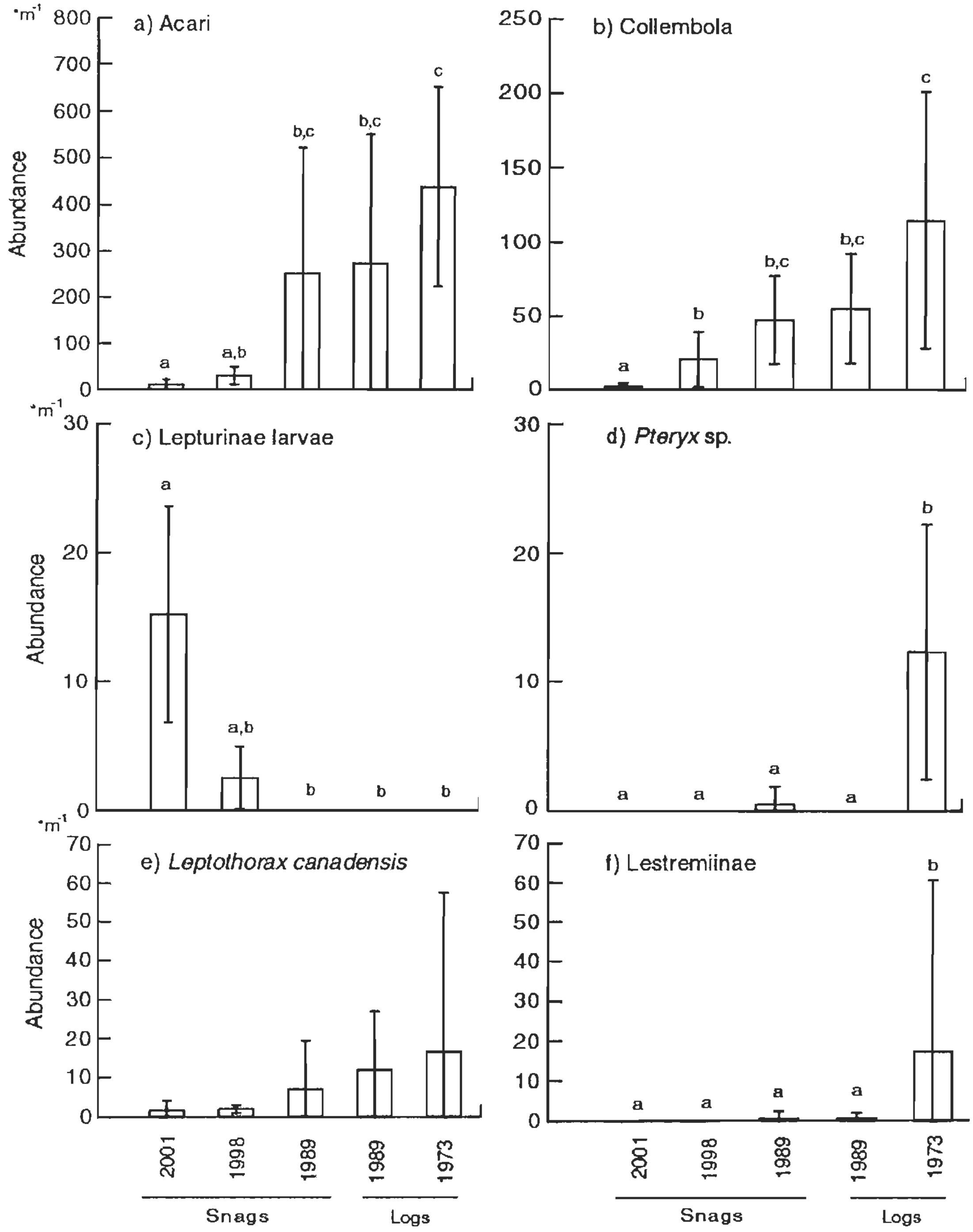

Figure 5. Mean and ± 1 SD abundance of Acari, Collembola, Lepturinae larvae and *Pteryx* sp. Coleoptera, *Leptothorax canadensis* ants and Lestremiinae Diptera collected from CWD rearing samples of each burned site. Significant differences in post-hoc multiple comparison test ($\alpha = 0.05$) are represented by letters.

Appendix 1. List of arthropod taxa collected from trunk-window-traps (TWT) and rearing

Class	Order	Family		Total abundance	
				TWT	Rearing
Arachnida	Araneae	Not determined		143	117
	Acariformes	Not determined		7684	6014
	Opiliones	Not determined		13	0
	Pseudoscorpiones	Not determined		0	6
Collembola		Not determined		810	1430
Insecta	Coleoptera	Anobiidae	*Ernobius* sp. *(granulatus ?)*	1	0
			Hemicoelus carinatus (Say)	2	0
		Boridae	*Boros unicolor* Say	7	5
			Lecontia discicollis (LeConte)	12	0
		Buprestidae	*Anthaxia inornata* (Randall)	1	0
			Chrysobothris trinervia (Kirby)	4	0
			Oxypteris acuminata (DeGeer)	11	1
		Byrrhidae	*Arctobyrrhus subcanus* (LeConte)	2	0
			Byrrhus kirbyi LeConte	2	0
			Cytilus alternans (Say)	5	0
		Cantharidae	*Malthodes* sp.	12	0
			Podabrus sp.	6	0
		Carabidae	*Calathus ingratus* Dejean	1	0
			Lebia sp.	1	0
			Sericoda obsoleta (Say)	41	7
			Sericoda quadripunctata (DeGeer)	11	0
		Carabidae	*Syntomus americanus* (Dejean)	2	0
		Cerambycidae	*Acmaeops proteus* (Kirby)	90	0
			Arhopalus foveicollis Haldeman	120	1
			Gnathacmaeops pratensis (Laicharting)	229	0

continued...

Class	Order	Family		Total abundance	
				TWT	Rearing
			Lepturinae (larvae)	0	106
			Monochamus scutellatus (Say)	2	2
			Pachyta lamed liturata Kirby	20	0
			Rhagium inquisitor (Linnaeus)	12	0
			Trachysida aspera brevifrons Howden	2	5
		Chrysomelidae	*Gonioctena notmani* (Schaeffer)	5	0
		Ciidae	*Cis* sp. 1 Blatchley	0	2
			Cis cf. *striolatus* Casey	42	16
		Clambidae	*Clambus* sp.1	1	0
			Clambus sp.2	2	0
		Cleridae	*Thanasimus undatulus nubilus* Klug	558	0
			Cleridae (larvae; Probably *T. undatulus*)	0	12
		Coccinellidae	*Adalia bipunctata* (L.)	2	0
			Scymnini sp.	2	0
		Corylophidae	Corylophidae sp. 1	1	0
			Sacium fuscum Harold	82	14
		Cryptophagidae	*Anchicera* sp.	2	0
			Antherophagus ochraceus Melsheimer	3	0
			Atomaria sp.	20	0
			Atomariinae (larvae)	0	12
			Caenoscelis ferruginea Sahlberg	18	1
			Cryptophagus pilosus Gyllenhal	0	5
			Henoticus serratus (Gyllenhal)	5	6
		Cucujidae	Cucujidae (larvae ; Probably *P. fuscus*)	0	10
			Pediacus fuscus Erichson	54	1
		Curculionidae	*Crypturgus borealis* Swaine	4	0
		Curculionidae	Curculionidae sp. 1	1	0

continued…

Class	**Order**	**Family**		**Total abundance**	
				TWT	**Rearing**
			Curculionidae sp. 2	1	0
			Dryocoetes affaber (Mannerheim)	2	0
			Dryocoetes autographus (Ratzeburg)	22	0
			Hylobius congener Dalla Torre et Hustache	23	0
			Hylobius warreni Wood	1	0
			Hylurgops rugipennis pinifex (Fitch)	1	0
			Ips pini (Say)	4	3
			Neocimberis elongatus (Leconte)	1	0
			Orthotomicus caelatus (Eichhoff)	4	0
			Pityophthorus sp.	8	0
			Polygraphus rufipennis (Kirby)	2	0
			Rhyncolus macrops Buchanan	0	2
			Scolytus piceae Swaine	1	0
			Trypodendron lineatum (Olivier)	1	0
		Elateridae	*Agriotes limosus* (Leconte)	2	0
			Ampedus sp. (larvae)	0	33
			Ampedus laurentinus Brown	31	1
			Ampedus melsheimeri (Leng)	1	2
			Ampedus quebecensis Brown	7	0
			Ctenicera kendalli (Kirby)	47	0
			Ctenicera spinosa (Leconte)	2	0
			Ctenicera triundulata (Randall)	252	2
			Eanus decoratus (Mannerheim)	5	0
			Elateridae sp.1	1	0
			Negastrius tumescens (LeConte)	5	0
			Sericus incongruus (L.)	119	0

continued...

Class	Order	Family		Total abundance	
				TWT	Rearing
		Hydrophilidae	*Hydrochus* sp.	1	0
		Lampyridae	*Ellychnia corrusca* (L.)	4	0
		Latridiidae	*Cartodere constrictus* (Gyllenhal)	97	1
			Corticaria spp.	5519	13
		Lycidae	*Dictyopteusa aurora* (Herbst)	4	0
		Melandryidae	Melandryidae sp.1	1	0
			Serropalpus coxalis Mank	10	0
			Serropalpus substriatus Haldeman	4	0
			Xylita laevigata (Hellenius)	98	1
			Xylita livida Sahlberg	25	0
		Melyridae	*Hoppingiana hudsonicus* (Leconte)	11	0
		Mordellidae	*Tomoxia borealis* (Leconte)	11	0
		Nitidulidae	*Epuraea obliquus* Hatch	1	0
			Epuraea obtusicollis Reitter	4	0
		Ptilidae	*Acrotrichis* sp.	1	0
			Pteryx sp.	0	77
			Ptiliolum sp.	1	0
			Ptinella sp.	0	1
		Pythidae	*Priognathus monolicornis* (Randall)	2	0
		Salpingidae	*Sphaeriestes virescens* (LeConte)	243	0
		Scirtidae	*Cyphon variabilis* Thunberg	4	0
		Scraptidae	*Anaspis nigrina* (Csiki)	6	1
			Canifa pallipes (Melsheimer)	1	0
		Scydmanidae	*Parascydmnus (corpusculus?)* sp.	11	0
			Stenichnus badius (Casey)	0	1
		Silphidae	*Nicrophorus investigator* Zetterstedt	1	0
			Nicrophorus vespilloides Herbst	1	0

continued...

Class	Order	Family		Total abundance	
				TWT	Rearing
		Silvanidae	*Dendrophagus cygnaei* Mannerheim	1	0
		Staphylinidae	*Acidota crenata* (F.)	4	0
			Aleocharinae (others)	28	7
			Carpelimus sp.	4	0
			Encephalus americanus Seever	2	0
		Staphylinidae	*Eusphalerum* sp. (pothos?)	14	0
			Gyrophaena keeni Casey	1	0
			Heterothops sp.	32	0
			Nudobius cephalus (Say)	11	1
			Phloenomus lapponicus (Zetterstedt)	51	0
			Placusa sp.	6	0
			Porrhodites fenestralis Zetterstedt	3	0
			Pselaphinae sp.1	1	0
			Pselaphinae sp.2	3	10
			Pselaphinae sp.3	3	2
			Quedius sp.	1	1
			Silusa sp.	3	0
			Staphylinidae (larvae)	0	41
			Stenus sp.	1	0
			Tachyporinae sp.	2	0
			Thinobius sp.	4	0
	Diptera	Anthomyiidae	Not determined	226	0
		Anisopodidae	Not determined	5	0
		Asilidae	Not determined	7	0
		Athericidae	Not determined	1	0
		Bibionidae	Not determined	5	0
		Calliphoridae	Not determined	350	2

continued...

Class	**Order**	**Family**		**Total abundance**	
				TWT	**Rearing**
		Carnidae	Not determined	3	0
		Cecidomyiidae	Not determined	177	0
			Asynapta sp.	-	1[a]
			Cecidomyiinae sp.	-	36[a]
			Lestremiinae sp.	-	113[a]
			Winnertzia sp.	-	12[a]
		Ceratopogonidae	Not determined	1928	0
			Forcipomyia sp.	-	11[a]
		Chironomidae	Not determined	923	18
		Chloropidae	Not determined	658	6
		Culicidae	Not determined	5	0
		Dolichopodidae	Not determined	161	0
			Medetera sp.	-	11[a]
		Drosophilidae	Not determined	5	0
		Empididae	Not determined	82	10
		Heleomyzidae	Not determined	77	0
		Lauxaniidae	Not determined	53	0
		Lonchaeidae	Not determined	390	0
		Milichiidae	Not determined	98	0
			Neophyllomyza sp.	-	17[a]
		Muscidae	Not determined	679	0
		Mycetophilidae	Not determined	347	0
			Monoclona sp.	-	9[a]
			Macrocera sp.	-	1[a]
		Phoridae	Not determined	3069	1
		Piophilidae	Not determined	1	0
		Platypezidae	Not determined	47	0

continued...

Class	**Order**	**Family**		**Total abundance**	
				TWT	**Rearing**
		Platystomatidae	Not determined	1	0
		Psychodidae	Not determined	0	1
		Sarcophagidae	Not determined	14	0
		Scatophagidae	Not determined	2	0
		Scatopsidae	Not determined	25	2
		Sciaridae	Not determined	212	0
			Bradysia sp.	-	63[a]
			Lycoriella sp.	-	15[a]
			Pnyxia scabiei (Hopkins)	-	6[a]
			Sciara sp.	-	1[a]
		Sciomyzidae	Not determined	17	0
		Simulidae	Not determined	6	0
		Sphaeroceridae	Not determined	1	0
		Syrphidae	Not determined	8	0
		Tabanidae	Not determined	1	0
		Tachinidae	Not determined	65	5
		Therevidae	Not determined	4	0
		Tipulidae	Not determined	5	0
		Brachycera sp.	Not determined	79	0
	Ephemeroptera	Not determined		14	0
	Hemiptera	Not determined		0	11
		Anthocoridae	Not determined	10[b]	0
		Aradidae	*Aradus* sp. (larvae)	23	37
			Aradus abbas Bergroth	104	0
			Aradus lugubris Fallen	47	0
		Lygaeidae	Not determined	28[b]	0
		Miridae	Not determined	34[b]	0

continued…

Class	**Order**	**Family**		**Total abundance**	
				TWT	**Rearing**
		Saldidae	Not determined	2[b]	0
		Thyreocoridae	Not determined	1[b]	0
	Homoptera	Not determined		59	14
	Hymenoptera	Andrenidae	Not determined	7	0
		Apidae	Not determined	183	0
		Braconidae	Not determined	27	4
		Ceraphronidae	Not determined	5	3
		Chrysididae	Not determined	3	1
		Diapriidae	Not determined	4	6
		Encyrtidae	Not determined	19	6
		Eucoilidae	Not determined	2	0
		Eulophidae	Not determined	3	0
		Eupelmidae	Not determined	0	1
		Formicidae	*Camponotus herculeanus* (L.)	4	3
			Formica neorufibarbis Emery	105	45
		Formicidae	*Formica aserva* Forel	84	0
			Formica podzolica (Wheeler)	6	0
			Leptothorax canadensis Provancher	19	234
			Myrmica alaskensis Wheeler	323	30
			Myrmica fracticornis Forel	99	0
			Tapinoma sessile (Say)	1	0
			Leptothorax sp.B	4	0
		Halictidae	Not determined	65	0
		Ichneumonidae	Not determined	16	0
		Megachilidae	Not determined	55	0
		Megaspilidae	Not determined	1	0
		Melittidae	Not determined	8	0

continued...

Class	**Order**	**Family**		**Total abundance**	
				TWT	**Rearing**
		Mymaridae	Not determined	10	2
		Platygastridae	Not determined	3	0
		Pteromalidae	Not determined	5	6
		Scelionidae	Not determined	14	8
		Sphecidae	Not determined	2	0
		Tenthredinidae	Not determined	3	0
		Trichogrammatidae	Not determined	4	0
		Vespidae	Not determined	17	0
	Lepidoptera	Not determined		355	12
	Orthoptera	Not determined		3	0
	Plecoptera	Not determined		9	0
	Psocoptera	Not determined		49	15
	Thysanoptera	Not determined		146	49
	Trichoptera	Not determined		14	0

[a] Identified only from rearing
[b] Identified only from TWT

Appendix 2. List of saproxylic coleopteran species collected from trunk-window-traps and their relative standardized abundance in each burned site

Family	Species	Trophic role[a]	Sources[§]	Standardized abundance (ind.100days^{-1})			
				2002	2001	1998	1989
Anobiidae	*Ernobius* sp. *(granulatus ?)*	X[*]	1	0	1.16	0	0
	Hemicoelus carinatus (Say)	SN	1	3.57	0	0	0
Boridae	*Boros unicolor* Say	UW	2	3.57	3.49	2.38	0
	Lecontia discicollis (LeConte)	UW	2	0	12.79	1.19	0
Buprestidae	*Anthaxia inornata* (Randall)	X	1	0	0	1.19	0
	Chrysobothris trinerva (Kirby)	X	1	1.79	2.33	0	1.16
	Oxypteris acuminata (DeGeer)	X	1	12.5	2.33	2.38	0
Carabidae	*Calathus ingratus* Dejean	P	1	0	1.16	0	0
	Lebia sp.	P	1	0	0	1.19	0
	Sericoda obsoleta (Say)	P	1	42.86	18.6	1.19	0
	Sericoda quadripunctata (DeGeer)	P	1	19.64	0	0	0
	Syntomus americanus (Dejean)	P	1	1.79	1.16	0	0
Cerambycidae	*Acmaeops proteus* (Kirby)	X	1	142.86	9.3	0	2.33
	Arhopalus foveicollis Haldeman	X	1	205.36	5.81	0	0
	Gnathacmaeops pratensis (Laicharting)	X	1	233.93	77.9	33.33	3.49
	Monochamus scutellatus (Say)	X	1	3.57	0	0	0
	Pachyta lamed liturata Kirby	X	1	32.14	1.16	1.19	0
	Rhagium inquisitor (Linnaeus)	X	1	0	12.79	1.19	0
	Trachysida aspera brevifrons Howden	X	1	0	2.33	0	0
Ciidae	*Cis* cf. *striolatus*	M[*]	3	3.57	30.23	9.52	6.98
Clambidae	*Clambus* sp.1	M	4	1.79	0	0	0

continued...

Family	Species	Trophic role[a]	Sources[§]	Standardized abundance (ind.100days^{-1}) 2002	2001	1998	1989
	Clambus sp.2	M	4	0	1.16	1.19	0
Cleridae	*Thanasimus undatulus nubilus* Klug	P	5	710.71	146.51	40.48	0
Coccinellidae	*Scymnini* sp.	P	6	0	0	1.19	1.16
Corylophidae	Corylophidae sp. 1	M	7	1.79	0	0	0
	Sacium fuscum Harold	M	7	50	60.47	2.38	0
Cryptophagidae	*Anchicera* sp.	M	8	1.79	0	1.19	0
	Antherophagus ochraceus Melsheimer	M	8	0	0	1.19	2.33
	Atomaria sp.	M	8	14.23	5.81	5.95	2.33
	Caenoscelis ferruginea Sahlberg	M	8	26.79	1.16	1.19	1.16
	Henoticus serratus (Gyllenhal)	M	8	7.14	0	1.19	0
Cucujidae	*Pediacus fuscus* Erichson	P[1]	9	28.57	19.77	16.67	8.14
Curculionidae	*Crypturgus borealis* Swaine	X	1	5.36	0	1.19	0
	Dryocoetes affaber (Mannerheim)	X	1	0	0	2.38	0
	Dryocoetes autographus (Ratzeburg)	X	1	10.71	16.28	2.38	0
	Hylobius congener Dalla Torre and Hustache	X	1	25	4.65	4.76	0
	Hylobius warreni Wood	X	1	0	1.16	0	0
	Hylurgops rugipennis pinifex (Fitch)	X	1	0	1.16	0	0
	Ips pini (Say)	X	1	0	4.65	0	0
	Orthotomicus caelatus (Eichhoff)	X	1	1.79	3.49	0	0
	Pityophthorus sp.	X	1	0	0	9.52	0
	Polygraphus rufipennis (Kirby)	X	1	0	0	2.38	0
	Scolytus piceae Swaine	X	1	0	0	1.19	0
	Trypodendron lineatum (Olivier)	X	1	0	1.16	0	0

continued...

Family	**Species**	**Trophic role**[a]	**Sources**[§]	**Standardized abundance (ind.100days^{-1})**			
				2002	**2001**	**1998**	**1989**
Elateridae	*Ampedus laurentinus* Brown	S	10	3.57	3.49	19.05	11.63
	Ampedus melsheimeri (Leng)	S	10	0	0	0	1.16
	Ampedus quebecensis Brown	S	10	0	2.33	1.19	4.65
Lampyridae	*Ellychnia corrusca* (L.)	P	1	0	0	2.38	2.33
Latridiidae	*Cartodere constrictus* (Gyllenhal)	M	11	75	25.58	23.81	15.12
	Corticaria spp.	M	11	8435.71	267.44	532.14	137.21
Lycidae	*Dictyoptera aurora* (Herbst)	M	12	0	1.16	2.38	1.16
Melandryidae	*Serropalpus coxalis* Mank	X[2]	13	10.71	3.49	1.19	0
	Serropalpus substriatus Haldeman	X[2]	13	5.36	1.16	0	0
	Xylita laevigata (Hellenius)	X[2]	13	0	70.93	25	18.6
	Xylita livida Sahlberg	X[2]	13	0	9.3	11.9	8.14
Mordellidae	*Tomoxia borealis* (LeConte)	UW[3]	14	0	0	11.9	1.16
Nitidulidae	*Epuraea obliquus* Hatch	M	15	0	1.16	0	0
	Epuraea obtusicollis Reitter	M	15	1.79	1.16	0	2.33
Ptilidae	*Acrotrichis* sp.	M	16	1.79	0	0	0
	Ptiliolum sp.	M	16	0	0	1.19	0
Pythidae	*Priognathus monolicornis* (Randall)	P	17	0	2.33	0	0
Salpingidae	*Sphaeriestes virescens* (LeConte)	P[4]	18	153.57	179.07	3.57	0
Scraptidae	*Anaspis nigrina* (Csiki)	UW	19	0	0	2.38	4.65
	Canifa pallipes (Melsheimer)	UW	19	0	0	1.19	0
Scydmanidae	*Parascydmnus* sp. *(corpusculus?)*	P	20	3.57	5.81	1.19	3.49
Silvanidae	*Dendrophagus cygnaei* Mannerheim	M	9	0	1.16	0	0
Staphylinidae	*Acidota crenata* (F.)	P	20	0	1.16	2.38	1.16
	Carpelimus sp.	S[5]	20	0	1.16	3.57	0
	Encephalus americanus Seever	M	1	0	0	2.38	0
	Gyrophaena keeni Casey	M	22	0	0	0	1.16

continued...

Family	**Species**	**Trophic role**[a]	**Sources**[§]	**Standardized abundance (ind.100days^{-1})**			
				2002	**2001**	**1998**	**1989**
	Heterothops sp.	P	22	10.71	6.98	19.04	4.65
	Nudobius cephalus (Say)	P	22	0	5.81	5.95	1.16
	Phloenomus lapponicus (Zetterstedt)	P	22	10.71	52.33	0	0
	Placusa sp.	M	23	3.57	4.65	0	0
	Porrhodites fenestralis Zetterstedt	P	22	1.79	0	1.19	1.16
	Pselaphinae sp.1	P	21	0	0	0	1.16
	Pselaphinae sp.2	P	21	0	1.16	1.19	1.16
	Pselaphinae sp.3	P	21	0	1.16	0	2.32
	Quedius sp.	P	22	1.79	0	0	0
	Silusa sp.	M	1	0	2.32	0	1.16
	Stenus sp.	P	21	0	1.16	0	0
	Thinobius sp.	S[5]	20	0	1.16	3.57	0

[a] M = Mycetophagous ; P = Predator ; S = Saprophagous ; X = Xylophagous ; UW = Unknown but found in wood ; SN = Saproxylic but not in *Picea*.
[*] Include xylem borer, root feeders, phloeophagous and ambrosia beetles.
[**] Include polypores, ascomycetes and myxomycetes feeders, spores feeders and microphagous.
[1] Cucujinae may be facultative predators (Lawrence 1991c)
[2] According to Lawrence (1991d) larvae may feed on rotting wood previously infested with fungi.
[3] May breed in *Gleophyllum* spp. (Lawrence 1991e)
[4] Muona and Rutanen (1994) reported that *Sphaeriestes stockmanni* is predator under bark.
[5] May be alga-feeders (Newton et al. 2001) but Hammond (1996) identified *Carpelimus* as saprophagous

[§]**Sources** : 1) Downie and Arnett 1996 ; 2) Pollock 2002a; 3) Lawrence 1971; 4) Lawrence 1991a; 5) Lawrence 1991b; 6) Vanderberg 2002; 7) Bowestead and Leschen 2002; 8) Leschen and Skelley 2002; 9) Lawrence 1991c; 10) Boris Büche pers. comm.; 11) Andrews 2002; 12) Miller 2002; 13) Lawrence 1991d ; 14) Lawrence 1991e; 15) Lawrence 1991f; 16) Hall 2001; 17) Pollock 2002b; 18) Muona and Rutanen 1994; 19) Young 1991; 20) O'keefe 2001; 21) Newton et al. 2001; 22) Klimaszewski 2000 ; 23) Klimaszewski et al. 2001.

Appendix 3. Diversity, trophic role and total abundance of Coleoptera from rearing samples

Family	Species	Trophic role[a]	Sources[§]	Total abundance (ind.)				
				2001 Snags	1998 Snags	1989 Snags	1989 Logs	1973 Logs
Boridae	*Boros unicolor* Say	UW	1	0	4	1	0	0
Buprestidae	*Oxypteris acuminata* (DeGeer)	X*	2	1	0	0	0	0
Carabidae	*Sericoda obsoleta* (Say)	P	2	4	1	0	0	2
Cerambycidae	*Arhopalus foveicollis* Haldeman	X	2	0	0	0	1	0
	Lepturinae larvae	X	2	91	15	0	0	0
	Monochamus scutellatus Say (larvae)	X	2	2	0	0	0	0
	Trachysida aspera brevifrons Howden	X	2	0	0	0	5	0
Ciidae	*Cis* cf. *striolatus*	M**	3	0	0	0	2	0
	Cis sp. 1	M	3	0	1	8	7	0
Cleridae	Cleridae larvae	P	4	8	1	1	0	2
Corylophidae	*Sacium fuscum* Harold	M	5	14	0	0	0	0
Cryptophagidae	Atomariinae larvae	M	6	2	0	0	0	10
	Caenoscelis ferruginea Sahlberg	M	6	0	0	0	1	0
	Cryptophagus pillosus Gyllenhal	M	6	2	0	0	1	2
	Henoticus serratus (Gyllenhal)	M	6	3	1	1	1	0
Cucujidae	Cucujidae larvae *(*Probably *P. fuscus)*	P[1]	7	0	0	0	0	10

continued...

Family	**Species**	**Trophic role[a]**	**Sources[§]**	**Total abundance (ind.)**				
				2001 Snags	**1998 Snags**	**1989 Snags**	**1989 Logs**	**1973 Logs**
	Pediacus fuscus Erichson	P[1]	7	0	0	0	0	1
Curculionidae	*Ips pini* (Say)	X	2	3	0	0	0	0
	Rhyncolus macrops Buchanan	X	2	0	0	0	0	2
Elateridae	*Ampedus* sp. larvae	S	8	0	2	1	12	18
	Ampedus laurentinus Brown	S	8	0	0	0	0	1
	Ampedus quebecensis Brown	S	8	0	1	0	0	1
	Ctenicera triundulata (Randall)	NS	8	1	0	1	0	0
Lathridiidae	*Cartodere constrictus* (Gyllenhal)	M	9	0	1	0	0	0
	Corticaria sp.	M	9	6	1	1	2	3
Melandryidae	*Xylita laevigata* (Hellenius)	X[2]	10	0	0	0	1	0
Ptilidae	*Pteryx* sp.	M	11	0	0	3	0	74
	Ptinella sp.	M	11	0	0	0	0	1
Scraptidae	*Anaspis nigrina* (Csiki)	UW	12	0	0	0	0	1
Scydmaenidae	*Stenichnus badius* (Casey)	P	11	0	0	0	0	1
Staphylinidae	Aleocharinae sp.	Various	13	0	0	0	1	6
	Nudobius cephalus (Say)	P	14	0	1	0	0	0
	Pselaphinae sp.	P	13	0	1	1	0	0

continued...

Family	**Species**	**Trophic role**[a]	**Sources**[§]	**Total abundance (ind.)**				
				2001 Snags	**1998 Snags**	**1989 Snags**	**1989 Logs**	**1973 Logs**
	Quedius sp.	P	14	0	0	0	0	1
	Staphylinidae larvae	Various	15	36	2	0	0	3

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[a] M = Mycetophagous ; P = Predator ; S = Saprophagous ; X = Xylophagous ; UW = Unknown but found in wood ; NS = Not saproxylic.

[*] Include xylem borer, root feeders, phloeophagous and ambrosia beetles.

[**] Include polypores, ascomycetes and myxomycetes feeders, spores feeders and microphagous.

[1] Cucujinae may be facultative predators (Lawrence 1991b)

[2] According to Lawrence (1991d) larvae may feed on rotting wood previously infested with fungi.

[§] **Sources** : 1) Pollock 2002; 2) Downie and Arnett 1996; 3) Lawrence 1971; 4) Lawrence 1991b; 5) Bowestead and Leschen 2002; 6) Leschen and Skelley 2002; 7) Lawrence 1991c; 8) Boris Büche, pers. comm. 9) Andrews 2002; 10) Lawrence 1991d; 11) Arnett and Thomas 2001; 12) Young 1991; 13) Newton et al. 2001; 14) Klimaszewski 2000; 15) Frank 2001.

2. Conclusions générales

2.1 Stockage des débris ligneux

Il appert que le volume de débris ligneux après feu en milieu subarctique québécois est particulièrement faible comparativement à ce qui est observé en Europe septentrionale (Krankina et al., 2002; Siitonen 2001). Toutefois, les DLG d'épinette noire après feu présentent une masse équivalente à ce qui fut préalablement noté à l'intérieur de pessières noires nordiques similaires (Bond-Lamberty et al., 2002). Par conséquent, la faible accumulation de DLG après feu en raison de la faible productivité ligneuse avant perturbation fait en sorte que ceux-ci ne procurent qu'entre 2,84 et 13,87 $Mg.ha^{-1}$ de carbone à l'intérieur des sites brûlés.

2.2 Succession des arthropodes saproxyliques en relation avec la décomposition du substrat ligneux

La lenteur à laquelle s'effectue la décomposition de la matrice ligneuse dans la région étudiée (k = 0.0041-0.0101) serait inhérente à la fois à des facteurs s'exprimant à grande et petite échelles. La faible température moyenne annuelle (-3.6°C) serait partiellement responsable des faibles taux de décomposition, l'activité microbienne et fongique étant principalement dépendantes de la température (Wang et al., 2002; Chambers et al., 2000). De ce fait, ces taux de décomposition conjugués aux faibles volumes de DLG occasionnent des pertes de carbone ligneux relativement faibles lorsque comparées à celles enregistrées à l'intérieur de peuplements plus méridionaux (Mattson et al., 1987).

Toutefois, le feu lui-même ralentirait le processus de décomposition en influençant le taux de fragmentation de l'écorce. La variation dans le taux de chute de l'écorce pourrait être reliée à l'intensité du feu, l'écorce calcinée se fragmentant plus rapidement que sur les sections troncales intactes (Wikars, 2002). Les individus conservant leur écorce durant une plus longue période pourraient maintenir un taux d'humidité suffisant afin de faciliter la colonisation fongique. L'humidité limite fréquemment la décomposition de la nécromasse ligneuse (Wang et al., 2002; Laiho et Prescott, 1999) puisque les basidiomycètes saproxyliques ne peuvent atteindre l'eau sous le seuil de saturation des fibres, communément fixé à 30 % (Harmon et al., 1986; Erickson et al., 1985). Ceci serait d'autant plus vrai pour les basidiomycètes à carie blanche, lesquels possèdent des capacités enzymatiques supérieures aux espèces de carie brune d'où une efficacité plus élevée pour dégrader la matrice ligneuse (Boddy et Watkinson, 1995; Renvall, 1995; Niemelä, 1985; Swift, 1977a). Puisque les champignons à carrie brune auraient davantage de facilité à s'établir sur des substrats secs (Renvall, 1995), les arbres incendiés et colonisés par ces espèces sont susceptibles de présenter de faibles taux de décomposition.

Qui plus est, malgré que la colonisation initiale par l'entomofaune saproxylique soit abondante et diversifiée (voir ci-dessous), il appert que la colonisation larvaire de certaines espèces, notamment des perceurs de xylèmes, soit particulièrement déficiente. Il est reconnu que ces insectes favorisent l'établissement de champignons saproxyliques en fournissant l'accès au xylème par l'intermédiaire des galleries larvaires ou par une inoculation passive et/ou active par les adultes (Six and Bentz, 2003; Zhong et Schowalter, 1989). Une faible densité larvaire pourrait alors réduire le potentiel de colonisation et de croissance de certains champignons saproxyliques, réduisant du même coup les taux de décomposition du substrat.

La diversité des coléoptères saproxyliques peu de temps après feu est inférieure à celle notée en pessière noire méridionale (Saint-Germain 2004a,b). Qui plus est, les communautés saproxyliques se distinguent de celle observée dans les pessières méridionales. La diversité totale des coléoptères saproxyliques demeurent inférieure à celle associée au débris ligneux d'épinette en milieu subarctique européen (Sippola et al., 2002; Olberg et al., 2001). Toutefois, la faible diversité pourrait être inhérente aux techniques d'échantillonnage utilisées ainsi qu'à la durée de la chronoséquence étudiée lesquelles amènent une sous-représentation des espèces associées aux stades de décomposition avancés.

Néanmoins, cette étude, qui est la première à documenter la succession saproxylique à long terme après feu au Canada, démontre clairement que le patron successionnel se présente en deux vagues de colonisation distinctes. En fait, la colonisation initiale débute peu de temps après la perturbation alors qu'il faut attendre la chute du chicot pour que s'amorce la deuxième phase de colonisation.

2.2.1 Colonisation saproxylique et décomposition des chicots

La diversité des coléoptères saproxyliques peu de temps après perturbation est essentiellement influencée par l'apport d'espèces pyrophiles lesquelles déclinent graduellement par la suite. Ces espèces regroupent notamment prédateurs subcorticaux, xylophages et certaines espèces associées aux ascomycètes se développant en région subcorticale (Muona et Rutanen, 1994).

Les coléoptères de la famille des Cerambycidae demeurent les xylophages les plus abondants à l'intérieur des deux techniques d'échantillonnage. L'abondance de ce dernier groupe est maximale l'année même du feu alors qu'elle décroît dans les sites plus âgés, plusieurs espèces étant fréquemment associées au bois brûlé (Werner, 2002; Wikars et Schimmel, 2001; McCullough et al., 1998; Lundberg, 1984; Gardiner, 1957; Richmond et Lejeune, 1945). La plupart de ces espèces se nourrissent à l'état larvaire dans la région subcorticale (Haack and Slansky, 1986) laquelle se décompose très rapidement comparativement aux tissus sous-jacents (Schowalter et al., 1998) rendant le substrat inapproprié au développement larvaire (Howdie et Vogt, 1951). Parallèlement, la rapide dégradation des tissus subcorticaux pourrait expliquer le déclin soudain peu de temps après feu de certaines espèces mycétophages (Coléoptères cucujoides, *Aradus* sp.) s'alimentant de spores d'ascomycètes (Wikars, 2002; Dajoz 1998).

On observe une augmentation de la diversité saproxylique l'année suivant le feu malgré que la plupart des espèces colonisatrices, notamment certains Scolytidae, soient peu communes. L'arrivée désynchronisée des Scolytidae pourrait refléter des changements dans la concentration et la nature des composés organiques volatiles en fonction de la décomposition des tissus subcorticaux (Lindgren et Miller, 2002a, 2002b; Fletchmann, 1999).

À ce point dans la chronoséquence, à la fois la diversité et l'abondance des coléoptères saproxyliques associés aux chicots diminuent à mesure que l'on s'éloigne de l'incidence de la perturbation. D'aucun envisagerait un changement dans les communautés saproxyliques en fonction des changements physiques de la matrice ligneuse (Hammond, 1997, 1996; Essen et al., 1997). Toutefois, malgré que la plupart des espèces colonisatrices initiales déclinent ou disparaissent en fin de chronoséquence, la succession vers des espèces associées à des stades de décomposition plus avancés est virtuellement inexistante dans les chicots. Ce phénomène résulterait du faible taux de décomposition mesuré dans le cadre de cette étude, notamment celui des chicots, lequel retarderait l'accession de substrats propices pour ces espèces.

Ainsi, le taux de décomposition des DLG sur pied est 2,5 fois plus lent que celui des DLG au sol. De façon concomitante, on observe que le degré d'humidité des chicots quatre ans et plus après feu demeure inférieur à 30 %, soit sous le seuil de saturation des fibres. Le taux d'humidité limité chez les chicots retarde, ou à tout le moins ralentit, la respiration fongique, influençant directement le taux de décomposition. Pour cette raison, la production de chicots après feu engendre la création d'un réservoir majeur de carbone en forêt boréale (Kasischke, 2000b).

2.2.2 La chute du chicot, la colonisation saproxylique et la décomposition subséquente

Une fois le débris au sol, l'augmentation de l'humidité favorise la croissance des tissus fongiques et conséquemment la dégradation de la nécromasse. Cette augmentation du taux de décomposition de la matrice ligneuse présumément stimule la deuxième phase de colonisation saproxylique. En plus d'affecter favorablement la disponibilité en eau ainsi que la température du substrat (Jonsell et Weslien, 2003), la chute du débris ligneux provoque l'arrivée d'espèces microphages et saprophages associées aux tissus fongiques (mycélium et carpophores) (Rukke, 2002; Irmler et al., 1996). Qui plus est, l'augmentation de l'abondance de taxons épigés en fin de chronoséquence résulte directement de l'accessibilité plus importante des DLG au sol (Hammon et al., 2001; Irmler et al., 1996). Ce processus est probablement accéléré à l'intérieur des sites à drainage déficient où la paludification rapide hâte l'incorporation de la nécromasse ligneuse au sol en raison de la croissance rapide des bryophytes.

2.3 Retour sur le patron de succession saproxylique

Simandl (1993) est d'avis que les patrons successionnels de colonisation par l'entomofaune saproxylique sont influencés par la différentiation spatiotemporelle des niches écologiques. À ce sujet, la succession des communautés d'arthropodes notée dans la présente étude semble s'effectuer par étape plutôt que graduellement. Plusieurs auteurs (ex. : Kaila et al., 1997; Økland et al., 1996; Howdie et Vogt, 1951) ont préalablement démontré que les propriétés physiques du bois telles que le stade de décomposition, la colonisation fongique et la position du débris, lesquels fluctuent en fonction du temps suite à la mort de l'arbre, demeurent les principaux facteurs susceptibles d'influencer les communautés saproxyliques. Notre étude suggère que ces communautés exhibent un patron de succession différent de celui-ci décrit par Essen et al. (1997) pour les arbres tués par chablis en Fennoscandie. Ces différences pourraient être reliées au type de perturbation, les arbres tués par chablis profitant probablement de conditions d'humidité plus favorables tout au long du processus de décomposition. Ceci maintiendrait le processus de succession saproxylique alors que celui-ci ne peut se poursuivre chez les arbres incendiés qu'une fois l'individu tombé au sol. Par conséquent, puisque la chute au sol du débris ligneux influence fortement les propriétés physiques de la matrice ligneuse, ce phénomène joue un rôle majeur dans la succession des communautés saproxyliques en milieu subarctique.

2.4 Le cyclage de l'azote

L'évolution du processus de décomposition et de succession saproxylique se réflète directement à l'intérieur des variations du contenu en azote de la matrice ligneuse. En fait, en considérant les pertes de masse engendrées par la dégradation fongique du substrat, l'azote suit trois phases distinctes en relation avec le temps suite à la perturbation. On observe ainsi une perte nette d'azote peu de temps après feu, suivi d'une période (~10 ans) de relative stabilité à laquelle succède une hausse du contenu en azote en fin de chronoséquence où la majorité des débris se retrouvent au sol. Ainsi, les pertes initiales d'azote seraient attribuables à la décomposition rapide des tissus subcorticaux lesquels renferment des concentrations relativement élevées d'azote (Cowling and Merrill, 1966). Le lessivage (Harmon et al., 1986) ainsi que la consommation de ces mêmes tissus par les xylophages subcorticaux (Schowalter et al., 1998) pouraient partiellement expliquer ce phénomène. Les faibles activités hétérotrophiques (arthropodes et champignons) dans les chicots pourraient expliquer la stabilité du contenu en azote par la suite. La chute du débris ainsi que la colonisation fongique subséquente amène une translocation active d'azote à l'intérieur du substrat via le mycélium (Schowalter et al., 1998; Boddy et Watkinson, 1995; Edmonds et Eglitis, 1989; Ausmus, 1977) ce qui se traduit par un gain net d'azote.

2.5 Ouverture et perspectives de recherche

L'élaboration de modèles concernant le stockage et les pertes de carbone provenant des DLG produits après feu dans le nord de la forêt boréale québécoise requiert de plus amples spécifications sur la variation du stockage en DLG. Celui-ci est affecté à la fois par la productivité primaire nette (PPN), l'historique des feux et les taux de décomposition, le tout variant le long d'un gradient latitudinal et longitudinal. L'hétérogénéité spatiale des DLG et des taux de décomposition à grande échelle peut être consédérable selon l'action de divers facteurs biotiques et abiotiques (Rouvinen et al. 2002). Au Québec nordique, la fréquence des feux est très variable, diminuant vers les hautes latitudes (Payette et al. 1989) et à proximité des influences marines de l'Atlantique (Foster 1985) et des baies de James et d'Hudson (Parisien et Sirois 2003) alors que les taux de décomposition et la PPN devraient diminuer vers le nord à mesure que le climat devient plus rude. L'inclusion de ces modèles conjuguée aux données provenant du stockage des débris ligneux avant feu devrait donner une image plus précise du stockage du carbone et de son cyclage dans la forêt boréale canadienne.

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