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EFFETS DES BRÛLAGES DIRIGÉS SUR LA RÉGÉNÉRATION DU PIN BLANC ET LA DIVERSITÉ DES COLÉOPTÈRES DU PARC NATIONAL DU CANADA DE LA MAURICIE

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Résumé

Les écosystèmes de pin blanc du parc national du Canada de la Mauricie (PNCLM) ont été altérés par les coupes forestières et la suppression des incendies forestiers depuis 1850. En raison de ces altérations, la trajectoire écologique des écosystèmes de pin blanc a été modifiée et ils ne sont plus en mesure de se perpétuer naturellement, la majorité des sites n'ayant aucun individu au stade de gaule. Ainsi, dans ces écosystèmes, les gaules de pin blanc sont presque absentes et les gaules de sapin baumier, très abondantes, compétitionnent fortement les semis de pin blanc pour l'espace et la lumière. Depuis 1991, le brûlage dirigé est utilisé pour restaurer les écosystèmes de pin blanc du parc national du Canada de la Mauricie. Ces pratiques s'inscrivent dans la politique d'intégrité écologique de Parcs Canada. Sept sites brûlés entre 1995 et 2005 et neuf sites non-brûlés ont été étudiés afin d'évaluer l'effet des brûlages dirigés sur différentes composantes biotiques du milieu, notamment la densité des gaules de sapin baumier et la densité des semis de pin blanc. Les brûlages dirigés ont tué plus de 67% des gaules de sapin baumier, éliminant ainsi une partie significative de la compétition faite aux semis de pin blanc. Dans les sites brûlés où la régénération en pin blanc a eu lieu, ces derniers sont quatre fois plus abondants dans les sites brûlés que dans les sites non-brûlés (moyenne de 21 333 vs 5 135 semis/ha). Le sapin n'a pas réintroduit les sites brûlés tandis que la banque de semis de pin blanc est abondante et stable, les plus grands spécimens atteignent 50 cm de hauteur 11 ans après le passage du feu. À court terme, les objectifs de régénération du pin blanc fixés par Parcs Canada ont donc été atteints. Cependant, la croissance des semis établis devra faire l'objet de suivis périodiques afin d'assurer le succès à moyen et long terme de ce programme de restauration. Par ailleurs, l'impact de ce traitement sur la diversité des communautés animales a aussi été étudié en utilisant les assemblages d'espèces de coléoptères comme modèle. En effet, il s'agit de l'ordre d'insectes le plus diversifié et le mieux connu, comptant entre autre de nombreuses espèces associées aux arbres moribonds et morts, une composante importante résultant de l'utilisation du brûlage dirigé. Les analyses portant sur l'abondance, la richesse et la rareté des coléoptères démontrent que les assemblages des sites brûlés et non-brûlés diffèrent énormément. Les résultats indiquent que les assemblages de coléoptères des peuplements non-brûlés possèdent moins d'espèces saproxyliques que les sites brûlés. La majorité des différences entre les communautés proviennent de la forte présence d'espèces "rares" et capturées principalement ou uniquement dans les sites brûlés. L'analyse de redondance des espèces saproxyliques abondantes a démontré de fortes relations entre la majorité des espèces et le bois mort récemment rendu disponible par le traitement. Les effets sur l'abondance et la diversité des coléoptères saproxyliques est maximale entre trois et spet ans après le traitement. En l'absence de feux naturels et malgré leur faible intensité, les brûlages dirigés semblent donc générer des conditions propices pour de nombreuses espèces saproxyliques.

Abstract

Ecosystems with Eastern white pine of La Mauricie National Park of Canada (LMNPC) have been affected by logging and forest fire suppression since 1850. Because of these alterations, the ecological trajectory of these ecosystems has been changed and they are no longer capable of persisting naturally, as saplings of this species were almost absent of unburbed forests. Thus, in these forests, Eastern white pine saplings are almost absent and balsam fir saplings competing strongly Eastern white pine seedlings for space and light. Since 1991, prescribed burning was used to restore the ecosystems of Eastern white pine. These practices have been initiated following Parks Canada ecological integrity restoration policies. Seven sites burned between 1995 and 2005 and nine unburned sites were studied to assess the effect of burning on various components of the biotic environment, including the density of balsam fir saplings and the density of Eastern white pine seedlings. The burns have killed more than 67% of balsam fir saplings, thus eliminating a significant part of the competition to Eastern white pine seedlings. In burned sites where Eastern white pine regeneration has occurred, they are four times more abundant than in unburned sites (mean 21 333 vs. 5 135 seedlings / ha). Balsam fir has not reintroduced burned sites while the Eastern white pine seedlings bank is abundant and stable, larger specimens reaching up to 50 cm of height 11 years after prescribed burning. In the short term, the objectives established by Parks Canada have been met. Seedling growth now established should be monitored periodically to ensure success in the medium and long-term. We have also studied the impact of prescribed burning on the diversity of animal communities through Coleoptera species assemblages. Analysis on the abundance, richness and rarity of beetles demonstrate that communities of burned sites differ greatly than those in unburned sites. Results indicate that beetle assemblages in unburned sites have fewer saproxylic species than burned sites. Differences mainly aroused from "rare" species caught mainly or only in burned sites. The redundancy analysis of abundant saproxylic species showed strong relationships between species captured and recent snags generated by the treatment. The beneficial effects on the abundance and diversity of saproxylic beetles, however, abate with time after the treatment, these being highest between three and seven years after the fire. In the absence of natural fires and despite the low intensity of prescribed burning, this treatment appears to create adequate conditions to maintain several saproxylic insects.

Avant-Propos

Ce projet a été réalisé grâce au partenariat de trois organismes soit, l'Université Laval, Parcs Canada et Ressources Naturelles Canada. Les travaux de terrain se sont déroulés au parc national du Canada de la Mauricie tandis que l'identification des insectes a eu lieu au centre de foresterie des Laurentides, dans le laboratoire d'écologie et diversité des insectes forestiers (EcoDIF) du Dr. Christian Hébert. Les fonds investis proviennent du programme de gestion des feux à Parcs Canada. Ce projet n'aurait pu être possible sans la participation de mon directeur Louis Bélanger (Université Laval), mon co-directeur Christian Hébert (Ressources Naturelles Canada), Victor Kafka, Michel Thériault et Raymond Queneville de Parcs Canada.

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Ton attitude détermine ton altitude

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Introduction

Au cours des dernières décennies, les forêts de l'Amérique du Nord ont subi d'importantes modifications et la raréfaction de certaines essences forestières pourrait menacer le maintien de la biodiversité (Bergeron et al. 2001; Reich et al. 2001). Dans les forêts précoloniales de l'Est de l'Amérique du Nord, le pin blanc (*Pinus strobus* Linnaeus) fût jadis une essence abondante (Sargent 1947; Horton et al. 1960; Peattie 1966; McRae et al. 1994; Carleton et al. 1996; Davis 1996 ; Quenneville et Thériault 1998). À l'arrivée des premiers européens dans le nord-est de l'Amérique, vers le 16^e siècle, d'immenses forêts de pin blanc étaient présentes dans la vallée du fleuve Saint-Laurent et des Grands Lacs (Sargent 1947; Peattie 1966; Weyenberg et al. 2004). Le pin blanc est une essence indigène à l'Amérique du Nord et son aire de répartition va de la côte atlantique, à l'est, jusqu'au Manitoba, à l'ouest. Il atteint sa limite nordique à Terre-Neuve, et au sud il atteint l'état de la Georgie aux États-Unis (Horton et Brown 1960; Farrar 1995; Abrams 2001; Vlasiu et al. 2001; Lorimer 2008). Le pin blanc est l'arbre qui atteint les plus grandes tailles dans l'est de l'Amérique du Nord, atteignant jusqu'à 30-50 m de hauteur et un diamètre à hauteur de poitrine de plus de 100 cm (Farrar 1995). Il pousse sur une grande variété de sols, mais plus souvent sur les terres arides et les sols acides où les espèces compétitives n'obtiennent pas d'aussi bons résultats (Wendel et Smith 1990; Abrams 2001). C'est une précieuse ressource forestière étant un élément important de l'économie, de la culture et de la médecine des anciens colonisateurs, ainsi que de l'histoire de certains peuples autochtones (Day 1953). Cette espèce de conifère est aussi utilisée comme nourriture et abri par plusieurs espèces fauniques (Naylor 1994).

Le pin blanc est associé aux incendies forestiers et autres perturbations naturelles (Maissurow 1935; Sargent 1947; Horton et al. 1960; Weyenberg et al. 2004). Bien que ses cônes ne soient pas sérotineux, il profite des nouvelles conditions crées par le feu pour bien s'installer. Il possède une écorce épaisse et ses premières branches sont hautes, conséquemment les flammes des feux de surface ne les atteignant que très rarement (Maissurow 1935; Sargent 1947; Horton et Brown 1960; Weyenberg et al. 2004). Selon la sévérité de la perturbation et des essences présentes sur le site, le feu améliore le lit de germination du pin blanc, élimine la compétition moins bien adaptée à ces évènements et ouvre le couvert du peuplement à la lumière en tuant certaines essences plus vulnérables tels le sapin et le bouleau blanc. Les semis de pin blanc peuvent coloniser divers habitats perturbés, dont ceux créés par les feux (Carleton et al. 1996; Dovčiak et al. 2001; Elliott et al. 2002).

La diminution de l'abondance de cette essence en Amérique du Nord semble grandement attribuable à la colonisation européenne (Watson 1923; Day 1953; Baker 1992; Frelich 1995; Östlund et al. 1997; Turbis 2005). En effet, le pin blanc a été une des essences forestières les plus exploitées en Amérique du Nord au début de la colonisation (Watson 1923; Carleton et al. 1996). Au départ, les grands semenciers ont été coupés pour la construction navale en Grande-Bretagne (Carlton 1939; Mirov et Hasbrouck 1976; Burgess et Methven 1977; Wilkins et Kiceluk 1994). Dans l'Est du Canada, l'impact de l'exploitation forestière s'est fortement fait sentir à la fin du 19^e et au début du 20^e siècle (Watson 1923; Palik et Pregitzer 1994; Weyenberg et al. 2004). Ces pratiques ont été si intenses que plusieurs peuplements ont été coupés une deuxième et même une troisième fois pour y récolter les tiges laissées lors de la première coupe (Burgess et Methven 1977). L'élimination des arbres matures et semenciers sur de grandes superficies a favorisé le remplacement de plusieurs forêts de pin blanc par des forêts mélangées de conifères de fin de succession et de feuillus tolérants (Quenneville and Thériault 1998). Cela a contribué à entraîner une diminution importante de l'abondance du pin blanc dans nos forêts actuelles par rapport aux forêts précoloniales (Watson 1923; Davis 1996; Pelletier 1998; Weyenberg et al. 2004).

La forte réduction des feux de forêt au cours des dernières décennies a grandement modifié les cycles de feux qui prévalaient autrefois dans les forêts de pin blanc (Baker 1994; McCullough et al. 1998; Carleton 2003; Backer et al. 2004). La réduction des feux a eu pour effet de permettre l'accroissement de l'abondance de certaines essences moins résistantes aux feux (Brown et al. 2004) comme le sapin baumier (*Abies balsamea* Linneaus) (Methven et Murray 1977;

Pelletier 1998). Sous les pins blancs matures, la régénération naturelle de ce dernier est négativement affectée et les gaules sont très rares en absence de perturbation (Watson 1923; Burgess et Methven 1977; Ziegler 1995; Carleton et al. 1996; Quenneville et Thériault 1998; Abrams 2001; Dovčiak et al. 2001; Weyenberg et al. 2004).

Avant la création du Parc National du Canada de la Mauricie (PNCLM), les coupes forestières ont été importantes sur ce territoire. Depuis la création du PNCLM en 1970, le pin blanc est présent en faible proportion dans quelques secteurs du parc. La présence de plusieurs souches de pin blanc sans tiges au sol sur le territoire du PNCLM confirme l'intense activité forestière du passé. De plus depuis le début de la colonisation, il a été estimé que l'abondance du pin blanc serait passée de 5-12% à 0.5% du volume forestier du parc tandis que celle du sapin baumier serait passée de 13.1% à 31.8% (Richard 1975; Pelletier 1998; Barrette 2004). L'augmentation du sapin baumier dans la mosaïque forestière nuit grandement à la régénération du pin blanc car il capte la majorité de la lumière nécessaire aux semis de pins (Quenneville et Thériault 1998). La suppression des incendies forestiers a aussi grandement contribué à l'augmentation du sapin baumier. Au PNCLM, le groupe Dryade (1986) a évalué que depuis la création du parc, le cycle de feu moyen des territoires forestiers appartenant au PNCLM s'est allongé drastiquement. Cet allongement marqué a eu plusieurs effets sur les peuplements de pin blanc dont l'écologie est souvent rattachée aux incendies forestiers (Baker 1992; Abrams 2001).

Les insectes et les incendies forestiers

Les espèces vivantes des forêts de pin blanc de l'est de l'Amérique du Nord étaient intimement liées aux processus naturels qui prévalaient dans ces habitats (Naylor 1994). De plus le feu, qui affecte l'hétérogénéité des peuplements (Methven et Murray 1974; Granström 2001; Weyenberg et al. 2004), représente un facteur important dans le maintien de la diversité des espèces animales au niveau du paysage forestier (Louck 1970; Attiwill 1994). Conséquemment, la réduction des incendies forestiers a eu des effets sur certains groupes, plus particulièrement sur les coléoptères forestiers (Baker 1992; Wikars 1997; Wikars 2002; Backer et al. 2004; Brown et al. 2004; Varner III et al. 2005). Il s'agit d'un ordre d'insecte très diversifié et reconnu pour réagir aux différentes perturbations. Ces derniers jouent différents rôles trophiques faisant d'eux un excellent groupe taxonomique pour évaluer l'impact des feux de forêts et la suppression des incendies forestiers sur la diversité des communautés animales (Niemelä et al. 1993; Buddle et al. 2006; Toivannen et Kotiaho 2007).

En Scandinavie, l'altération de certains processus naturels comme les incendies forestiers a eu pour effet de modifier les communautés d'insectes rattachées à ces perturbations (Wikars 1997; McCullough et al. 1998; Martikainen et al. 2000). La suppression des incendies forestiers dans les forêts actuelles étant très efficace, plusieurs attributs et composantes des peuplements se sont modifiés (McCullough et al. 1998). En Scandinavie par exemple, le volume de bois mort brûlé a été réduit à une petite fraction de ce qu'il était autrefois (Siitonen 2001; Toivannen et Kotiaho 2007). Plusieurs coléoptères profitent des habitats forestiers brûlés où le bois mort et moribond est disponible en grande quantité (Wikars 1997). C'est le cas des espèces saproxyliques, qui dépendent de ce type de bois durant une partie de leur vie, des champignons qui s'y développent ou de la présence d'une ou plusieurs autres espèces saproxyliques (Speight 1989). En Scandinavie, l'aménagement intensif des forêts a réduit considérablement le volume de bois mort ou moribond en forêt et, par conséquent, plusieurs espèces saproxyliques sont en déclin et se retrouvent sur les listes rouges d'espèces en danger (Similä et al. 2002; Väisänen et al. 1993). Ces espèces sont souvent associées à certaines parties très précises ou stades de décomposition du bois mort. Les attributs importants du bois mort sont l'essence, la position (couché ou debout), l'exposition au soleil et le stade de décomposition (Økland et al. 1996; Jonsell et al. 1998; Jonsell et al. 1999; Siitonen 2001; Simila et al. 2002 ; Harmond et al. 2004 ; Jonsell et al. 2004). Plusieurs espèces saproxyliques et de milieux ouverts associées à ces perturbations; certaines d'entre elles peuvent même détecter les signaux émis par le feu et les habitats brûlés (Evans 1966; Muona et Rutanen

1994; Wikars 1997; McCullough et al. 1998). En Europe, le feu via la création de grande quantités de bois mort est donc un facteur important dans le maintien de certaines espèces saproxyliques (Wikars 1997), dont certaines sont des espèces rares et menacées (Simila et al. 2002; Hyvärinen et al. 2005), et pour le maintien de la richesse spécifique rattachée à ces peuplements (Muona et Rutanen 1994; Wikars 1997; Hyvärinen et al. 2005). En Europe, la réduction des incendies forestiers et l'aménagement intensif des forêts a mené plusieurs espèces saproxyliques et de milieux ouverts au bord de l'extinction (Wikars 1997; Siitonen 2001; Simila et al. 2002; Hyvärinen 2005; Toivanen et Kotiaho 2007).

La gestion active à Parcs Canada: Les brûlages dirigés

La Loi sur les parcs nationaux du Canada exige le maintien ou le rétablissement de l'intégrité écologique des parcs à travers la protection des ressources naturelles et des processus écologiques. L'intégrité écologique est définie comme "un état jugé caractéristique de sa région naturelle et susceptible de durer, qui comprend les composantes abiotiques et la composition de même que l'abondance des espèces indigènes et des communautés biologiques, les rythmes de changement et les processus qui les soutiennent » (Département de Justice du Canada 2000). Parce que plusieurs parcs ont été créés dans des endroits précédemment perturbés par l'exploitation forestière (Bonnicksen et Stone 1985; White et Mladenoff 1994; Conseil canadien des parcs 2007), les gestionnaires de Parcs Canada ont souvent besoin de développer de nouvelles approches de gestion active afin de restaurer ces écosystèmes.

Alors que la politique du «laisser brûler» ne peut être mise œuvre dans un petit parc comme le PNCLM, la gestion active est nécessaire pour rétablir les conditions qui prévalaient dans les forêts de pin blanc du parc. Les gestionnaires de Parcs Canada ont choisi les brûlages dirigés afin d'émuler les effets des feux de surface de faible intensité qui sévissaient autrefois dans les forêts de pin blanc préindustrielles et précoloniales (Attiwill 1994; Haeussler et Kneeshaw 2003). Ce traitement émule les effets du feu de surface et diminue les conséquences de l'utilisation passée de nos forêts (Barden et Woods 1976; Linder et al. 1998; Kouki et al. 2001; Uotila et al. 2002; Hyvärinen et al. 2005; Partel et al. 2005). En Europe, ce traitement a déjà été utilisé comme méthode de restauration dans le but d'augmenter les volumes de bois mort disponibles dans les parcs et réserves (Juninnen et al. 2008).

Depuis 1991 au PNCLM, 10 peuplements à dominance de pin blanc ont été traité avec la technique du brûlage dirigé. L'objectif à court terme de ce traitement était de générer des conditions écologiques qui permettraient d'accroître la densité des semis de pin blanc à plus de 1000/ha et de diminuer la compétition faite par le sapin. A moyen et long terme, les objectifs sont d'augmenter la densité des gaules jusqu'à 100/ha dans le but d'accroître éventuellement la couverture de pin blanc à 3-4% du territoire forestier du parc (Quenneville et Thériault 1998).

Objectifs et hypothèse

La régénération naturelle du pin blanc ainsi que les effets du brûlage dirigé sur la régénération de cette essence ont été étudiées à l'intérieur de 16 sites d'étude. Pour le premier volet du projet, les objectifs étaient 1) de documenter la situation de la régénération du pin blanc dans les forêts du PNCLM et 2) de déterminer si le brûlage dirigé réduisait la compétition faite par le sapin et favorisait la régénération du pin blanc. Nous avançons les hypothèses que le feu réduira la compétition faite par le sapin baumier et que la régénération en pin blanc sera significativement plus abondante que dans les forêts non-brûlées.

Dans le but de connaître les effets du brûlage dirigé sur les communautés animales, les assemblages de coléoptères ont été étudiés `l'intérieur de 15 sites. Pour les familles de coléoptères abondantes, ainsi que les espèces saproxyliques et non-saproxyliques, nous avions pour objectifs de caractériser la richesse spécifique, l'abondance et la rareté dans les forêts brûlées et non-brûlées. Nous avons émis l'hypothèse 1) que la richesse spécifique des coléoptères sera plus élevée dans les sites traités, 2) que les communautés de coléoptères des forêts brûlés seraient différentes et distinctes de celles des forêts non-brûlées, particulièrement pour les espèces saproxyliques, et 3) que les assemblages d'espèces saproxyliques sont associées au bois mort récent généré par les brûlages dirigés. Nous avons aussi mesuré l'effet du temps depuis le brûlage dirigé sur les assemblages d'espèces capturés en comparant les données des forêts brulées entre 1995 et 2005. Bien que certaines études aient laissé entendre que des avantages pour la régénération du pin blanc pouvait être attendus en utilisant les brûlages dirigés, il existe peu de dispositifs qui ont permis d'étudier les effets de ces derniers sur la végétation et les communautés animales (Simberloff 2001; Niwa et Peck 2002). Le programme de restauration du pin blanc au PNCLM représente donc une occasion unique d'évaluer les impacts du brûlage dirigé.

Effects of prescribed burning used to restore Eastern white pine in forests of La Mauricie National Park of Canada

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Résumé

Les écosystèmes de pin blanc du parc national du Canada de la Mauricie (PNCLM) ont été altérés par les coupes forestières depuis 1850 et la suppression des incendies forestiers plus récemment. En raison de ces altérations, la trajectoire écologique des écosystèmes de pin blanc a été modifiée et ils ne sont plus en mesure de se perpétuer naturellement, la majorité des sites n'ayant aucun individu au stade de gaule. Ainsi, dans ces écosystèmes, les gaules de pin blanc sont presque absentes et les gaules de sapin baumier compétitionnent fortement les semis de pin blanc pour l'espace et la lumière. Depuis 1991, Parcs Canada utilise le brûlage dirigé pour restaurer les écosystèmes de pin blanc. Sept sites brûlés entre 1995 et 2005 et neuf sites non-brûlés ont été étudiés afin d'évaluer l'effet des brûlages dirigés sur différentes composantes biotiques du milieu, notamment la densité des gaules de sapin baumier et des semis de pin blanc. Les brûlages dirigés ont tué plus de 63% des gaules de sapin baumier, éliminant ainsi une partie significative de la compétition faite aux semis de pin blanc. Ces derniers sont quatre fois plus abondants dans les sites brûlés que dans les sites non-brûlés (moyenne de 21333 vs 5178 semis/ha). Le sapin n'a pas réoccupé les sites brûlés tandis que la banque de semis de pin blanc est abondante et stable, les plus grands spécimens pouvant atteindre 50 cm de hauteur après 11 ans. À court terme, les objectifs de régénération du pin blanc fixés par Parcs Canada ont donc été atteints. La croissance des semis maintenant établis devra faire l'objet de suivis périodiques afin d'assurer le succès à moyen et long terme de ce programme de restauration des écosystèmes à pins blancs.

Abstract

Eastern white pine forests of La Mauricie National Park of Canada (LMNPC) have been affected by logging since the 1850s and, more recently, by forest fire suppression. Because of these alterations, the ecological trajectory of Eastern white pine ecosystems has been changed and they now appear hardly sustainable. In these ecosystems, Eastern white pine saplings are nearly absent and balsam fir saplings are strong competitors of Eastern white pine seedlings for space and light. Since 1991, Parks Canada has been using prescribed burning as a means of restoring Eastern white pine ecosystems. Seven sites burned between 1995 and 2005 and nine non-burned sites were studied in order to evaluate the effects of prescribed burnings on different biotic components of the environment, particularly the density of balsam fir saplings and Eastern white pine seedlings. Prescribed burnings killed more than 63% of balsam fir saplings, thus eliminating a significant part of the competition to Eastern white pine seedlings. These were four times more abundant in burned than in unburned sites (21 333 vs. 5 178 seedlings/ha). Balsam fir has not re-established itself in the burned sites while the Eastern white pine seedlings bank is abundant and stable, the largest individuals reaching 50 cm in height after 11 years. In the short term, the Eastern white pine regeneration objectives established by Parks Canada have been achieved. The growth of seedlings that are now well established will need to be monitored periodically to ensure the mid- and long-term success of this restoration program of Eastern white pine ecosystems.

Introduction

Over the last decades, changes in the forest composition from primeval stages and the reduction in the abundance of noble tree species have become critical issues for biodiversity (Bergeron et al. 2001; Reich et al. 2001). In the pre-settlement forests of North America, Eastern white pine (*Pinus strobus* L.) was more prevalent than it is today (Sargent 1947; Peattie 1966; McRae and al. 1994; Carleton and al. 1996). Selective logging of mature Eastern white pines during the 18th and 19th centuries has reduced the density of seed trees and made regeneration much more difficult to establish (Ahlgren 1976; Mirov and Hasbrouck 1976; Palik and Pregitzer 1994). Thus, the majority of these harvested stands have been converted into stands where Eastern white pine abundance has decreased progressively (Smidt and Puettmann 1998; Burgess et al. 2005). Moreover, fire suppression policies have also altered the natural dynamics of Eastern white pine stands by allowing shade-tolerant species to outcompete pine seedlings (Watson 1923; Burgess and Methven 1977; Ziegler 1995; Carleton et al. 1996; Quenneville and Thériault 1998; Abrams 2001; Dovčiak et al. 2001; Weyenberg et al. 2004).

Eastern white pine is native to North America and distributed from the Atlantic coast in the east to Manitoba, Canada, in the west; it reaches Newfoundland, Canada, in the north and Georgia, USA, in the south (Horton and Brown 1960; Farrar 1995; Abrams 2001; Vlasiu et al. 2001; Lorimer 2008). Eastern white pine is the tallest tree in eastern North America; it can grow up to 30-50 m and reach a diameter at breast height larger than 100 cm (Farrar 1995). It grows on a wide variety of soils but is more often found on dry and acid soils where competing species do not perform as well (Wendel and Smith 1990; Abrams 2001). It is a valuable timber resource and an important component of the present and past economy. Furthermore, it has been recognized as an important part of the culture, medicine and history of Native peoples and early settlers (Day 1953). This conifer species is also used as food and shelter by several wildlife species (Naylor 1994).

The historical role of fire in maintaining Eastern white pine stands in North America has often been reported (Maissurow 1935; Mayall 1941; Heinselman 1981). In these stands, surface fires are known to improve seedbed quality, increase light availability and reduce competition from saplings of other tree species (Methven and Murray 1974; Van Lear and Waldrop 1991; Clinton et al. 1993; McRae et al. 1994). Mature trees of Eastern white pine survive most surface fires due to their thick bark (Hengst et al. 1994), branch-free lower trunks, and a moderately deep rooting habit (Beverly and Martell 2003). Their needles have a low content of resin and thus are not highly flammable (Landers 1991). Prescribed burning provides excellent seedbeds for Eastern white pine because it burns the upper organic layer of the soil, making it more suitable to Eastern white pine seed germination (McRae et al. 1994). Fire suppression policies have favoured non fire-resistant species (Brown et al. 2004) such as balsam fir (*Abies balsamea* L.), which grows better than Eastern white pine under shady conditions (Horton and Bedell 1960; Methven and Murray 1974; Wendel and Smith 1990; Krueger and Puettmann 2004).

The *Canada National Parks Act* requires maintaining or restoring the ecological integrity of the parks through the protection of natural resources and ecological processes. Ecological integrity is defined as "a condition that is determined to be characteristic of its natural region and likely to persist, including abiotic components and the composition and abundance of native species and biological communities, rates of change and supporting processes" (Department of justice Canada 2000). Because several parks have been established in areas previously disturbed by logging, Parks Canada often needs to develop active management approaches to restore these ecosystems. For example, in La Mauricie National Park of Canada (hereafter LMNPC), Eastern white pine proportion in pre-settlement forests has been estimated at 5-12% but it now represents only 0.5% of the current forest composition (Richard 1975; Pelletier 1998; Barrette 2004). During the same period, balsam fir abundance has been estimated to shift from 13.1% to 31.8% in LMNPC (Richard 1975; Pelletier 1998). These changes are due to past logging and current fire management policies (Quenneville and Thériault 1998). LMNPC is a small park (536 km^2) where all ignitions are suppressed for safety reasons. Thus, the objective of restoring the ecological integrity of Eastern white pine ecosystems to pre-settlement conditions, or at least within their historic range of variability (Brown et al. 2004), can be achieved by using prescribed burning as a management approach (Barden and Woods 1976). Since 1991, a total of 10 Eastern white pine stands have been treated with prescribed burning at LMNPC. The objectives of this treatment are to generate ecological conditions that increase Eastern white pine seedlings density (short-term objective) to bring saplings density up to 100/ha (mid-term objective) in order to increase the cover of Eastern white pine dominated stands to 3-4% (long-term objective) in the future forested area of the park (Quenneville and Thériault, 1998). As the number of published studies addressing the ecological effectiveness of management practices in protected areas is limited (Gaston et al., 2006), this restoration program represents a unique opportunity to evaluate the effects of prescribed burning, as a management practice in a national park. We hypothesized that prescribed burning would kill the vast majority of balsam fir saplings, thus reducing competition for light and promoting Eastern white pine regeneration. In LMNPC, balsam fir is the most important competitor of Eastern white pine seedlings (Quenneville and Thériault 1998) and by far the most abundant sapling species in this study, so we will pay special attention to it throughout the paper. The objectives of this study were 1) to provide an appraisal of the issue of Eastern white pine regeneration in LMNPC forests, and 2) to determine if prescribed burning reduces competition and favours Eastern white pine regeneration.

Materials and methods

Study area and stand selection

Study sites were located in LMNPC, Quebec, Canada (Figure 1-1). The park is a 536 km^2 plateau located north of the St.Lawrence River, just beside one of its most important affluent, the St.Maurice River. It belongs to the Sugar Maple – Yellow Birch bioclimatic domain (Ministère des ressources naturelles du Québec 2003) and is a typical Laurentian Mountains landscape moulded with hills and lakes. Annual precipitations vary between 900 and 1400 mm and annual mean temperatures vary between 2.5 and 5.0 °C (Gosselin 2001). For our study, seven sites treated with prescribed burning between 1995 and 2005, and nine unburned sites, were selected over an area of 40 km^2 (Figure 1-1). The 16 selected sites had an altitude ranging from 217 to 341 m and slope varying between 1% and 47% (Table 1-1). Balsam fir was the most abundant understory species while Eastern white pine and spruces dominated the overstory (Table 1-2).

Prescribed burning was used in forest stands where Eastern white pine density was >15 trees/ha, the slope was <50% and balsam fir saplings dominated the understory. In these sites, Eastern white pine seedling and sapling densities were considered to be too low to ensure Eastern white pine renewal and thus to preclude the park from reaching its objective of maintaining ecological integrity (Quenneville and Thériault 2002). Burning prescriptions were elaborated using the Canadian Forest Fire Danger Rating System (Forestry Canada Fire Danger Group 1992) and the software FBP97 for forecasting fire behaviour (Remsoft Inc. 1997). Prescribed burnings were done in spring because conditions are better before budflushing of broadleaved trees and shrubs (Vlasiu et al. 2001). When these conditions were met, fire was ignited using burners (driptorch) or a helicopter equipped with a Premo MK3 aerial ignition device. Low-intensity surface fires were isolated and controlled with natural and artificial firebreaks.

Forest inventory

Three 400 m^2 circular plots located 50 m apart along a transect and at a minimum distance of 50 m from the edges of the stand or treatment were set up in each site to survey and describe the forest environment. In each plot, the slope (%), altitude (m), surface deposit, drainage and soil organic layer (litter and humus) thickness were recorded (Table 1-1). Flame height and length were recorded during each prescribed burning event by LMNPC's staff and were used to estimate fire intensity based on the Canadian forest fire behaviour prediction system (Forestry Canada Fire Danger Group 1992) (Table 1-1). For low intensity surface fires, these classes usually range from 1 (frontal fire intensity <10 kw/m; flame length <0.2 m; flame height <0.1 m) to 5 (frontal fire intensity >4000 kw/m; flame length >3.5 m; flame height >2.5 m). Fire intensity in burned sites was mostly of class 3 (frontal fire intensity 500-2000 kw/m; flame length 1.4-2.6 m; flame height 1.0-1.9 m), the only exception being for a site burned in 1999 where fire intensity reached the class 4 (frontal fire intensity 2000-4000 kw/m; flame length 2.6-3.5 m; flame height 1.9-2.5 m) and killed many mature trees including some Eastern white pines.

Species, diameter at breast height (hereafter DBH) and decay class of each standing tree ≥9.1 cm at DBH were recorded. Decay classes were determined according to Hunter's (1990) classification, which recognizes nine classes for trees (1: alive and 2: declining) and snags (3: dead tree with bark intact up to 9: stump). Because most of red and Eastern white pine trees are large and tall, their density was rather low and, to get more accurate estimates of their basal area, we enlarged the sampled plots up to 1200 m^2 (radius = 19.55 m). In each 400 m^2 plot, four smaller plots of 25 m^2 (radius = 2.82 m) and four micro plots of 4 m^2 (radius = 1.13 m) were established at 8.46 m from the plot centre, in each cardinal direction (Figure 1-2). Saplings and seedlings were recorded in the 25 m^2 and 4 m^2 plots respectively. Saplings were young trees in which DBH ranged between 1 and 9 cm, whereas DBH of seedlings was smaller than 1 cm (Canada 1992). Sapling DBH was measured and seedling height was recorded into 5 cm classes. Eastern white pine relative dominance was estimated on the basis of its relative basal area (hereafter BA, in m^2/ha) in 1200 m^2 plots, in relation to BA of other tree species estimated in 400 m^2 plots. The area covered (1-5%, 6-10% and then by 10% classes) by non-commercial tree, shrub, herbaceous, fern and moss species was also estimated in the 25 m^2 plots. The most abundant non-commercial trees or shrubs encountered were blueberry (*Vaccinium sp.*), mountain maple (*Acer spicatum* Lamarck) and beaked hazel (*Corylus cornuta* Marshall), while bush honeysuckle (*Diervilla lonicera* Mill.), wild sarsaparilla (*Aralia nudicaulis* L.) and Canadian mayflower (*Maianthemum canadense* Desf.) were the most prevalent herbaceous plants. The only dominant fern species was bracken fern (*Pteridium aquilinum* (L.) Kuhn.). Bryophytes were not identified and simply recorded as mosses.

Statistical analysis

Because Eastern white pine seedling establishment probably involves interactions with many variables, a multiple linear stepwise regression was used to identify variables that significantly influence natural Eastern white pine seedling density in unburned plots. This procedure tests variables one by one and these were retained when $\alpha \leq 0.10$. Variables known to influence Eastern white pine regeneration are mainly related to local site conditions, forest openings and competition for light (Wilkins and Kiceluk 1994; Carleton et al. 1996; Quenneville et al. 1998; Dovčiak et al. 2001; Elliott et al. 2002). Thus, the variables tested in the model were slope, thickness of the organic soil layer, live sapling density, live tree BA, live Eastern white pine BA, and % cover by shrub, fern and herbaceous species (see Table 1-1). Analyses were made at the plot level because Eastern white pine regeneration was considered to be a highly localized process. Multi-colinearity among environmental variables was assessed using variance inflation factors (VIF), but none was removed from the analysis as VIF ranged from 1.32 to 2.57 for all variables; VIF >10 indicate multi-colinearity (Graham 2003). Linear and quadratic regressions were tested to relate variables that were significant in the multiple regression model predicting Eastern white pine seedling density. The technique described by McDonald (2008) was used to determine if linear and quadratic curves were significantly different. Regressions showing the highest R-square values were retained.

We also tested the short-term effects of prescribed burning on various components of the forest environment to assess how the treatment generates favourable conditions for the establishment of Eastern white pine seedlings. Considering that stands had not been sampled before treatment, the short-term effects of prescribed burning were assessed using the percentage of recent tree or sapling mortality. Tree BA and sapling density (stems/ha) of each decay class were calculated for Eastern white pine, balsam fir, spruces and broadleaved species. Then, the percentages of recent mortality (Hunter classes 3 and 4) were calculated for both burned and unburned sites. Student's t-tests were used to compare recent mortality of trees and saplings in both stands types. Such analyses were also performed to compare the thickness of the soil organic layer and ground cover of shrub, herbaceous, fern and moss species between burned and unburned sites. For these variables, recovery after burning was assessed using simple linear regressions relating them with the time elapsed (years) since burning. Sites burned in 1995 and 1997 were excluded from further analyses because some of these variables had already returned to levels found in unburned forests and could not represent the short term effects of prescribed burning.

Finally, to determine if prescribed burning made it possible to achieve the short-term objective of increasing Eastern white pine seedling density, we used Student's t-tests to compare the density in burned and unburned sites. Sites burned in 2004 and 2005 were excluded from the seedling analysis because no seed crop has occurred since the treatment, thus precluding the establishment of regeneration in these sites. Logarithmic transformations (log x+1) were used to normalize the distribution and stabilize variances when necessary. When transformations did not achieve equality of variances, we used results obtained with Satterthwaite's approximate t-test, a method that belongs to the Behrens-Welch family (Armitage et al. 2001). All t-tests and regressions were performed using SAS software v. 9.1. (SAS Institute 2000).

Results

Current status of Eastern white pine in LMNPC forests

Forest composition of unburned sites was dominated by conifers, with slightly more than 75% of the tree basal area belonging to Eastern white pine and other conifers, mostly spruces and red pine (Table 1-2). Balsam fir represented less than 10% of tree basal area, and broadleaved trees slightly more than 15%. Eastern white pines represented more than a quarter of the total BA and were well distributed among DBH classes, reaching maximum densities between 20 and 60 cm of DBH (Figure 1-3; bottom right). However, small balsam fir trees ($\leq$20 cm) as well as saplings outnumbered Eastern white pine (Figure 1-3; bottom right and middle). Balsam fir saplings represented 80.1% of total sapling density while

Eastern white pine represented only 0.9% (Table 1-5). Eastern white pine seedling density was lower than that of balsam fir in each height class observed (Figure 1-3) and they represented only 26.7% of all seedlings in unburned sites (Table 1-5). Moreover, they never reached more than 75 cm in height (Figure 1-3; top right).

The multiple regression model, aimed to predict Eastern white pine seedling density in unburned plots, was significant ($p = 0.0003$), and two of the eight variables tested were retained ($\alpha \leq 0.10$). The slope showed a highly significant and positive relationship while the density of live saplings had a slightly negative relationship with Eastern white pine seedlings density (Table 1-3). These relationships were confirmed by quadratic regressions, the strongest relation arising from plot slope ($R^2 = 0.6673$; $p < 0.0001$) (Figure 1-4 a, b).

Prescribed burning impact on the forest environment

Prescribed burnings significantly increased the mortality of balsam fir and broadleaved trees, with 38.2% and 39.0% of mortality in burned sites compared with 3.7% and 14.3% in unburned sites (Table 1-2). Mature Eastern white pine trees and other conifers were not significantly affected by the burning treatment. Saplings of balsam fir and broadleaved species were significantly affected by the burning treatment (Table 1-2). Mortality averages of 67.4% and 37.0% were measured respectively for balsam fir and broadleaves saplings in burned sites compared with 9.2% and 6.1% in unburned sites (Table 1-2). The most severely burned site (1999) had a percentage of recent mortality of 93% for balsam fir, which was 25% higher than in any other burned sites. Overall, mortality of saplings was significantly higher in burned sites (63.6%) than in unburned ones (9.2%) (Table 1-2). However, after burning, the density of balsam fir saplings was still high, mostly because some patches of the forest remained unburned in some sites (Fig. 1-1; left middle).

Shrub and fern covers were similar in both burned and unburned sites, but herbaceous plant cover increased significantly in burned sites while mosses and organic layer thickness decreased significantly (Table 1-4). Simple linear regressions showed that two variables (herbaceous cover and organic layer thickness) were significantly related to the number of years after burning (Figure 1-5). Shrubs, ferns and mosses were not significantly related to the number of years after burning (Figure 1-5).

Prescribed burning effect on Eastern white pine

Prescribed burnings increased significantly the density of Eastern white pine seedlings when compared with unburned sites (Table 1-5), their proportion increasing from 26.7% to 83.7% of all seedlings in burned sites. By contrast, the proportion of balsam fir seedlings decreased from 39.6% in unburned sites to 20.6% in burned ones (Table 1-5). However, Eastern white pine seedlings were largely dominant in the first five height classes (1-25 cm) and they rarely exceeded 50 cm. Balsam fir seedlings were more evenly distributed up to 130 cm and dominated Eastern white pine seedlings in all height classes higher than 25 cm (Figure 1-3; top left).

No distinctive pattern in Eastern white pine seedling growth was observable along the burning chronosequence. Sites burned in 2004 and 2005 only harboured 417 seedlings of Eastern white pine per hectare because these sites (1-2 years after burning) have not yet benefited from a good seed year (Frelich 1992; Nolet et al. 1999). The stand burned in 2003 (3 years) was exposed to a good seed crop the summer after the treatment and regeneration was the most plentiful in the 5-10 cm height class. The site burned in 2001 (5 years) was exposed to a good seed crop two years after the treatment and seedlings were a slightly more abundant than in the stand burned in 2003, with almost all seedlings being found in the 5-10 cm height class (Figure 1-6). In the site burned in 1999 (7 years), Eastern white pine seedlings were asymmetrically distributed to the right of the 5-10 cm height class, with seedlings reaching 25-30 cm (Figure 1-6). However, the site burned in 1997 (9 years), which benefited from two good seed crops (1998, 2003), did not harbour more Eastern white pine seedlings than the other sites, with its seedlings being mainly found in the first two height classes (1-5 cm and 5-10 cm) (Figure 1-6). In the oldest burned stand (1995; 11 years), which benefited from three good seed crops, seedlings were mainly found in the first two height classes. However, Eastern white pine seedlings reached their maximum height (40-45 cm) in this stand. Balsam fir seedlings <50 cm high were not abundant in any of these five burned sites compared with Eastern white pine seedlings, the only one showing more than 10 000 balsam fir seedlings/ha being the one that burned in 1997 (Figure 1-6).

Discussion

As elsewhere in North America, Eastern white pine suffers from shade tolerant tree competition at LMNPC. Almost no saplings of Eastern white pine were observed in the forest stands studied. At LMNPC, fire suppression has remained active since the 1930s, and no large fire has been recorded over the last 80 years. This means that competing species of Eastern white pine regeneration, such as balsam fir, have been growing in the absence of fire for at least the last 80 years (Richard 1975; Pelletier 1998). Many studies have reported the same pattern of occupation by balsam fir in Eastern white pine forests over the last decades (Alhgren 1976; Heinselman 1981; Wendel and Smith 1990; Carleton et al. 1996; Abrams 2001; Burgess et al. 2005; Ontario Ministry of Natural Resources 2009). According to McRae et al. (1994), survival of the remaining Eastern white pine stands in Canada may need the reintroduction of fire into these forests. Logging has also probably affected Eastern white pine abundance and stand dynamics by removing most of the mature seed-bearing trees. In the Mauricie region, massive exploitation of Eastern white pine started around 1850 (Boucher 1952). It has been recognized that more than 90% of Eastern white pine trees were harvested before the park's creation (Boucher 1952; Quenneville and Thériault 1998). Our observation of several Eastern white pine stumps larger than 75 cm of diameter in each study site are in agreement with this statement. In LMNPC, Eastern white pine volume went down from 12% (pre-settlement level) to 0.5% (now) (Richard 1975; Pelletier 1998). However, it could be very appropriate to conduct scientific projects to confirm the abundance of white pine in the preindustrial and precolonial forests of LMNPC. Some authors also pointed out declines in Eastern white pine abundance following logging across eastern Canada and United States.

For example, in northeastern Minnesota, Eastern white pine represented 20% of the basal area in pre-settlement forests and it now represents less than 2% (Frelich 1995; Davis 1996; Weyenberg et al. 2004).

Current status of Eastern white pine in LMNPC forests

An obvious problem with Eastern white pine seedling growth was observed in unburned stands at LMNPC. In these stands, even if mature Eastern white pines were present in relatively high densities (mean of 84/ha) and bank seedlings averaged 5135/ha, it seems that some suppression occurred because seedlings were restricted to the lower height classes and Eastern white pine saplings were absent from almost all unburned sites. Other authors also described this growth problem in Eastern white pine stands (Wendel and Smith 1990; McRae et al. 1994; Carleton et al. 1996). They found that fir and broadleaved species were exercising suppression on Eastern white pine seedlings by reducing light availability, thus limiting pine regeneration success. In our unburned sites, the density of Eastern white pine seedlings was negatively related to total sapling density. Several authors have concluded that balsam fir competition was the main factor explaining the failure of Eastern white pine regeneration and growth (Methven and Murray 1974; Burgess and Methven 1977; Smidt and Puettmann 1998; Abrams 2001; Dovčiak et al. 2001; Beverly and Martell 2003). In our unburned stands, balsam fir was also the main sapling species to compete with Eastern white pine seedlings for light. In these stands, only a few Eastern white pines reached the sapling stage, while the vast majority of seedlings remained suppressed.

Eastern white pine regeneration in unburned sites

A significant and positive relationship was found between the density of Eastern white pine seedlings and the slope in unburned sites. Eastern white pine seedling density was particularly high when the slope was >25% while saplings (mainly balsam fir) were less abundant. It has been demonstrated that competition to

Eastern white pine seedlings by other species is less important in low-productive sites located on rocky slopes (McRae et al. 1993; Carleton et al. 1996). Balsam fir is known to perform better in soils with high humidity levels (Ritchie 1959; Farrar 1995). Steep slopes of white pine stands are expected to have thinner soils and a better drainage that may poorly retain water, thus providing conditions that may limit balsam fir establishment in these sites. When appropriate soil conditions are not met, balsam fir and broadleaved species cannot grow optimally, thus favouring Eastern white pine regeneration (McRae et al. 1993; Carleton et al. 1996).

The few Eastern white pine saplings found in unburned sites were all located in forest gaps where light availability is higher, which favours growth. Local disturbances caused by windthrows (Quinby 1991; Carleton et al. 1996; Powers et al. 2008) can thus provide conditions favourable to Eastern white pine growth. One of our unburned sites (Control 6), which is located on an island, had a high density of Eastern white pine saplings (100/ha) even though its seedling density was rather low (625/ha). This site had been disturbed by a small wind storm due to its location on an island. Gaps created in the forest cover were large enough to favour the growth of Eastern white pine seedlings up to the sapling stage. This is important for Eastern white pine forest renewal as Stiell (1985) demonstrated that pine's ability to compete is greatly improved when the sapling stage is reached. Even if all the saplings surveyed in our unburned sites were to reach the canopy, their numbers would still be below the density objective of 100/ha (Quenneville and Thériault 1998).

Prescribed burning effect on the forest environment

Prescribed burnings were efficient in reducing sapling competition, balsam fir being the species most affected in our study. Balsam fir is not resistant to fire because of its thin bark and the high degree of inflammability of its needles (Ontario Parks 2008), so these high percentages of recent mortality are not surprising. However, some unburned patches still remained. Several factors may explain these green patches, including terrain heterogeneity and remaining snow patches in dense conifer stands at the time of the burn. Weather conditions may also constrain fire spread rate and fire sustainability. Unburned patches should be kept at a minimum because their presence facilitates balsam fir recolonization and subsequent dominance in the understory (Methven and Murray 1974). In their study, these authors showed that balsam fir reintroduced itself in the seedling community rapidly after prescribed burning and was still an important component of the understory. Its competition was weaker in burned sites than in unburned ones but still high enough in some cases to restrain pine growth. Furthermore, according to Heinselman (1981), balsam fir is efficient at reinvading burned sites from seeds blown in from islands of unburned neighbouring stands. Weyenberg et al. (2004) reported that fire was efficient at regenerating Eastern white pine if it inhibits competition for at least 10 years after the burn. In our study, post-treatment reoccupation by balsam fir seedlings does not appear to be of major concern. At each burned site, Eastern white pine seedlings were largely more abundant than balsam fir seedlings. This is important because reducing balsam fir competition was one of the objectives of the prescribed burning program. Mature Eastern white pines were not significantly affected by prescribed burnings so they remained abundant, which is important since these sites need substantial Eastern white pine seed supply to regenerate at high levels (Burgess et al. 2002; Weyenberg et al. 2004).

Prescribed burning effect on Eastern white pine regeneration

The prescribed burning treatment made it possible to increase Eastern white pine seedling density up to an average of 21133 seedlings/ha in burned sites, compared with 5135 seedlings/ha in unburned sites. Methven and Murray (1974) observed 12000 seedlings/ha 5 years after a prescribed burn in a Eastern white pine stand at the Petawawa forest research station located in Ontario. Lynham and Curran (2003) reported a high density of 45000 seedlings/ha 4 years after a natural surface fire in mixed stands of Eastern white pine across Ontario. Compared with these seedling densities, prescribed burnings at LMNPC seem to have been efficient at regenerating Eastern white pine in burned sites.

Sites burned in 2004 and 2005 had a very low density of Eastern white pine seedlings when compared with other burned sites. It is probable that this low-level regeneration results from the absence of a good seed crop in these sites since the treatment was applied. However, in these sites, the bracken fern species (*P. aquilinum*) was abundant with an average cover of 26%. This fern was highly competitive in recolonizing burned sites where it was present prior to treatment. It is a fire-adapted species that possesses deep fire-resistant rhizomes (Gleissman 1978). Bracken ferns are strong competitors for light and their presence is known to increase the level of competition for the establishment of Eastern white pine seedlings (Horton and Bedell 1960). In the future, after a first good seed year, it would be important to monitor and measure the regeneration of Eastern white pine and the effect of the abundance of this fern on the dynamics of this tree species. The sites burned (2001 and 2003), and exposed to a good seed crop in 2003 had a high number of seedlings, approximating 20000 seedlings/ha. Most pine seedlings were grouped in the 5-10 cm height class and showed a normal growth rate for Eastern white pine (Horton and Bedell 1960). The site burned in 1999 was submitted to the highest fire intensity and showed the highest recent mortality of trees, including some pines. It also had taller Eastern white pine seedlings than the site burned 2 years before. No competition reinvaded this site and the good seed crop of 2003 seems to have allowed the regeneration of Eastern white pine, even if it occurred four years after the treatment. Furthermore, the taller seedlings observed indicate better growth conditions in this site, probably linked with a higher penetration of light due to higher tree mortality. Finally, the tallest Eastern white pine seedlings were observed in the oldest burned site, but these only reached 50 cm of height, which shows a slow growth rate after 11 years (Horton and Bedell 1960).

Implications for management

Active management is an important approach for restoring the ecological integrity of ecosystems in Canadian national parks. The current policy states that when park ecosystems have been seriously altered by human activities and natural processes alone cannot achieve restoration objectives, intervention may be prescribed. In LMNPC, the ecological integrity of Eastern white pine ecosystems has been altered by logging and fire suppression. On a short-time scale (10-15 years), the prescribed burning program implemented in LMNPC has been successful in increasing significantly Eastern white pine seedling density. However, in the near future, it would be important to continue monitoring each burned site to determine Eastern white pine seedling growth rates under different local environmental conditions. Initial growth of Eastern white pine usually averages 10-15 cm after 5 years (Horton and Bedell 1960), which is slow compared with faster growing competitors such as firs and hardwoods (Wendell and Smith 1990). It would also be important to survey balsam fir in burned sites to make sure that it will not compete against Eastern white pine seedlings and preclude them from reaching the sapling stage. In order to evaluate the ecological integrity of a national park, Timko and Innes (2009) recently recommended such monitoring for assisting managers in evaluating the effectiveness of their management actions.

According to Ontario Ministry of Natural Resources (2009), Eastern white pine seedlings that receive more than 45% of full light have a higher probability of reaching the sapling stage. Otherwise, these seedlings will probably survive but might not be able to grow rapidly enough to compete with fir and broadleaved species. In such cases, it might be necessary to use further treatment to reach the objective of restoring Eastern white pine forest ecosystems. It might be the case in burned sites of LMNPC as the densities of Eastern white pine seedlings are high, but their growth remains clearly slow. It might be necessary to open the canopy by different methods to allow better penetration of light. This objective could be achieved by girdling mature trees (mostly spruces) or by increasing fire intensity in future prescribed burnings. Continuous monitoring of seedling growth in burned sites would help managers to determine if such actions could be useful in helping LMNPC to restore Eastern white pine ecosystems. These evaluations would also promote adaptive management and ensure that decision-making is based on sound science (Pullin et al., 2004).

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References

Abrams, M.D. 2001. Eastern white pine versatility in the pre-settlement forest. BioScience 51: 967-979.

Ahlgren, C.E. 1976. Regeneration of red pine and white pine following wildfire and logging in norteastern Minnesota. Journal of Forestry 74: 135-140.

Armitage, P., G. Berry and J.N.S. Matthews. 2001. Statistical methods in medical research, 4th Edition. Blackwell Science Ltd, oxford, U.K., 832 p.

Barden, L.S. and F.W. Woods. 1976. Effects of fire on pine and pine-hardwood forests in the southern Appalachians. Forest Sciences 22: 399-403.

Barrette, M. 2004. Caractérisation du paysage primitive de la region écologique ds hautes collines du Bas-Saint-Maurice pour une gestion des écosystèmes du parc national du Canada de la Mauricie. Thèse de doctorat. Université Laval, Québec. 129 p.

Bergeron, Y., S. Gauthier, V. Kafka, P. Lefort and D. Lesieur. 2001. Natural fire frequency for the eastern Canadian boreal forest: consequences for sustainable forestry. Canadian Journal of Forest Research 31: 384-391.

Beverly, J.L. and D.L. Martell. 2003. Modeling *Pinus strobus* mortality following prescribed fire in Quetico Provincial Park, northwestern Ontario. Canadian Journal of Forest Research 33: 740-751.

Boucher, T. 1952. Mauricie d'autrefois. Éditions du bien public, Trois-Rivières, Canada, Collection l'histoire régionale. No. 11.

Brown, R.T., J.K. Agee and J.F. Franklin. 2004. Forest restoration and fire: principles in the context of place. Conservation Biology 18: 903-912.

Burgess, D.M. and I.R. Methven. 1977. The historical interaction of fire, logging and pine: a case study at Chalk River, Ontario. Canadian Forest Service, Petawawa National Forest Research Institute, Information report PS-X-66.

Burgess D., F. Pinto and S. Wetzel. 2002. Some management implications from an eastern white pine regeneration experiment. Natural Resources Canada, Canadian Forest Service, Pacific Forestry Centre. Technology Transfert Note No. 28.

Burgess, D., C. Robinson and S. Wetzel. 2005. Eastern white pine response to release 30 years after partial harvesting in pine mixedwood forests. Forest Ecology and Management 209: 117-129.

Canada 1992. Silvicultural terms in Canada. Science and Sustainable Development Directorate, Forestry Canada. 63 p.

Carleton, T.J., P.F. Maycock, R. Arnup, and A.M. Gordon. 1996. *In Situ* regeneration of *Pinus strobus* and *P. resinosa* in the Great Lakes forest communities of Canada. Journal of Vegetation Science 7: 431-444.

Clinton, B.D., J.M. Vose and W.T. Swank 1993. Site preparation burning to improve southern Appalachian pine-hardwood stands: vegetation composition and diversity of 13-year-old stands. Canadian Journal of Forest Research 23: 2271-2277.

Davis, M.B. 1996. Eastern old-growth forests. Edited by Mary Byrd Davis. Foreword by John Davis. Island Press, Washington. 383 p.

Day, G.M. 1953. The Indian as an ecological factor in the northeastern forest. Ecology 34: 329-346.

Department of Justice Canada. 2000. Canada National Parks Act (2000, c. 32) Ottawa, Canada. Available online at: http://laws.justice.gc.ca/en/N-14.01/index.html.

Dovčiak, M., L.E. Frelich, and P.B. Reich. 2001. Discordance in spatial patterns of white pine (*Pinus strobus*) size-classes in a patchy near-boreal forest. Journal of Ecology 89: 280-291.

Elliott, K.J., J.M. Vose and B.D. Clinton. 2002. Growth of eastern white pine (*Pinus strobus* L.) related to forest floor consumption by prescribed fire in the southern Appalachians. Southern Journal of Applied Forestry 26: 18-25.

Farrar, J.L. 1995. Les Arbres du Canada. Service canadien des forêts, Ressources Naturelles Canada. Les éditions Fides. Saint-Laurent, Canada, 502 p.

Forestry Canada Fire Danger Group. 1992. Development and structure of the Canadian forest fire behaviour prediction system. Forestry Canada Information Report ST-X-3. 63p.

Frelich, L.E. 1992. The relationship of natural disturbances to white pine stand development, pp.27-37 In: Stine R.A. and M.J. Baughman (Eds.), Proceedings of white pine symposium: history, ecology, policy and management, University of Minnesota, St. Paul, USA, pp. 27-37.

Frelich, L.E. 1995. Old forest in the Lake States today and before European settlement, Natural Areas Journal 15: 157-167.

Gaston, K.J., Charman, K., Jackson, S.F., Armsworth, P.R., Bonn, A., et al., 2006. The ecological effectiveness of protected areas: the United Kingdom. Biological Conservation 132, 76-87.

Gleissman, S.R. 1978. The establishment of bracken following fire in tropical habitats. American Fern Journal 68: 41-44.

Gosselin, J. 2001. Guide de reconnaissance des types écologiques – Région écologique 3c - Hautes collines du Bas-Saint-Maurice. Ministère des ressources naturelles et de la faune du Québec, Québec, Canada, 121 p.

Graham, M.H. 2003. Confronting multicollinearity in ecological multiple regression. Ecology 84: 2809–2815.

Heinselman, M.L. 1981. Fire intensity and frequency as factors in the distribution and structure of northern ecosystems. In: Mooney H.A., Bonnicksen, T.M., Christensen, N.L., Lotan, J.E. and Reiner, W.A. (Eds.), Fire regimes and ecosystem properties, USDA Forest Service, General Technical Report WO-26.

Hengst, G.E. and J.O. Dawson. 1994. Bark properties and fire resistance of selected tree species from the central hardwood region of North America. Canadian Journal of Forest Research 24: 688–696.

Horton, K.W. and G.H.D. Bedell. 1960. White and red pine: ecology, silviculture and management. Canadian Department of Northern Affairs and Natural Resources, Forestry Branch, Ottawa, Canada, Bulletin 124, 185 p.

Horton, K.W. and W.G.E. Brown. 1960. Ecology of white and red pine in the Great Lakes-St. Lawrence Forest Region. Canadian Department of Northern Affairs and Natural Resources, Forestry Branch, Ottawa, Canada. Technical Note No. 88, 22 p.

Hunter, M.L. 1990. Wildlife, forests and forestry. Principles of managing forests for biological diversity. Prentice Hall Inc., Lebanon, USA. 345 p.

Krueger, J.A. and K.J. Puettmann. 2004. Growth and injury patterns of eastern white pine (*Pinus strobus* L.) seedlings as affected by hardwood overstory density and weeding treatments. Northern Journal of Applied Forestry 21: 61-68.

Landers, J.L. 1991. Disturbance influences on pine traits in the southeastern United States. In: Proceedings, 17th Tall Timbers fire ecology conference; 1989 May 18-21; Tallahassee, FL. Tallahassee, FL: Tall Timbers Research Station: 61-95.

Lorimer, C.G. 2008. Eastern white pine abundance in 19th century forests: A re-examination of evidence from land surveys and lumber statistics. Journal of Forestry 106: 253-260.

Lynham, T.J. and T.R. Curran. 2003. Vegetation recovery after wildfire in old-growth red and white pine. Natural Resources Canada, Frontline Express Bulletin No. 31.

Maissurow, D.K. 1935. Fire as a necessary factor in the perpetuation of white pine. Journal of Forestry 33: 373-378.

Mayall, K. M. 1941. White pine succession as influenced by fire (interim report). National Research Council of Canada Publication No. 989.

McRae, D.J., T.J. Lynham and R.J. Frech. 1993. Implementing a successful understory red pine and white pine prescribed burn. Proceedings paper from the white pine/red pine workshop, Chalk River, Ontario. October 7-9, 1993. 11 p.

McRae, D.J., T. J. Lynham, and R. J. Frech. 1994. Understory prescribed burning in red pine and white pine. The Forestry Chronicle 70: 395-401.

Methven, I.R. and W.G. Murray. 1974. Using fire to eliminate understory balsam fir in pine management. The Forestry Chronicle 50: 77-79.

Ministère des ressources naturelles du Québec. 2003. *Vegetation zones and bioclimatic domains in Quebec*. Gouvernement du Québec, Available online at: http://www.mrnf.gouv.qc.ca/english/publications/forest/publications/zone-a.pdf.

Mirov, N.T. and J. Hasbrouck. 1976. The story of pines. Indiana University Press, Bloomington, USA. 148 p.

Naylor, B.J. 1994. Managing wildlife habitat in red pine and white pine forests of central Ontario. The Forestry Chronicle 70: 411-419.

Nolet, P., F. Doyon and P. D. Vlasiu. 1999. L'aménagement par coupe par trouées des strates de feuillus d'essences tolérantes avec pin blanc. Institut québécois d'aménagement de la forêt feuillue, Ripon, Canada. 33 p.

Ontario Ministry of Natural Resources. 2009. Ecology and management of eastern white pine in the Lake Abitibi (3E) and Lake Temagami (4E) ecoregions of Ontario. Ontario Ministry of Natural Resources. Sault Ste. Marie, Canada. 79 p.

Ontario Parks. 2008. Quetico: Statement of fire intent. Government of Ontario, Ontario Parks, Toronto, Canada. 40 p.

Palik, B.J. and K.S. Pregitzer. 1994. White pine seed-tree legacies in an aspen landscape: influences on post-disturbance white pine population structure. Forest Ecology and Management 67: 191-201.

Peattie, D. C. 1966. A natural history of trees of eastern and central North America. Houghton Mifflin Co., Boston, USA. 606 p.

Pelletier, H. 1998. Plan de conservation des écosystèmes terrestres. Parcs Canada, Parc National du Canada de la Mauricie, Service de la conservation des ressources naturelles, Shawinigan, Canada. 320 p.

Powers, M.D., K.S. Pregitzer and B.J. Palik. 2008. Physiological performance of three pine species provides evidence for gap partitioning. Forest Ecology and Management 256: 2127-2135.

Pullin, A.S., Knight, T.M., Stone, D.A., Charman, K., 2004. Do conservation managers use scientific evidence to support their decision-making? Biological Conservation 119, 245-252.

Quenneville, R. and M. Thériault. 1998. Cadre pour la restauration écologique du pin blanc au Parc National de la Mauricie. Parcs Canada, Service de la conservation des ressources naturelles, Shawinigan, Canada. 39 p.

Quenneville, R. and M. Thériault. 2002. Plan de gestion du feu: Parcs Canada, Parc National du Canada de la Mauricie. Service de la conservation et des écosystèmes, Shawinigan, Canada. 19 p.

Quinby, P.A. 1991. Self-replacement in old-growth white pine forests of Temagami, Ontario. Forest Ecology and Management 41: 95-109.

Reich, P.B., P. Bakken, D. Carlson, L.E. Frelich, S.K. Friedman and D.F. Grigal. 2001. Influence of logging, fire, and forest type on biodiversity and productivity in southern boreal forests. Ecology 82: 2731-2748.

Remsoft Inc.. 1997. Software FBP97. Remsoft, Fredericton, Canada.

Richard, P. 1975. La vulgarisation des travaux paléobiogéographiques effectués dans le parc national de la Mauricie (Rapport final). Service de la recherche en analyse pollinique, Université du Québec à Chicoutimi, Chicoutimi, Canada. 132 p.

Ritchie, G. A. 1959. Trees of knowledge: a handbook of maritime trees. Tay Tree & Land Services, Fredericton, Canada. Cat. No. Fo42-244/1996E

Sargent, C. S. 1947. The silva of North America: A description of the trees which grow naturally in North America exclusive of Mexico. Volume XI (Coniferae). Houghton Mifflin Co., Boston, USA. 163 p.

SAS Institute Inc. 2000. SAS for Windows: Version 9.1. SAS Institute Inc., Cary, USA.

Smidt, M.F. and K.J. Puettmann. 1998. Overstory and understory competition affect underplanted eastern white pine. Forest Ecology and Management 105: 137-150.

Stiell, W. M. 1985. Silviculture of eastern white pine. Proceedings of the Entomological Society of Ontario 116: 95-107.

Timko, J.A., Innes, J.L., 2009. Evaluating ecological integrity in national parks: case studies from Canada and South Africa. Biological Conservation 142, 676-688.

Van Lear, D.H. and T.A. Waldrop. 1991. Prescribed burning for regeneration. In: Duryea, M.L. and P.M. Dougherty. (Eds.). Forest regeneration manual. Kluwer Academic Publishers, Dordrecht, The Netherlands. Pp 235-250.

Vlasiu, P.D., P. Nolet and F. Doyon. 2001. Le pin blanc : Revue de littérature. Institut québécois d'aménagement de la forêt feuillue, Ripon, Canada. 91 p.

Watson, R. 1923. Forest devastation in Michigan. Journal of Forestry 21: 425-451.

Wendel, G.W. and H.C. Smith. 1990. *Pinus strobus* L., eastern white pine. In: Burns, R.M. and B.H. Honkala. (Eds.). Silvics of North America, Vol. 1, Conifers. USDA Forest Service, Agriculture Handbook 654, Washington, D.C. pp. 476-488.

Weyenberg, S.A., L.E. Frelich and P.B. Reich. 2004. Logging versus fire: How does disturbance type influence the abundance of *Pinus strobus* regeneration? Silva Fennica 38: 179-194.

Wilkins, C. and L. Kiceluk. 1994. The mythic white pine is in trouble. Canadian Geographic 114: 58-66.

Ziegler, S.S. 1995. Relict eastern white pine (*Pinus strobus* L.) stands in southwestern Wisconsin. American Midland Naturalist 133: 88-100.

Table 1-1: Description of the 16 study sites at LMNPC.

			Soil - Topography					Cover (%)				Trees (alive)		Saplings (alive)	
Site	Year of burning	Class of intensity	Depot	Drainage	Humus (cm.)	Alt. (m.)	Slope (%)	Moss	Herb	Shrub	Fern	Density (Stem/ha)	BA (m^2/ha)	Density (Stem/ha)	BA (m^2/ha)
Burn 2005	2005	3	Fluvio-glacial	Good	2.7	242	4	20.0	8.9	21.3	6.4	383	14,56	1766	1,77
Burn 2004	2004	3	Fluvio-glacial	Rapid	4.3	245	2	16.7	9.0	26.3	8.5	550	17.63	833	0,98
Burn 2003	2003	3	Till	Good	3.7	341	41	9.6	8.7	0.0	10.9	383	23.78	1233	2.07
Burn 2001	2001	3	Fluvio-glacial	Rapid	5.3	286	26	10.4	6.9	5.0	8.6	775	37.55	1167	1.52
Burn 1999	1999	4	Fluvio-glacial	Rapid	6.7	217	5	8.8	7.2	10.0	7.9	300	30.93	0	0.00
Burn 1997	1997	2	Fluvio-glacial	Rapid	7.3	250	4	37.9	7.2	5.0	10.6	683	34.70	2967	4,93
Burn 1995	1995	2	Fluvio-glacial	Good	6.7	262	1	35.4	6.7	11.3	10.4	700	31.43	2233	3.11
Control 1	-	-	Fluvio-glacial	Rapid	6.0	259	5	49.6	8.7	12.5	17.1	833	29.39	3033	4.46
Control 2	-	-	Fluvio-glacial	Rapid	9.0	314	38	19.2	5.5	8.3	9.6	775	35.92	2900	2.95
Control 3	-	-	Till	Good	9.3	303	47	18.6	6.3	0.0	7.3	966	41.00	2267	1.63
Control 4	-	-	Fluvio-glacial	Rapid	6.7	220	1	75.0	5.3	6.8	6.3	725	20.89	3133	7.82
Control 5	-	-	Till	Good	6.7	277	46	18.3	5.4	0.0	5.0	950	40.60	1433	1.08
Control 6	-	-	Fluvio-glacial	Rapid	5.3	249	9	21.3	5.4	5.0	15.6	1075	37.89	1200	2.27
Control 7	-	-	Till	Good	4.3	264	16	15.0	5.7	5.0	7.1	1075	28.59	3333	5.97
Control 8	-	-	Till	Good	5.7	259	18	25.0	5.4	5.0	6.2	876	23.52	3967	5.43
Control 9	-	-	Fluvio-glacial	Rapid	9.3	239	9	24.2	5.8	5.7	7.5	651	36.56	2867	4.03

Table 1-2: Comparison of average (± S.E.) initial tree basal area and sapling density (before burning) and of the % of recent mortality of different species in burned and unburned stands. Student t-tests were used to compare mortality averages between treatments (significant ones are in bold).

Stage	Species	Initial BA[1] or density[2] of live trees		% of recent mortality		df	t	p
		Burned	Unburned	Burned	Unburned			
Tree	*P. strobus*	13.7 ± 2.8	11.4 ± 2.0	1.4 ± 0.8	2.4 ± 1.5	14	0.52	0.6109
	A. balsamea	3.1 ± 0.7	3.1 ± 1.1	**38.2 ± 12.7**	**3.7 ± 2.1**	**14**	**3.20**	**0.0064**
	Other conifers	14.6 ± 2.7	18.1 ± 2.9	18.4 ± 6.8	10.7 ± 2.8	14	1.07	0.3036
	Broadleaves	6.1 ± 1.3	5.8 ± 1.2	**39.0 ± 8.8**	**14.3 ± 3.3**	**14**	**2.81**	**0.0138**
	Total	37.8 ± 3.4	38.1 ± 2.2	18.8 ± 4.5	11.3 ± 1.8	14	1.65	0.1203
Saplings	*P.strobus*	9.0 ± 6.0	26.0 ± 11.0	0.0 ± 0.0	0.0 ± 0.0	-	-	-
	A.balsamea	2590.0 ± 372.0	2396.0 ± 427.0	**67.4 ± 7.3**	**9.2 ± 2.6**	**14**	**4.28**	**0.0008**
	Otherconifers	214.0 ± 144.0	437.0 ± 132.0	43.4 ± 18.0	4.1 ± 2.0	14	1.37	0.1922
	Broadleaves	238.0 ± 57.0	189.0 ± 44.0	**37.0 ± 11.7**	**6.1 ± 3.2**	**14**	**2.42**	**0.0296**
	Total	3052.0 ± 333.0	3048.0 ± 391.0	**63.6 ± 6.9**	**9.2 ± 2.3**	**14**	**4.46**	**0.0005**

[1] basal area for trees (Burned sites = 7 / Unburned sites = 9)
[2] density for saplings (Burned sites = 5 / Unburned sites = 9)

Table 1-3: Results of a stepwise multiple regression ($\alpha = 0.10$) predicting the number of Eastern white pine seedlings per control plot as a function of eight environmental variables.

Variables	Mean	S.E.	Min.	Max.	R^2	Rel.	F	Significance at last step
Slope	**21.3**	**17.9**	**0.0**	**60.0**	**0.5154**	+	**25.53**	**< 0.0001**
Total sapling alive / plots	**26.1**	**12.5**	**4.0**	**51.0**	**0.5793**	-	**3.49**	**0.0744**
Shrubs	8.8	4.7	5.0	20.0	-		-	-
Humus thickness	6.9	3.1	3.0	15.0	-		-	-
Ferns	4.8	4.2	0.0	18.0	-		-	-
Herbaceous	5.8	1.2	5.0	10.0	-		-	-
Total Eastern white pine BA	0.5	0.4	0.0	2.0	-		-	-
Total tree BA	1.3	0.5	0.4	2.7	-		-	-

Model is globally significant at $p = 0.0003$

Table 1-4: Comparison of the coverage (%) by ferns, herbaceous, mosses and shrubs and of the organic layer thickness (cm) (mean ± S.E.) in burned (n=5) and unburned (n=9) sites. Statistical comparisons were done using Student t-tests.

Species group	Burning (n=5)	Control (n=9)	df	F	p
Ferns	11.7 ± 5.1	4.9 ± 1.2	12	0.85	0.4093
Herbaceous	**8.1 ± 0.4**	**5.7 ± 0.2**	**12**	**5.99**	**< 0.0001**
Mosses	**11.6 ± 2.2**	**29.5 ± 6.6**	**12**	**- 2.98**	**0.0114**
Organic layer	**4.5 ± 0.7**	**7.5 ± 0.6**	**12**	**- 3.04**	**0.0104**
Shrubs	8.1 ± 0.6	8.8 ± 1.3	12	- 0.35	0.7314

Table 1-5: Comparison of living sapling and seedling densities of Eastern white pine and balsam fir in burned (n=5; 2004-2005 excluded) and unburned sites (n=9).

Stage	Species	Density / ha (mean ± SE)		P	Proportion (%)	
		Burned	Unburned		Burned	Unburned
Seedlings	Balsam fir	5250.0 ± 1869.7	7592.9 ± 2451.8	0.5434	20.6	39.6
	Eastern white pine	**21333.0 ± 1368.7**	**5135.8 ± 1716.6**	**<0.0001**	**83.7**	**26.7**
Saplings	**Balsam fir**	**746.4 ± 250.6**	**2017.2 ± 296.1**	**0.0160**	**52.0**	**80.1**
	Eastern white pine	6.6 ± 6.6	24.2 ± 9.7	0.2551	0.3	0.9

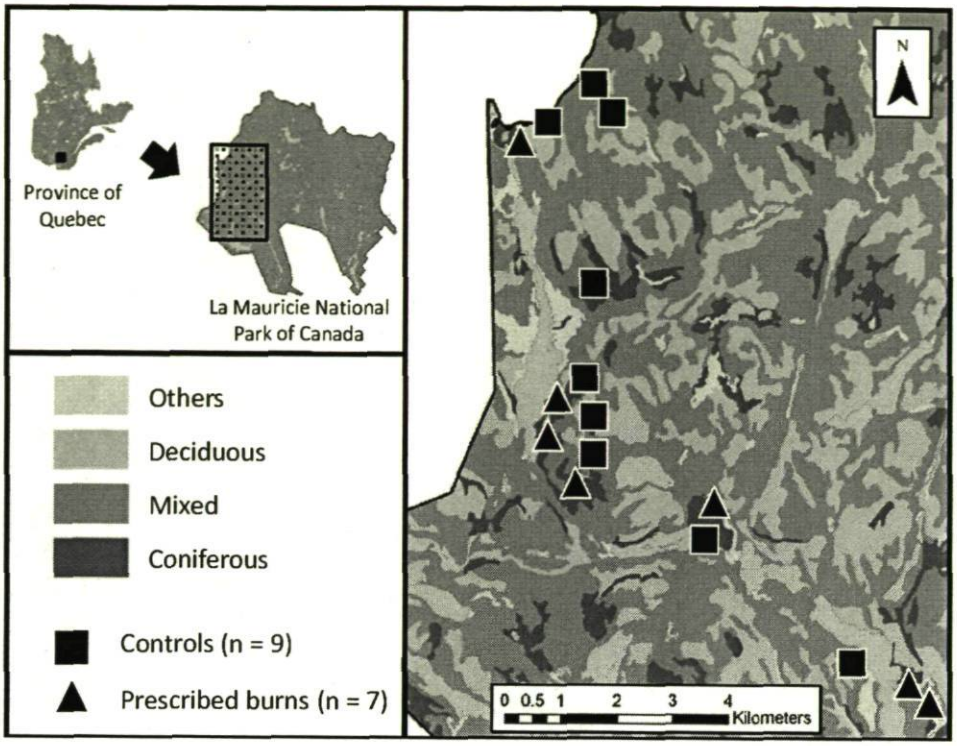

Figure 1-1: Location of the study sites in La Mauricie National Park of Canada.

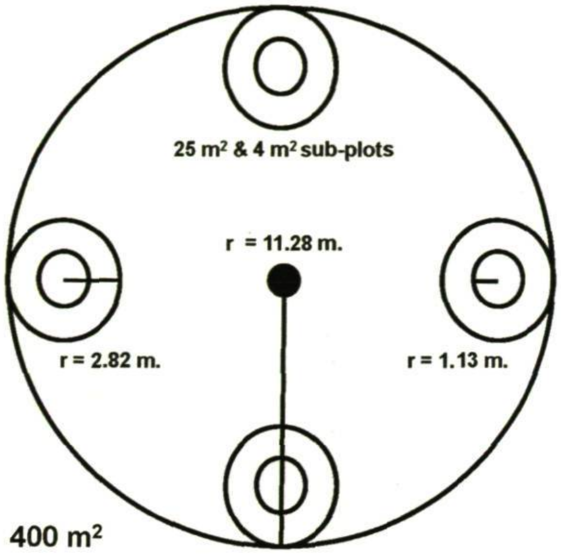

Figure 1-2: Sampling plot, subplots and sub-subplots used to measure trees, saplings and seedlings respectively.

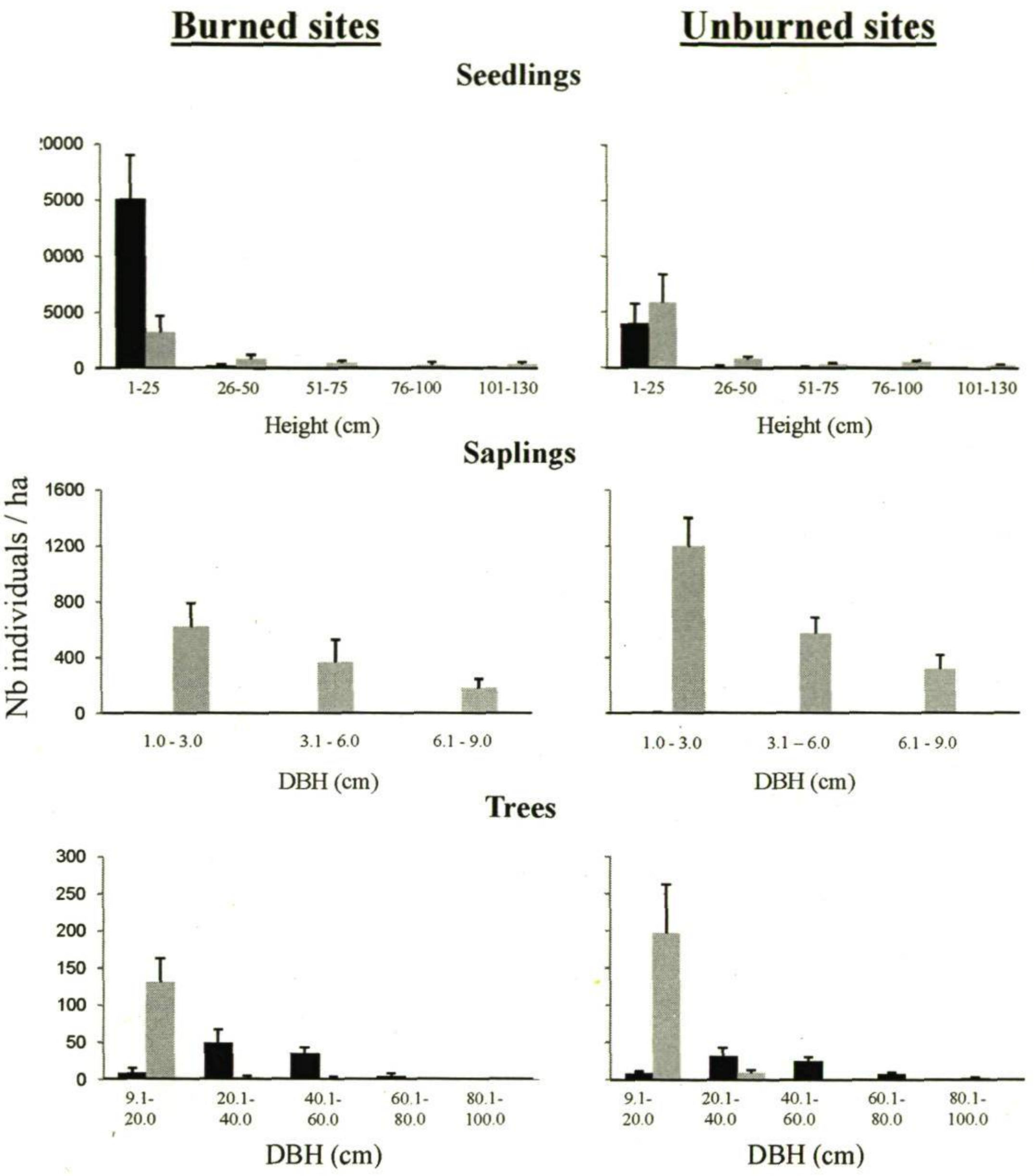

Figure 1-3: Comparisons of Eastern white pine (black columns) and balsam fir (pale grey columns) seedling, sapling, and tree densities (mean± S.E) between burned (n = 7; 2004 and 2005 included) and unburned sites (n = 9).

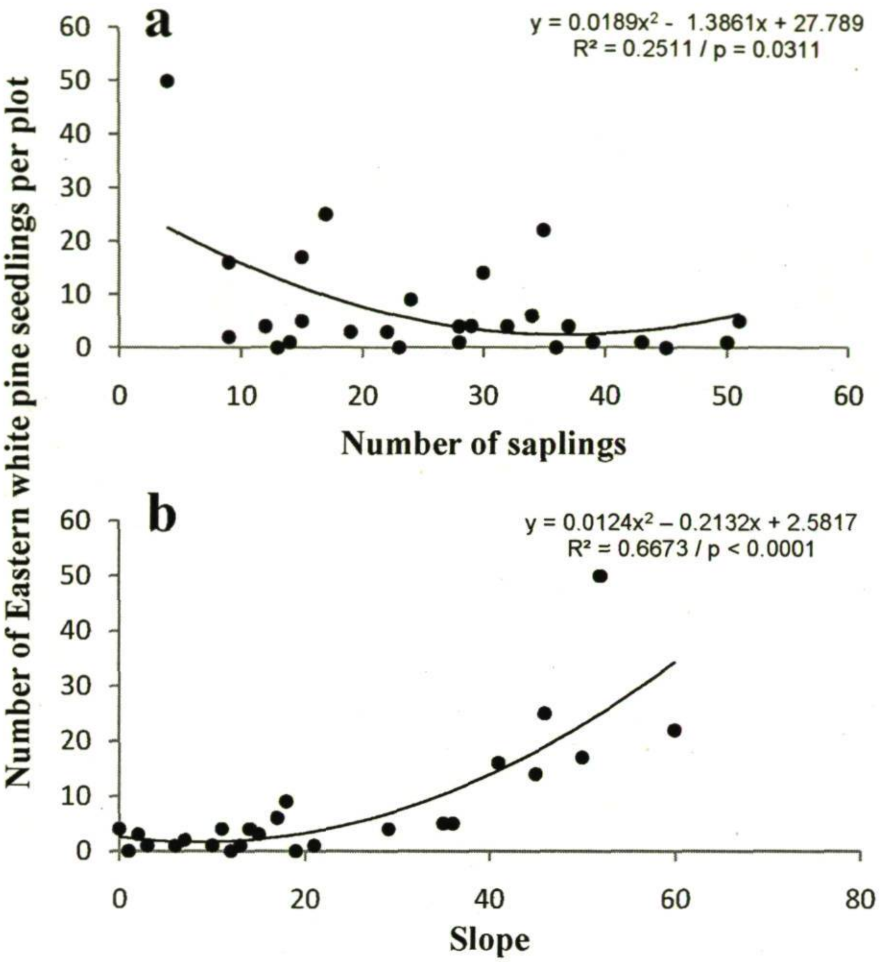

Figure 1-4: Relationships between the number of Eastern white pine seedlings and (a) the total number of tree saplings or (b) slope in 27 unburned plots of forest stands.

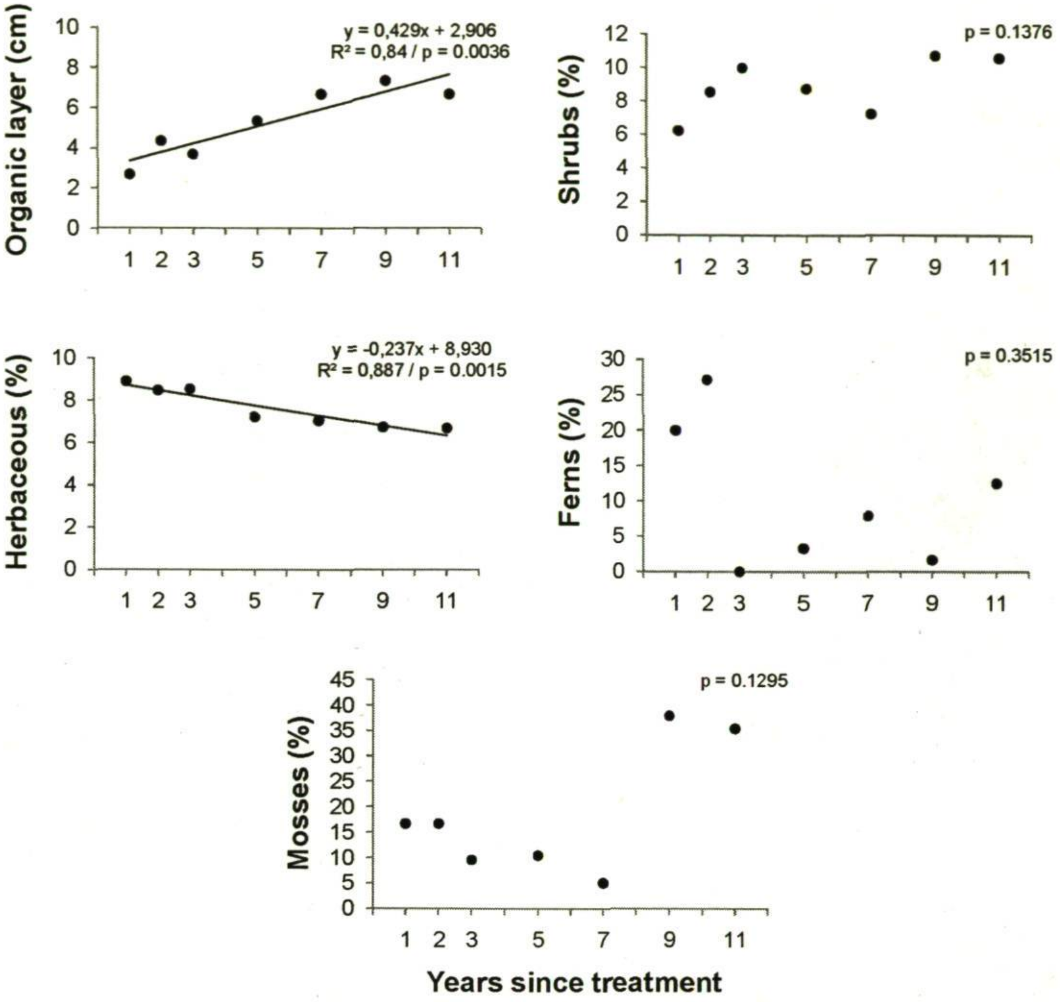

Figure 1-5: Relationships between five ground cover variables and the number of years after treatment.

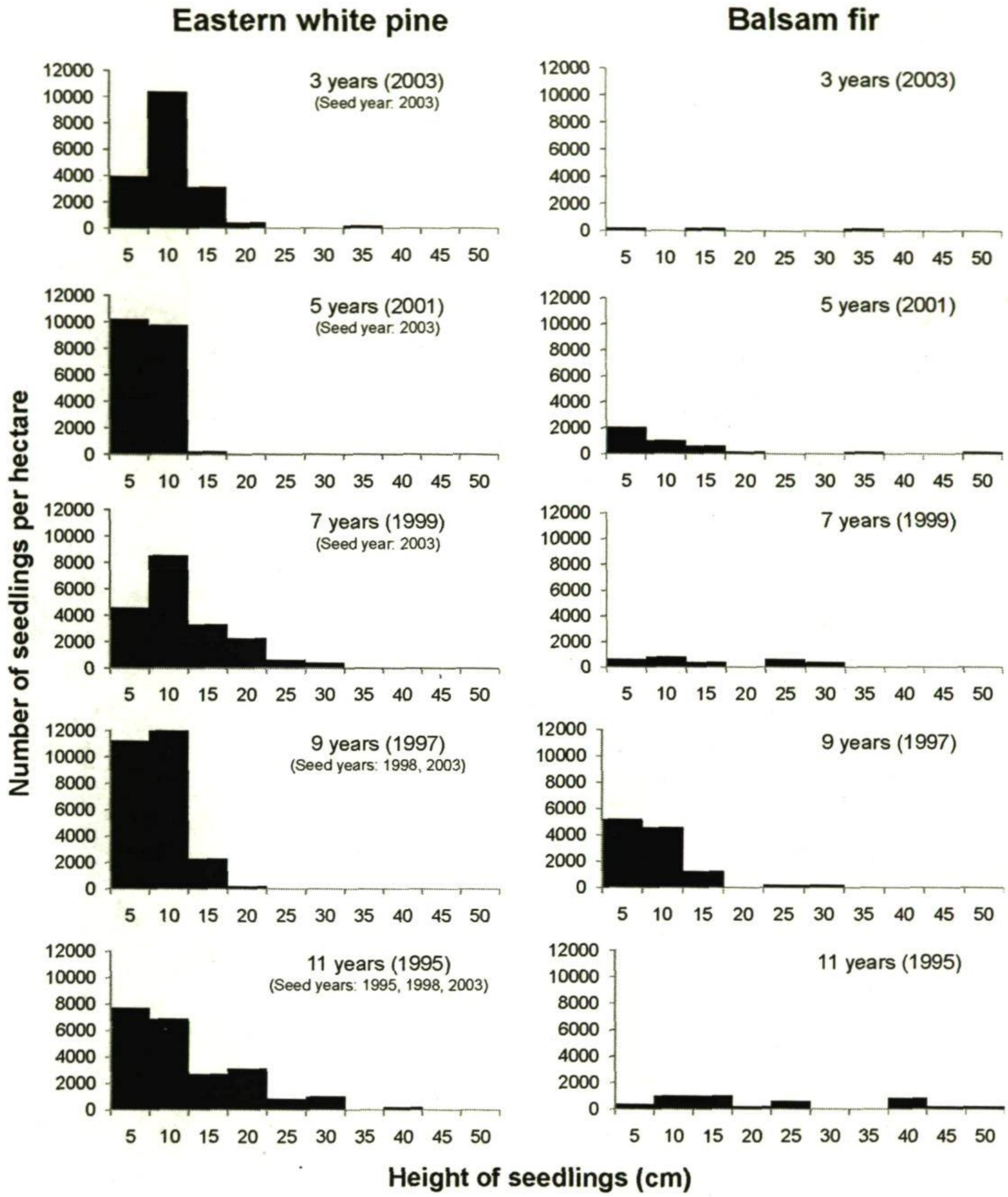

Figure 1-6: Distribution of Eastern white pine and balsam fir seedlings among 5 cm height classes in burned sites of different ages at LMNPC. No Eastern white pine seedling exceeded 45 cm of height.

Effects of prescribed burning on the diversity and species assemblages of Coleoptera in Eastern white pine stands of La Mauricie national park of Canada

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Résumé

L'altération des peuplements de pin blanc de l'Est au PNCLM par les coupes forestières et la suppression des incendies forestiers a modifié la dynamique naturelle de ces peuplements. Face à ces changements, les gestionnaires de Parcs Canada ont décidé d'utiliser les brûlages dirigés afin de restaurer l'intégrité écologique de ce type de peuplement forestier. Ces traitements sont reconnus pour être efficaces en éliminant la compétition et en stimulant la régénération du pin blanc de l'Est. La chronoséquence de brûlage dirigés offre une occasion intéressante d'étudier les effets des ces traitements sur les communautés d'insectes. Il semble que les brûlages dirigés ont aussi d'importants impacts sur les communautés de coléoptères des sites traités. En effet, le feu augmente l'abondance et la richesse spécifique des espèces saproxyliques. De nombreuses espèces saproxyliques ont été détectées uniquement ou en très grande proportion dans les sites brûlés. Beaucoup de ces espèces ont été favorisées par le volume de bois mort généré par les brûlages. Un total de 10 espèces (neuf saproxyliques) et six genres (cinq saproxyliques) ont été identifiés comme indicateurs des sites brûlés alors qu'aucune espèce indicatrice n'a été identifiée pour les sites non brûlés. De plus, la mortalité des arbres et surtout des gaules ont permis la mise en place de conditions post-traitement favorables à certaines espèces de coléoptères floricoles. Plus d'espèces saproxyliques et non-saproxyliques considérées "rares" ont été capturées dans les sites brûlés. Les brûlages dirigés, malgré leur faible intensité, semblent donc être un outil très intéressant et efficace dans le but de restaurer l'intégrité écologique des peuplements de pin blanc de l'Est. Il est cependant difficile d'évaluer le niveau d'intégrité écologique atteint en ce qui concerne les communautés de coléoptères étudiées puisqu'il n'existe pas de référence préindustrielle. Cependant, le nombre élevé d'espèces saproxyliques indique clairement que les communautés observées se rapprochent davantage de celles de sites naturellement brûlés que de sites non-brûlés. En plus de régénérer les forêts de pin blanc de l'Est, ces traitements ont aussi des effets positifs sur les groupes d'insectes habituellement rattachés aux incendies forestiers.

Abstract

The alteration of Eastern white pine stands by logging and forest fire suppression has modified the natural dynamics of these forest stands in LMNPC. Faced to these changes, managers of Parks Canada decided to use prescribed burning in order to restore the ecological integrity of this type of stands. This treatment has been effective by eliminating competition and stimulating Eastern white pine seedling establishment. This chronosequence of prescribed burning represent an interesting opportunity to study the effects of this treatment on the insects. It seems that prescribed burning also has significant impacts on beetle communities. Indeed, increases in abundance and species richness of saproxylic species have been observed in burned stands. Many saproxylic species were detected only or mostly in burned sites. Many of these species have been favoured by the volume of deadwood generated by the burning. Overall, 10 species (nine saproxylics) and six genera (five saproxylics) were identified as indicators of burned sites while no indicator of unburned sites was identified. In addition, mortality of trees and saplings allowed the establishment of favourable post-treatment conditions for certain species of beetles attracted by flowering plants. Furthermore, we captured significantly more non-saproxylic and saproxylic species considered "rare" in the burned sites. The burn, despite its low intensity, seems to be an effective tool for restoring the ecological integrity of Eastern white pine stands. It is however difficult to estimate the level of ecological integrity achieved in regards to species assemblages because we do not have a preindustrial reference. However, the high numbers of saproxylic species indicate that the communities are closer to those of naturally burned sites than unburned sites. In addition of their usefulness to regenerate the Eastern white pine forests, these treatments also have positive effects on groups of insects usually associated with forest fires.

Introduction

Forest harvesting has resulted in important changes of forest composition in many countries (Hansen et al. 1991; Hyvärinen et al. 2005). At the time of European settlement in North America, Eastern white pine (*Pinus strobus* L.) was an important component of coniferous forests (Horton and Brown 1960; Quenneville and Thériault 1998). European newcomers were the first to use Eastern white pine but intensive harvesting mostly occurred during the last 100-150 years, causing major alterations in both structure and composition of these forests (Boucher 1952; Baker 1994; Similä et al. 2002). Almost all accessible Eastern white pine stands were harvested and even the trees of lower quality were cut (Mirov and Hasbrouck 1976; Burgess and Methven 1977). This has lead to important reductions of Eastern white pine stocks and to the conversion of the majority of these forests into stands composed of late successional coniferous (mainly balsam fir) and tolerant hardwood trees (mainly maples) (Ziegler 1995; Carleton et al. 1996; Quenneville and Thériault 1998; Abrams 2001; Dovčiak et al. 2001; Weyenberg et al. 2004). In recent decades, the rare old-growth Eastern white pine forests still existing and residual logged stands also faced another threat. Fire, which has been historically an important natural disturbance for maintaining Eastern white pine stands (McRae et al. 1994; Carleton 2003), has gradually decreased in importance because of the implementation of fire suppression policies (Baker 1994; Quenneville and Thériault 1998). Remnant trees now die without having access to appropriate stand conditions for seedling establishment and growth that would ensure the persistence of Eastern white pine. Therefore, there is a growing concern about management of Eastern white pine forests (Carleton et al. 1996; Ontario Ministry of Natural Resources 2009).

At La Mauricie National Park of Canada (hereafter LMNPC), Eastern white pine stands are now rare and most often Eastern white pine is loosely distributed into a mosaic of different tree species. Before the creation of the park in 1970, Eastern white pine logging has been selective and intensive since at least a century (Boucher 1952; Valcourt and Gagnon 2000). This has led to a decrease in Eastern white pine prevalence from 5-12% of wood volume in the preindustrial forest to 0.5% in the actual forest (Pelletier 1998; Barrette 2004).

Furthermore, fire suppression remained active since the 1930's and no large fire has been recorded over the last 80 years. According to Dryade (1986), the fire cycle in LMNPC has drastically increased over the last decades. These changes in the natural dynamic of Eastern white pine stands have resulted in an increased abundance of balsam fir, a competing species which now dominates the understory of remnant Eastern white pine stands of LMNPC. The volume of this species has increased from 13.1% before the preindustrial period to 31.8% in the actual forest (Pelletier 1998).

In addition of being effective to regenerate several types of forests, natural fire enhances spatio-temporal heterogeneity of forests (Granström 2001; Weyenberg et al. 2004) by modifying age structure, tree species composition (Zackrisson 1977; Similä et al. 2002) and stocks of dead wood available for several years (Siitonen 2001; Wikars 2002). Recently burned forests provide abundant stressed or dead trees rarely seen in other phases of forest succession (Linder et al. 1998; Pedlar et al. 2002).

These volumes of dead wood are known to be important for many saproxylic beetles (Siitonen 2001; Grove 2002; Saint-Germain et al. 2004; Toivanen and Kotiaho 2007), those that depend on dead or dying wood, on wood-decaying fungi or on the presence of other saproxylic organisms during at least a part of their life cycle (Speight 1989). Saproxylic beetles often specialize on dead wood with particular characteristics such as tree species, size, decay stage, sun-exposure and position (lying, standing or on the ground) (Økland et al. 1996; Jonsell et al. 1998, 1999, 2004; Siitonen 2001). Some beetle species found in burned forests use sensory organs to detect chemicals released by dead or dying trees (mainly ethanol and monoterpenes), smoke, heat and infra-red to locate these high quality and competition-free habitats (Evans 1966; Montgomery and Wargo 1983; Schroeder 1988; Muona and Rutanen 1994; Wikars 1997; McCullough et al. 1998). Several fire-favoured beetles have become rare in European countries where fire suppression has been implemented (Muona and Rutanen 1994; Wikars 1997; Similä et al. 2002) and intensive forestry particles have been used. This has resulted in the addition of many fire-associated species on red-lists of threatened or endangered species (Wikars 1997; Siitonen 2001; Similä et al. 2002; Hyvärinen et al. 2005; Toivanen and Kotiaho 2007). Therefore, we may hypothesize that fire-favoured species might be adversely affected when under efficient fire suppression (Wikars 1997).

Because the "let it burn" policy cannot be implemented in a small park like LMNPC, management practices are thus needed to achieve the objectives of Parks Canada's ecological integrity policy, including those that concern the restoration of preindustrial Eastern white pine forests conditions. Since 1991, Parks Canada has developed a restoration program of Eastern white pine stands where prescribed burning is used to emulate low-intensity fires that prevailed in primeval forests (Attiwill 1994; Haeussler and Kneeshaw 2003).

In Eastern white pine forests, this treatment has already been used as a restoration method (Barden and Woods 1976; McRae et al. 1994); it has also been used for the restoration of different types of stands in parks and reserves (Juninnen et al. 2008). In North America, some authors have demonstrated its success in regenerating Eastern white pine (Methven and Murray 1974; McRae et al. 1994; Quenneville and Thériault 1998; Domaine et al. unpublished). The LMNPC restoration program represents a unique opportunity to evaluate the effects of several prescribed burning events carried out in Eastern white pine forest stands, and along a chronosequence covering 11 years.

Because they occupy almost all ecological niches and are highly sensitive to environmental changes, Coleoptera represent a powerful group to measure the effects of prescribed burning on biodiversity. Furthermore, several species of Coleoptera, mainly saproxylics, are known to be associated with fire or post-fire conditions (Evans 1966; Wikars 1997, 2002). These insects take advantage of fire because they are mostly decomposers and there is more food available for them. They have many characteristics required for use as a taxon that allow evaluating the impact of prescribed burning on the ecosystems fauna (Fernàndez Fernàndez and Salgado Costas 2004).

We may hypothesize that, based on several studies carried out in natural wildfires, prescribed burning could also affect biodiversity (Siitonen 2001; Grove 2002; Saint-

Germain et al. 2004; Toivanen and Kotiaho 2007). Few studies have investigated more than short term effects of a single fire event (Simberloff 2001). Furthermore, several studies have addressed the issue of natural fire and its effects on beetle diversity, but the effects of prescribed burning (low intensity surface fire) remain almost unexplored (Niwa and Peck 2002). The aim of our study was to determine how diversity and species assemblages of Coleoptera change after prescribed burning in Eastern white pine stands, along a chronosequence covering 11 years. More specifically, our objectives were to determine (1) if abundance, species richness and rarity increase after prescribed burning, (2) how species assemblages and β-diversity dispersion differ among burned and unburned sites, and (3) how long the changes induced by burning last in treated sites.

Materials and methods

Study area and sampling sites

Study sites were located in the La Mauricie National Park of Canada (LMNPC) (Figure 2-1), which is a vast plateau located north of the St-Lawrence River in Quebec, just beside one of its most important affluent, the St-Maurice River. The park has been created in 1970 and it covers 536 km^2. Annual precipitations vary between 900 and 1400 mm and the annual average temperature from 2.5 to 5.0°C (Gosselin 2001). LMNPC is located between two terrestrial Canadian ecozones, the boreal shield and the mixedwood plains. It is characterized by a typical landscape of Laurentian Mountains moulded with hills and lakes that belongs to the sugar maple – yellow birch bioclimatic domain (Ministère des ressources naturelles du Québec 2003). The park is a diversified land where over 30 forest types are found (Lalumière and Thibault 1988; Quenneville and Thériault 2002). Eastern white pine a small component of mixed forest stands, associated with spruces (*Picea* sp.), balsam fir (*Abies balsamea* (L.) Mill.) and deciduous trees. In LMNPC, it also grows more rarely in nearly pure stands or combined with red pine (*Pinus resinosa* Ait.).

Between 1995 and 2005, prescribed burning has been used in seven forest sites where the slope was <50%, Eastern white pine density >15 trees/ha, and balsam fir saplings were dominating the understory. In these sites, Eastern white pine seedling and sapling densities were considered to be too low to ensure Eastern white pine renewal. Thus, prescribed burnings were used to achieve the objective of restoring the ecological integrity in Eastern white pine ecosystems (Quenneville and Thériault 2002). Prescribed burnings were done in spring, before budflushing of broadleaved trees and shrubs (Vlasiu et al. 2001). When meteorological conditions were met, fire was ignited using burners (driptorch) or a helicopter equipped with Premo MK3 aerial ignition device. Low-intensity surface fires were isolated and controlled with natural and artificial firebreaks.

Eight closely located unburned sites were selected as reference sites to estimate the effect of the burning treatment on coleoptera diversity and species assemblages. All sites were located across a territory of 40 km^2 (Figure 2-1). The altitude of selected sites ranged from 217 to 341 m and slope varied between 1% and 47% (Table 2-1). Balsam fir was the most abundant understory tree species while Eastern white pine and spruces dominated the overstory.

Forest inventory

In each of the 15 sites, we established three 400 m^2 circular plots located 50 m apart. Plots were distributed along a transect and distanced by a minimum of 50 m from stand or treatment edges (Figure 2-2). We determined the slope (%), altitude (m), surface deposit and drainage for each plot (Table 2-1). Flame heights were recorded by LMNPC's crews during each prescribed burning event and were used to estimate fire intensity, based on the Canadian forest fire behaviour prediction system (Natural Resources of Canada 2008. Fire intensity of surface fires used during field operations was mostly of class 3 (frontal fire intensity 500-2000kw/m; flame length 1.4-2.6m; flame height 1.0-1.9m) except for the site burned in 1999 where fire intensity reached the class 4 (frontal fire intensity 2000-4000kw/m; flame length 2.6-3.5m; flame height 1.9-2.5m) and killed many mature trees including some Eastern white pines.

In the 400 m^2, we recorded the species, diameter at breast height (hereafter DBH) and decay class for each standing tree ≥9.1 cm at DBH. Decay classes were determined according to the Hunter (1990) classification that recognizes 9 classes for trees (1: alive and 2: declining) and snags (3: dead tree with bark intact... to 9: stump). In each 400 m^2 plot, four smaller plots of 25 m^2 (radius=2.82 m) and four micro plots of 4 m^2 (radius=1.13 m) were established at 8.46 m from the plot center, in each cardinal direction (Figure 2-2). Saplings and seedlings were recorded in the 25 m^2 and 4 m^2 plots respectively. Saplings were young trees in which DBH ranged between 1 and 9 cm, whereas DBH of seedlings was smaller than 1 cm (Canada 1992). For each sapling, we recorded the species, DBH and decay class while we classified seedlings by species and height in 5-cm classes. Coverages (1-5%, 6-10% and then by 10% classes) of non-commercial species of trees, shrubs, herbaceous, ferns and mosses were also estimated in the 25 m^2 plots. Bryophytes were not identified and simply recorded as mosses.

Volume of trees and saplings were calculated for two different groups of snags: recent (Hunter's decay classes 3 and 4) and old (decay classes 5 to 7) (Table 2-2). To estimate the volume of each snag, we used three different equations depending on the decay class of individual trees: (1) if crown was intact (Hunter's decay class 3), volume = cylinder x 0.50 (a paraboloid); (2) if crown was missing but large branches were present (Hunter's decay classes 4 and 5), volume = cylinder x 0.75 (intermediate between paraboloid and cylinder); (3) if branches were absent and only bole was present (Hunter's decay classes 6 and 7), volume = cylinder x 1.00 (a cylinder) (Tyrell and Crow 1994). Volume of downed woody debris was estimated using the line-intersection technique described by Van Wagner (1968). Three transects of 15 m (total length 45 m) and oriented at 0, 120, and 240 degrees were settled, each one beginning at the center of the plot. Each debri of more than 1 cm of diameter was recorded. Species, diameter at interception and decay class were recorded for each debris. For analyses, we classified volume of downed woody debris into two classes: recent deadwood (Hunter's decay classes for woody debris 1 and 2) and old deadwood (Hunter's decay classes for woody debris 3 to 5) (Table 2-2).

Coleoptera sampling

Coleoptera were continuously sampled between May 16th and August 17th 2006 in seven burned sites and eight unburned sites. Four pitfall traps and one multidirectional flight-interception trap were installed in each 400 m^2 plot (Figure 2-3). The multidirectional flight-interception trap was placed at the center of the plots, 0.5–1m above the ground for sampling flying Coleoptera. They were built using four 15 x 40 cm panels (two made of Plexiglas and two of mosquito net) mounted into a cross pattern, along a black ABS cylinder of 10 cm diameter, with two funnels leading to the top and bottom collecting bottles. This ''hybrid'' trap was designed to account for different behavioural responses shown among beetle families when hitting different types of interception panels (Saint-Germain et al. 2004). Four pitfall traps (MultiPher® traps) were buried into the ground, 7 m away from the multidirectional flight-interception trap in each cardinal direction, to sample ground-dwelling coleoptera (Figure 2-2). Thus, the pitfall traps were positioned in a square pattern around the center of the plot and at 10 m from each other. They had 10 cm diameter and were screened with a wire mesh (10 x 10 mm) to reduce vertebrate captures. An inner removable recipient was placed inside the trap to make insect collection easier. In both types of trap, a 40% ethanol solution with traces of household vinegar (5% acetic acid) was used as preservative. A detachable lid was placed on the top of each pitfall trap to protect samples from rain and reduce ethanol evaporation. Traps were emptied every two weeks and most beetles were identified at the species level whenever possible. Reference collections of labelled and identified beetle specimens are stored in the René-Martineau insect collection of the Laurentian Forestry Centre (Natural Resources of Canada).

Statistical analysis

Abundance, species richness and rarity in burned and unburned forests were compared using t-tests for saproxylic and non-saproxylic species, as well as for each of the six most abundant families, those in which at least 250 beetles were captured among the 16 study sites (Carabidae, Cerambycidae, Curculionidae, Elateridae, Lathridiidae and Nitidulidae). Because the Lathridiidae were identified at the genus level, we haven't tested species richness and rarity for this family. Staphylinidae were identified at the family level and were not included in further analyses. We used the Saproxylic Database (The Saproxylic Database 2009) and relevant literature to classify coleoptera as saproxylic (facultative and obligatory) or non-saproxylic species. In our study, species that were caught only three times or less, over the 15 sites, were considered to be "rare". We also compared the abundance of common and abundant species ($n>20$) to pinpoint differences between burned and unburned sites. When necessary, data were transformed ($\log x + 1$) to normalize distributions and stabilize variances. Analyses were performed using SAS version 9.1.3 for Windows (SAS Institute 2000). To better appraise the prevalence or not of species for burned sites, we also determined the proportion of species that were mostly found in burned versus unburned sites. First, we classified species according to their overall abundance: "rare" species (1-3), uncommon species (4-20), common species (21-100) and abundant species (≥ 101). Among "rare" species, those that were caught exclusively in burned sites were considered to have been favoured by the treatment. Any other species which have been caught at least 75% of the time in burned sites was considered to be favoured by the prescribed burning treatment. The resulting matrix (3x4 contingency table relating the number of species showing prevalence for burned or unburned sites or absence of prevalence X abundance classes) was compared using chi square analysis to determine if the prevalence or not for burned sites was equally distributed among abundance classes.

We used the Anderson's (2006) test for homogeneity of multivariate dispersions (using Betadisper in R) to pinpoint differences in beta diversity dispersion among species assemblages of burned and unburned groups of sites. Beta (β) diversity is defined as the variation in species composition among sites (Whittaker 1972). We composed *a priori* groups using treatment (burned and unburned) as a discriminant variable. The R procedure Betadisper compares the average distance of species assemblages of each site to their group centroid, defined in the space recognized by the Bray-Curtis measures. To test if the dispersions (variances) of burned and unburned groups were different, we used a test which permutes model residuals to generate a permutation distribution of F under the Null hypothesis of no difference in dispersion between groups (Anderson 2006; Anderson et al. 2006). These analyses were carried out using the R software (R development core team

2008). We also used the Indicator Value analysis (IndVal) to identify species that would be indicative of the burning treatment. To fully benefit from the potential of this analysis, sites were classified as recent (2004-2005), mid-aged (1999-2001-2003) or old burns (1995-1997) and, for unburned sites, those growing on steep slopes (>35%) or not (<20%). It has also been shown that Eastern white pine dynamic differed as a function of slope, sites located on steep slopes showing higher Eastern white pine seedling density and lower competition from balsam fir (Domaine et al. unpublished). Only significant (alpha = 0.05) species ($n \geq 10$ individuals at 1st and 2nd levels; $n \geq 5$ individuals at 3rd level) that had an indicator value > 55% (asymetrical indicators) were retained. The analysis was made using IndVal 2.0 Software (Dufrêne 1998).

Redundancy analysis (RDA) was performed to examine how environmental variables, including those resulting from the burning treatment, influenced non-saproxylic and saproxylic species assemblages. In RDA, species are arranged to maximise the explanatory power of the environmental variables. It is a multivariate method in which species are presumed to be linearly related to environmental gradients (Legendre and Legendre 1998). Burns were expected to generate characteristics that would form major gradients that may structure Coleoptera assemblages. Analysis was performed on raw data including all the species captured. We used Hellinger transformation to relativize the weights of abundant species (Legendre and Gallagher 2001). Environmental variables used in the RDA of non-saproxylic species were the mean percentages of ground covering by herbaceous and shrubs, plus fire intensity. Environmental variables used in the RDA of saproxylic species were the mean percentages of ground covering by each herbaceous and shrubs, fire intensity, the volume (m^3/ha) of snags and the volume (m^3/ha) of downed woody debris with respect to young decay classes (Hunter classes 3-4 for snags; Hunter classes 1-2 for debris) of either deciduous or coniferous trees.

Because the RDA makes it difficult to interpret the relationships between "rare" species and the environmental variables, we used linear regression to highlight their relationships with the volume of dead trees, dead saplings and downed woody debris. Deadwood was categorized as young (Hunter classes 3-4 for snags; Hunter classes 1-2 for debris) or old

(Hunter classes 5-9 for snags; Hunter classes 3-4 for debris). Simple linear regressions were also used to verify if the abundance and species richness of non-saproxylic beetles were related to the time elapsed (years) after the treatment. We also used second order polynomial regressions to relate the abundance and species richness of saproxylic beetles to the time elapsed (years) after the treatment. Regressions were performed using SAS 9.1 for Windows (SAS Institute 2000).

Results

A total of 14 203 coleoptera belonging to 62 families were captured throughout the study. Coleopteran fauna was dominated by seven families (Carabidae, Cerambycidae, Curculionidae, Elateridae, Lathridiidae, Nitidulidae and Staphylinidae) which accounted for 85% of the total abundance. Eight species were strongly dominant, each with more than 500 specimens captured, representing 69% of all beetles collected (Annexe 2). Among these, the weevil *Hylobius congener* ($p<0.0001$) and the Nitudilidae *Glischrochilus s. sanguinolentus* ($p=0.0127$) were more abundant in burned sites; the six other species were not significantly more abundant in either burned or unburned sites (Annexe 2). A minimum of 319 taxa were identified at different levels (1 family, 44 genera and 274 species), including 222 saproxylic taxa (23 genera and 199 species). Overall, 115 species were caught exclusively in the seven burned sites (27 from the site burned in 1999) compared to only 41 species in the eight unburned sites. The site burned in 1999 showed the highest species richness (142) among all sites, while the oldest burned site (1995) had the lowest species richness (90) of all burned sites; however its species richness was still higher than the average species richness found in unburned sites (Table 2-2).

Abundance and species richness

At the family level, only the Lathridiid beetles were significantly more abundant ($p<0.0001$) in burned than in unburned sites (Table 2-2). For this family, four out of six genera (*Corticaria, Corticarina, Cortinicara* and *Melanophtalma*) tested were significantly more abundant in burned sites (Annexe 2). Overall abundance, as well as that of saproxylic species were significantly higher in burned than in unburned sites (Table 2-2). Non-saproxylic species abundance was not significantly different in the two types of stands. However, species richness of both saproxylic and non-saproxylic species were significantly higher in burned sites, as well as total richness (Table 2-2). Among these, three families (Cerambycidae, Curculionidae and Nitidulidae) showed higher richness in burned sites (Table 2-2). High species richness in burned sites resulted from the presence of many "rare" species in four of the five abundant families (except the Nitidulidae) identified at the species level. The chi square analysis comparing the prevalence of species in burned versus unburned sites among abundance classes confirmed this pattern: more ""“rare”"" species (compared to the common and abundant classes) were found in burned sites than expected if distribution would have been random (Table 2-3). Nevertheless, some common and abundant species of Curculionidae and Elateridae were significantly more abundant in burned sites such as the weevils *Hylobius congener* ($p<0.0001$) and *Polygraphus rufipennis* ($p=0.0456$) (see Annexe 2) and the elaterid beetles *Agriotes stabilis* ($p=0.0290$) and *Melanotus castanipes* ($p=0.0315$) (see Annexe 2). However, abundances of the vast majority of common and abundant species were not significantly higher in burned than in unburned sites.

The abundance of non-saproxylic species was significantly and negatively related to the time elapsed (years) after the treatment (Figure 2-4). For saproxylic species, the mean species richness was significantly related to the time elapsed (years) after the treatment, species richness peaking between three to seven years after prescribed burning (Figure 2-4). Despite its non significance ($p=0,0765$), the quadratic regression relating the mean abundance of saproxylic species to the time elapsed (years) after the treatment showed the same pattern as for the saproxylic species richness (Figure 2-4).

Species assemblages and β-diversity

There was no significant difference in the dispersion of the non-saproxylic species assemblages between burned and unburned sites, the mean distances to the centroids being respectively of 0.3175 and 0.3357 (F = 0.28; df = 1; P = 0.6023). Control sites 4 and 6 mostly overlapped with the group composed of burned sites (Figure 2-5a). However, for saproxylic species assemblages, a significant difference was found among burned and unburned sites, the average distances to the centroids being respectively of 0.2619 and 0.3204 (F = 4.82; df = 1; P = 0.0468), showing that saproxylic species assemblages of burned forests were less variable than those of unburned sites. This was illustrated by the differences in the location of sites among groups in the ordination space (Figure 2-5b).

The IndVal analysis revealed that 16 taxa were indicators (10 species and six genera) of burned sites while no species was significantly indicative of unburned sites (Table 2-4). Species or taxa with the highest indicator values for burned sites were mostly saproxylic species such as *Corticarina sp.*, *Corticaria sp.*, *Silvanus bidentatus* and *Hylobius congener* (Table 2-4). Other less abundant species, such as *Acmaeops p. proteus* and *Dryopthorus americanus*, had lower indicator values but were exclusively found in burned sites. The analysis also recognized six indicators (five identified at the species level and one at genus) of recent burns, four indicators of mid-aged burns but no indicator of old burns (Table 2-4). Five out of six indicator species of recent burns were non-saproxylic species (mainly Carabidae) while all four indicators of mid-aged burns were saproxylic species (Table 2-4).

Relationships between environmental variables and species assemblages

The RDA allowed to determine how attributes affected by the burning treatments were connected or not to the non-saproxylic and saproxylic species assemblages. The model was not significant for non-saproxylic species (p=0.2821) but it was significant for saproxylic species (p=0.0290) when tested with 999 permutations. The eigenvalues of the first two axes of the ordination were 0.186 and 0.118 respectively, explaining 30.4 % of the variation in the dataset (Figure 2-6b). The first axis of the ordination (p=0.0447) clearly contrasted burned sites on the left, along with vectors of recent deadwood (including both trees and saplings), fire intensity and herbaceous covering; the unburned sites were mainly located on the right side of the axis, along with shrub coverage and downed woody debris (including both coniferous and deciduous) vectors (Figure 2-6b). The cloud of saproxylic species was located slightly at the left of the biplot center, along with burned sites. Simple linear regressions showed that recent deadwood variables (trees, saplings and downed woody debris) were significantly related to the number of "rare" species captured at each site (Figure 2-7 left). However, the old deadwood variables were not significantly related to the number of "rare" species captured at each site (Figure 2-7 right).

Discussion

Our study shows that the number of "rare" species of Coleoptera increases more than it would have been expected by random after prescribed burning in Eastern white pine forests. This results in higher species richness in burned than in unburned forests for both saproxylic and non saproxylic species, indicating that prescribed burning does not only increase the amount of recent deadwood necessary for saproxylic organisms but also favours other resources mostly linked with post-fire environment. Moreover, even if species richness returned to the level observed in unburned forests 11 years after the burning, saproxylic species assemblages were still different, indicating that the treatment effects last longer than a decade and that a new ecological trajectory may have been defined. Our results indicate prescribed burning creates conditions useful in restoring the ecological integrity of these ecosystems in a much larger sense. By favouring several "rare" species and saproxylics species favoured by the fire effects, prescribed burnings help to improve biodiversity conservation, an important aspect of the ecological integrity concept. This is particularly important in the context of a protected area such as La Mauricie National Park of Canada.

These newly generated habitats are used by several species of different abundant families (Cerambycidae, Curculionidae and Elateridae) known to be associated with post-fire conditions (Wikars 1992). Several saproxylic species (and genera) were identified as indicators of burned sites (*Corticarina sp.*, *Corticaria sp.*, *Silvanus bidentatus* and *Hylobius* *congener; Acmaeops p. proteus* for the recent burns group) while no species were identified for the group of unburned sites. Most of these taxa have been reported in several studies done after wildfires (Saint-Germain et al. 2004; Boulanger and Sirois 2007). By killing trees across wide areas (often several thousands of hectares), wildfires produce large amounts of deadwood that release chemicals and produce large plumes of smoke which are known to attract several saproxylic species (Evans 1971; Montgomery et al. 1983; McCullough 1998). Even if prescribed burnings are less intense than wildfires, they increased significantly the mortality of broadleaved and balsam fir trees and saplings, and they produced great amounts of smoke. This seems to be enough to induce responses of saproxylic species and significantly increase their abundance and richness compared to unburned sites.

As expected, different saproxylic species assemblages were found in burned sites when compared to unburned ones. Saproxylic species assemblages appeared tightly clustered, apart from the group of unburned sites, in the homogeneity of multivariate dispersions analysis. This, and results arising from the RDA, indicate that saproxylic species assemblages of burned sites, in addition of being richer, were clearly distinct from the species assemblages of unburned sites. Furthermore, the saproxylic assemblages were more homogenous than in unburned sites giving them a distinctive and important ecological value for species conservation. It is in agreement with Wikars (2002) who concluded that some species not only need deadwood as substrate but are also favoured by particular habitat characteristics. While placing scorched and non-scorched logs in burned and unburned forests, Wikars (2002) came to this conclusion when he found that scorched logs placed in burned forests hosted different saproxylic species than non-scorched logs placed in burned or unburned forests.

The distinction of non-saproxylic species assemblages of burned and unburned forests was not as clear as for saproxylic species, the RDA model being not significant. Several authors have demonstrated that immediately after a fire, post-fire habitats represent a favourable environment for open-habitat species (Muona and Rutanen 1994; Moretti and Barbalat 2004; Saint-Germain et al. 2004; Hyvärinen et al. 2005; Buddle et al. 2006; Toivanen and

Kotiaho 2007). In our study, we found significantly more non-saproxylic species (mainly carabidae) in burned sites, indicating that even if prescribed burnings do not kill as many trees as severe wildfires, they generate suitable conditions for many non-saproxylic species. For example, some non-saproxylic species were considered as indicators of recent burns (the carabids *Notiophilus aeneus* and *Syntomus americanus*). These species are known to use xeric open-habitat (Arnett and Thomas 2001; Larochelle and Larivière 2003). Saint-Germain et al. (2005) also found these two species to be restricted to recently burned spruces forests.

The RDA linked abundant saproxylic species to burned sites and to the higher amounts of recent deadwood (mainly coniferous trees and saplings) generated by prescribed burnings. Saproxylic species were more closely related to standing deadwood than to downed woody debris. Snags are probably more important for maintaining species associated with younger stages of decomposition while downed woody debris might be more important for maintaining species associated with older stages of decomposition (Jonsell et al. 2004). Saproxylic species abundances were also associated with herbaceous resources suggesting that a greater exposure to the sun favours flowering plants, which are important resources for several saproxylic and non-saproxylic beetles (Moretti and Barbalat 2004; Fayt et al. 2006).

Abundance and species richness of saproxylics were lower in the first and second years following treatment. Studied prescribed burnings were low intensity fires and appropriate conditions for many saproxylic species may take time to establish. This may explain that the abundance and species richness of the 2004-2005 sites were low compared to the mid-aged burned sites. Higher catches following the third year may reflect activities of beetles still attacking trees and emerging from these trees (a higher activity means higher trap captures). In Finland, Martikainen and Kaila (2004) observed dramatic decreases in longhorned beetle abundance seven years after a fire. This is probably due to the end of the tree mortality period caused by the burning and thus to the reduction in the abundance of recent snags of high quality that are used as substrate by wood-borers (Lachat et al. 2006). According to Ahnlund and Lindhe (1992), fire-favoured species use burned areas mostly during the first five years after a fire. In our study, the significant and nearly significant quadratic regressions concerning the abundance and the species richness of saproxylic species, as well as the decrease in the number of "indicator species" as a function of the time after burning (6 in recent burns, 4 in mid-aged burns and 0 in old burns) suggest that the burning "signal" may lose strength as time elapsed after treatment. A decreasing temporal pattern was found in the abundance of non-saproxylic species but not for species richness. Some species may have benefited from the recent post-fire habitat to increase in abundance. This differs from a logging disturbance where, according to Niemelä et al (1993), several years are needed to allow open-habitat species to establish in high numbers.

One of the objectives of prescribed burning was to emulate the effects of low-intensity fires. The highest species richness and the exclusive presence of several saproxylic species captured at the site that burned most severely suggest that prescribed burning of higher intensity in Eastern white pine forests would favor a richer and quite different biodiversity. Attractiveness of some saproxylic species toward burned forests has also been reported to increase with fire severity and habitat opening by Sullivan et al. (2003) and Moretti and Barbalat (2004). A better access to food resources (more deadwood and fungi associated with it) and increased sun-exposure provide better conditions for reproduction of several floricolous and saproxylic species (Kouki et al. 2001; Siitonen 2001; Toivanen and Kotiaho 2007). It has also been suggested that burnings of higher intensity would help to promote Eastern white pine growth (Domaine et al. unpublished). Therefore, increasing the variability of fire intensity in future prescribed burnings or using management practices that would increase light penetration into stands by killing more mature trees could help to improve this program toward restoring the ecological integrity of Eastern white pine ecosystems.

Implications for management

Fire is a disturbance that enhances habitat heterogeneity, which, in turn, is known to be linked with biodiversity (Janssen et al. 2009). It has been reported that many saproxylic species have become rare and threatened because of efficient fire suppression policies in several European countries (Muona and Rutanen 1994; Wikars 1997; Similä et al. 2002; Hyvärinen et al. 2005; Toivanen and Kotiaho 2007). Contrary to Europe, there is no red-list of threatened or endangered insect species in Canada. In such context, it is therefore more difficult to manage rare species. However, in our study, "rare" or uncommon saproxylic species were more frequently caught in burned sites, which is important for a conservation area like LMNPC. Furthermore, we found that the higher volumes of recent deadwood generated by the prescribed burnings were significantly related to the number of "rare" species. The higher frequency of "rare" and uncommon species in burned sites resulted in higher species richness in these sites. The rarity observed in the burned areas suggests that some species might be maintained at non detectable levels in unburned forest and may benefit from the conditions generated by the burning to aggregate and reproduce, thus becoming detectable in our sampling devices. The probability of local extinction of some of these "rare" species is unknown and we cannot estimate if species may have already disappeared because we have not found historical data on beetle communities in pre-settlement Eastern white pine stands. Nevertheless, prescribed burning appears as an efficient management practice in restoring the ecological integrity of the coleopteran communities that once characterized burned Eastern white pine ecosystems.

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References

Abrams, M.D. 2001. Eastern white pine versatility in the pre-settlement forest. Bioscience 51: 967-979.

Ahnlund, H. and A. Lindhe. 1992. Hotade vedinsekter i barrskogslandskapet – nagra synpunkter utifran studier av sörmländska brandfalt, hallmarker och hyggen. Entomologisk Tidskrift 113: 13-23.

Anderson, M.J. 2006. Distance-based tests for homogeneity of multivariate dispersions. Biometrics 62: 245–253.

Anderson, M.J., K.E. Ellingsen and B.H. McArdle. 2006. Multivariate dispersion as a measure of beta diversity. Ecology letters 9: 683-693

Arnett, R.H. and M.C. Thomas. 2001. American Beetles, Volume I: Archostemata, Myxophaga, Adephaga, Polyphaga: Staphyliniformia. C.R.C. press, Washington. 859 p.

Arnett, R.H., M.C. Thomas, P.E. Skelley and J.H. Frank. 2002. American Beetles, Volume II: Polyphaga: Scarabaeoidea through Curculionoidea. C.R.C. press, Washington. 443 p.

Attiwill, P.M. 1994. The disturbance of forest ecosystems: the ecological basis for conservative management. Forest Ecology and Management 63: 247-300.

Baker, W.L. 1994. Restoration of landscape structure altered by fire suppression. Conservation Biology 8: 763-769.

Barden, L.S. and F.W. Woods. 1976. Effects of fire on pine and pine-hardwood forests in the southern Appalachians. Forest Sciences 22: 399-403.

Barrette, M. 2004. Caractérisation du paysage primitive de la region écologique ds hautes collines du Bas-Saint-Maurice pour une gestion des écosystèmes du parc national du Canada de la Mauricie. Thèse de doctorat. Université Laval, Québec. 129 p.

Boucher, T. 1952. Mauricie d'autrefois. Éditions du bien public, Trois-Rivières, Canada, Collection L'histoire régionale. No. 11.

Boulanger, Y. and L. Sirois. 2007. Postfire succession of saproxylics arthropods, with emphasis on Coleoptera, in the north boreal forest of Quebec. Environmental Entomology 36: 128-141.

Bright, D.E. 1976. The insects and arachnids of Canada Part 2: The bark beetles of Canada and Alaska, Coleoptera: Scolytidae. Biosystematics research institute, Department of agriculture Canada, Ottawa. Publication 1576.

Buddle, C., D.W. Langor, G.R. Pohl and J.R. Spence. 2006. Arthropod responses to harvesting and wildfire: Implications for emulation of natural disturbance in forest management. Biological Conservation 128: 346-357.

Burgess, D.M. and I.M. Methven. 1977. The historical interaction of fire, logging and pine: a case study at Chalk River, Ontario. Edited by Petawawa experimental forest. Canadian Forest Service. 18 p.

Canada 1992. Silvicultural terms in Canada. Science and Sustainable Development Directorate, Forestry Canada. 63 p.

Carleton, T.J., P.F. Maycock, R. Arnup and A.M. Gordon. 1996. In situ regeneration of *Pinus strobus* and *P. resinosa* in the Great Lakes forest communities of Canada. Journal of Vegetation Science 7: 431-444.

Carleton, T.J. 2003. Old growth in the Great Lakes forests. Environmental Reviews 11: 115-S134.

Dovčiak, M., L.E. Frelich, and P.B. Reich. 2001. Discordance in spatial patterns of white pine (*Pinus strobus*) size-classes in a patchy near-boreal forest. Journal of Ecology 89: 280-291.

Dryade. 1986. Etude de l'importance du rôle écologique du feu dans les parcs nationaux de la région de Québec, 145 p.

Dufrêne, M. 1998. IndVal Version 2.0. Observatoire de la faune, de la flore et des habitats, Station de recherches forestières.

Evans, W.G. 1966. Perception of infrared radiation from forest fires by *Melanophila acuminata* De Geer (Buprestidae, Coleoptera). Ecology 47: 1061–1065.

Evans, W.G. 1971. The attraction of insects to forest fires. In: Tall timbers conference on ecological animal control by habitat management, Proceedings. Tall Timbers research station, Tallahassee, 115-127.

Fayt, P., M. Dufrêne, E. Branquart, P. Hastir, C. Ponégnie, J.M. Henin and V. Versteirt. 2006. Contrasting responses of saproxylics insects to focal habitat resources: the example of longhorned beetles and hoverflies in Belgian deciduous forests. Journal of Insect Conservation 101: 129-150.

Forestry Canada Fire Danger Group. 1992. Development and structure of the canadian forest fire behavior prediction system. Ottawa, Forestry Canada, 68 p., Information Report ST-X-3F.

Forman, R.T.T. and M. Gordon. 1986. Landscape Ecology. John Wiley and Sons, New York. 640 p.

Gosselin, J. 2001. Guide de reconnaissance des types écologiques – Région écologique 3c - Hautes collines du Bas-Saint-Maurice. Ministère des ressources naturelles et de la faune du Québec. 121 p.

Fernàndez Fernàndez, M.M. and J.M Salgado Costas. 2004. Recolonization of a burnt pine forest (*Pinus pinaster*) by Carabidae (Coleoptera). European Journal of Soil Biology40: 47-53.

Granström, A. 2001. Fire management for biodiversity in the european boreal forest. Scandinavian Journal of Forest Research 3: 62-69.

Grove, S.J. 2002. Saproxylic insect ecology and the sustainable management of forests. Annual Review of Ecology, Evolution and Systematics 33: 1-23.

Haeussler, S. and D. Kneeshaw. 2003. Comparing forest management to natural processes. Pages 307-368 in P. J. Burton, C. Messier, D. W. Smith, and W. L. Adamowicz, editors. Towards Sustainable Management of the Boreal Forest. NRC Research Press.

Hansen, A.J., T.A. Spies, F.J. Swanson and J.L. Ohmann. 1991. Conserving biodiversity in managed forests: lessons from natural forests. Bioscience 41: 382-392.

Horton, K.W. and W.G.E. Brown. 1960. Ecology of white and red pine in the Great lakes-St.Lawrence forest region. Government of Canada, Technical note 88, 22 p.

Hunter, M.L. 1990. Wildlife, forests, and forestry. Principles of managing forests for biological diversity. Prentice Hall, Englewood Cliffs, NJ, 370 p.

Hyvärinen, E., J. Kouki, P. Martikainen and H. Lappalainen. 2005. Short-term effects of controlled burning and green-tree retention on beetle (Coleoptera) assemblages in managed boreal forest. Forest Ecology and Management 212: 315-332.

Jonsell, M., J. Weslien and B. Ehnström. 1998. Substrate requirements of red-listed saproxylic invertebrates in Sweden. Biodiversity and Conservation 7: 749–764.

Jonsell, M., G. Nordlander and M. Jonsson. 1999. Colonization patterns of insects breeding in wood-decaying fungi. Journal of Insect Conservation 3: 145–161.

Jonsell, M., K. Nittérus and K. Stighäll. 2004. Saproxylic beetles in natural and man-made deciduous high stumps retained for conservation. Biological Conservation 118: 163–173.

Junninen, K., J. Kouki and P. Renvall. 2008. Restoration of natural legacies of fire in European boreal forests: an experimental approach to the effects on wood-decaying fungi. Canadian Journal of Forest Research 38: 202-215.

Kouki, J., S. Löfman, P. Martikainen, S. Rouvinen and A. Uuotila. 2001. Forest fragmentation in Fennoscandia: linking habitat requirements of wood-associated threatened species to landscape and habitat changes. Scandinavian Journal of Forest Research Supplement 3: 27–37.

Lachat, T., P. Nagel, Y. Cakpo, S. Attignon, G. Georgen, B. Sinsin and R. Pevelong. 2006. Dead wood and saproxylic beetle assemblages in a semi-deciduous forest in Southern Benin. Forest Ecology and Management 225: 27-38.

Lalumière, R. and M. Thibault. 1988. Les forêts du parc national du Canada de la Mauricie au Québec, Les Presses de l'Université Laval, 495 p.

Larochelle, A. and M.C. Larivière. 2003. A natural history of the ground-beetles (Coleoptera: Carabidae) of America north of Mexico. Pensoft, Bulagaria, 583 p.

Legendre, P. and E.D. Gallagher. 2001. Ecologically meaningful transformations for ordinations of species data. Oecologia 129: 271-280.

Legendre, P. and L. Legendre. 1998. Numerical Ecology. 2nd English edition. Elsevier, Amsterdam. 853 p.

Linder, P., P. Jonsson and M. Niklasson. 1998. Tree mortality after prescribed burning in an old-growth Scots pine forest in northern Sweden. Silva Fennica 32: 339–349.

Martikainen, P. and L. Kaila. 2004. Sampling saproxylic beetles: lessons from a 10-years monitoring study. Biological Conservation 120: 171-181.

McCullough, D.G., R.A. Werner and D. Neumann. 1998. Fire and insects in northern and boreal forest ecosystems of North America, Annual Review of Entomology 43: 107-127.

McRae, D.J., T.J. Lynham, and R.J. Frech. 1994. Understory prescribed burning in red pine and white pine. The Forestry Chronicle 70: 395-401.

Methven, I.R. and W.G. Murray. 1974. Using fire to eliminate understory balsam fir in pine management. The Forestry Chronicle 50: 77-79.

Ministère des ressources naturelles du Québec. 2003. Vegetation zones and bioclimatic domains in Quebec. Gouvernement du Québec, Available online at: http://www.mrnf.gouv.qc.ca/english/publications /forest/publications/zone-a.pdf.

Mirov, N.T. and J. Hasbrouck. 1976. The story of pines. Indiana University Press, Bloomington, USA. 148 p.

Montgomery, M. E. and P. M . Wargo. 1983. Ethanol and other host-derived volatiles as attractants to beetles that bore into hardwoods. Journal of chemical ecology 9 (2): 181-190.

Moretti, M. and S. Barbalat. 2004. The effects of wildfires on wood-eating beetles in deciduous forests on the southern slopes of the Swiss Alps. Forest Ecology and Management 187: 85-103.

Muona, J. and I. Rutanen. 1994. The short-term impact of fire on the beetle fauna in boreal coniferous forest. Annales Zoologici Fennici 31: 109-121.

Niemelä, J., D.W. Langor et J.R. Spence. 1993. Effects of clear-cut harvesting on boreal ground-beetle assemblages (Coleoptera: Carabidae) in western Canada. Conservation Biology 7: 551-562.

Niwa, C. and R.W. Peck. 2002. Influence of prescribed fire on carabid beetle (Carabidae) and spider (Araneae) assemblages in forest litter in southwestern Oregon. Community and Ecosystem Ecology 31: 785-796.

Økland, B., A. Bakke, S. Hagvar and K. Torstein. 1996. What factors influence the diversity of saproxylic beetles? A multiscaled study from a spruce forest in southern Norway. Biodiversity and Conservation 5: 75-100.

Ontario Ministry of Natural Resources. 2009. Ecology and management of eastern white pine in the Lake Abitibi (3E) and Lake Temagami (4E) ecoregions of Ontario. Ontario Ministry of Natural Resources. Sault Ste. Marie, Canada. 79 p.

Pedlar, J.H., J.L. Pearce, L.A. Venier and D.W. McKenney. 2002. Coarse woody debris in relation to disturbance and forest type in boreal Canada. Forest Ecology and Management 158: 189–194.

Pelletier, H. 1998. Plan de conservation des écosystèmes terrestres. Parcs Canada, Parc National du Canada de la Mauricie, Service de la conservation des ressources naturelles, Shawinigan, Canada. 320 p.

Quenneville, R. and M. Thériault. 1998. Cadre pour la restauration écologique du pin blanc au parc national de la Mauricie. Parcs Canada, Service de la conservation des ressources naturelles, Shawinigan, Canada. 39p.

Quenneville, R. and M. Thériault. 2002. Plan de gestion du feu: Parcs Canada, Parc National du Canada de la Mauricie. Service de la conservation et des écosystèmes, Shawinigan, Canada. 19 p.

R Development Core Team. 2008. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL http://www.R-project.org.

Saint-Germain, M., P. Drapeau and C. Hébert. 2004. Comparison of Coleoptera assemblages from a recently burned and unburned black spruce forests of northeastern North America. Biological Conservation 118: 583-592.

SAS Institute Inc. 2000. SAS for Windows: Version 9.1. SAS Institute Inc., Cary, North Carolina. # de pages

Schroeder, L.M. 1988. Attraction of the bark beetle *Tomicus piniperda* and some other bark and wood-living beetles to the host volatiles α-pinene and ethanol. Entomologia Experimentalis et Applicata 46: 203-210.

Siitonen, J. 2001. Forest management, coarse woody debris and saproxylic organisms: Fennoscandian boreal forests as an example. Ecological Bulletin 49: 11-41.

Simberloff, D. 2001. Management of boreal forest biodiversity: a view from the outside. Scandinavian Journal of Forest Research 16: 105-118.

Similä, M., J. Kouki, P. Martikainen and A. Uotila. 2002. Conservation of beetles in boreal pine forests: the effects of forest age and naturalness on species assemblages. Biological Conservation 106: 19-27.

Speight, M.C.D. 1989. Saproxylic Invertebrates and their Conservation. Council of Europe, Strasbourg, France. 82 p.

Sullivan, B.T., C.J. Fettig, W.J. Otrosina, M.J. Dalusky and C.W. Berisford. 2003. Association between severity of prescribed burns and subsequent activity of conifer-infesting beetles in stands of longleaf pine. Forest Ecology and Management 185: 327-340.

The Saproxylic Database. 2009. The Saproxylic Database : Biodiversity in dead wood. Wordpress, Available online at: http://www.saproxylic.org.

Toivanen, T. and J.S. Kotiaho. 2007. Mimicking natural disturbances of boreal forests: the effects of controlled burning and creating dead wood on beetle diversity. Biodiversity and Conservation 16: 3193-3211.

Tyrrell, L.E. and T.R. Crow. 1994. Structural characteristics of old-growth hemlock-hardwood forests in relation to age. Ecology 75: 370-386.

Valcourt, J. and R. Gagnon. 2000. Caractérisation des pinèdes du lac Anticagamac, Parc national de la Mauricie. Laboratoire d'écologie végétale, Université du Québec à Chicoutimi. 46 p.

Van Wagner, C.E. 1968. The line intersect method in forest fuel sampling. Forest Science 14: 20-26.

Vandervel, M.C., J.R. Malcolm, S.M. Smith and N. Islam. 2006. Insect community composition and trophic guild structure in decaying logs from eastern canadian pine-dominated forests. Forest Ecology and Management 225: 190-199.

Vlasiu, P.D., P. Nolet and F. Doyon. 2001. Le pin blanc : Revue de littérature. Institut québécois d'aménagement de la forêt feuillue, Ripon, Canada. 91 p.

Wermelinger, B, P. Duelli and M.K. Obrist. 2002. Dynamics of saproxylic beetles (Coleoptera) in windthrow areas in alpine spruce forests. Forest Snow and Landscape Research 77: 133-138.

Weyenberg, S.A., L.E. Frelich and P.B. Reich. 2004. Logging versus fire: How does disturbance type influence the abundance of *Pinus strobus* regeneration? Silvia Fennica 38: 179-194.

Whittaker, R. H. 1972. Evolution and measurement of species diversity. Taxon 21: 213–251.

Wikars, L.-O. 1992. Forest fires and insects (in Swedish). Entomologisk Tidskrif 113: 1-11.

Wikars, L.-O. 1997. Effects of forest fire and the ecology of fire-adaptated insects. Doctoral thesis, Uppsala University, Department of zoology, 35p.

Wikars, L.-O. 2002. Dependance on fire in wood-living insects: An experiment with burned and unburned spruce and birch logs. Journal of Insect Conservation 6: 1-12.

Yanega, D. 1996. Field guide to northeastern longhorned beetles (Coleoptera: Cerambycidae). Illinois natural history survey manual, 184p.

Zackrisson, O. 1977. Influence of forest fires on the north Swedish boreal forest. Oikos 29: 13–32.

Ziegler, S.S. 1995. Relict eastern white pine (*Pinus strobus* L.) stands in southwestern Wisconsin. American Midland Naturalist 133: 88-100.

Table 2-1: Description of the 16 study sites at LMNPC.

			Soil - Topography					Cover (%)				Trees (alive)		Saplings (alive)	
Site	Year of burning	Class of intensity	Depot	Drainage	Humus (cm.)	Alt. (m.)	Slope (%)	Moss	Herb	Shrub	Fern	Density (Stem/ha)	BA (m^2/ha)	Density (Stem/ha)	BA (m^2/ha)
Burn 2005	2005	3	Fluvio-glacial	Good	2.7	242	4	20.0	8.9	21.3	6.4	383	14,56	1766	1,77
Burn 2004	2004	3	Fluvio-glacial	Rapid	4.3	245	2	16.7	9.0	26.3	8.5	550	17.63	833	0,98
Burn 2003	2003	3	Till	Good	3.7	341	41	9.6	8.7	0.0	10.9	383	23.78	1233	2.07
Burn 2001	2001	3	Fluvio-glacial	Rapid	5.3	286	26	10.4	6.9	5.0	8.6	775	37.55	1167	1.52
Burn 1999	1999	4	Fluvio-glacial	Rapid	6.7	217	5	8.8	7.2	10.0	7.9	300	30.93	0	0.00
Burn 1997	1997	2	Fluvio-glacial	Rapid	7.3	250	4	37.9	7.2	5.0	10.6	683	34.70	2967	4,93
Burn 1995	1995	2	Fluvio-glacial	Good	6.7	262	1	35.4	6.7	11.3	10.4	700	31.43	2233	3.11
Control 1	-	-	Fluvio-glacial	Rapid	6.0	259	5	49.6	8.7	12.5	17.1	833	29.39	3033	4.46
Control 2	-	-	Fluvio-glacial	Rapid	9.0	314	38	19.2	5.5	8.3	9.6	775	35.92	2900	2.95
Control 3	-	-	Till	Good	9.3	303	47	18.6	6.3	0.0	7.3	966	41.00	2267	1.63
Control 4	-	-	Fluvio-glacial	Rapid	6.7	220	1	75.0	5.3	6.8	6.3	725	20.89	3133	7.82
Control 5	-	-	Till	Good	6.7	277	46	18.3	5.4	0.0	5.0	950	40.60	1433	1.08
Control 6	-	-	Fluvio-glacial	Rapid	5.3	249	9	21.3	5.4	5.0	15.6	1075	37.89	1200	2.27
Control 7	-	-	Till	Good	4.3	264	16	15.0	5.7	5.0	7.1	1075	28.59	3333	5.97
Control 8	-	-	Till	Good	5.7	259	18	25.0	5.4	5.0	6.2	876	23.52	3967	5.43
Control 9	-	-	Fluvio-glacial	Rapid	9.3	239	9	24.2	5.8	5.7	7.5	651	36.56	2867	4.03

Table 2-2: T-tests results of coleopteran abundance, richness and rarity for each abundant family (n > 250 individuals)., non-saproxylics, saproxylics and total species richness.

Family	Number of individuals			Number of species			Number of "rare" species		
	Burned	Unburned	p	Burned	Unburned	p	Burned	Unburned	p
Carabidae	217.3 ± 24.4	274.2 ± 66.4	0.6714	10.4 ± 0.9	9.6 ± 0.7	0.4950	**1.6 ± 0.6**	**0.3 ± 0.2**	**0.0316**
Cerambycidae	26.1 ± 6.0	18.8 ± 5.3	0.3712	**9.1 ± 1.8**	**4.6 ± 0.4**	**0.0160**	**2.6 ± 0.6**	**1.0 ± 0.2**	**0.0283**
Curculionidae	277.9 ± 46.8	180.8 ± 63.5	0.2513	**15.1 ± 1.3**	**9.3 ± 1.2**	**0.0066**	**2.3 ± 0.4**	**0.9 ± 0.4**	**0.0150**
Elateridae	49.9 ± 20.0	25.5 ± 2.8	0.2717	12.5 ± 1.4	9.9 ± 0.7	0.1056	**2.4 ± 0.5**	**1.0 ± 0.3**	**0.0343**
Lathridiidae	**45.4 ± 5.6**	**13.5 ± 2.3**	**<0.0001**	-	-	-	-	-	-
Nitidulidae	181.0 ± 36.7	94.6 ± 22.2	0.0589	**8.4 ± 0.9**	**6.1 ± 0.4**	**0.0129**	0.9 ± 0.6	0.3 ± 0.2	0.3236
Saproxylic	**723.9 ± 93.5**	**410.5 ± 76.4**	**0.0224**	**84.6 ± 6.0**	**57.0 ± 3.5**	**0.0012**	**13.6 ± 2.9**	**5.9 ± 0.8**	**0.0127**
Non-Saproxylic	261.1 ± 21.6	293.6 ± 65.8	0.9809	**29.3 ± 2.0**	**20.1 ± 0.7**	**0.0004**	**8.3 ± 1.3**	**4.0 ± 0.7**	**0.0116**
Total	**985.0 ± 91.4**	**679.1 ± 89.3**	**0.0330**	**114.1 ± 6.6**	**77.1 ± 4.0**	**0.0003**	**21.6 ± 3.8**	**9.9 ± 1.2**	**0.0050**

Table 2-3: Table of contingency using overall number of species categorized by classes of abundance. Predicted number of species having or not an habitat predilection are listed at the bottom of the table.

Frequency	**Class of abundance**		**Habitat of predilection** (number of species)			**X^2**	**p**
			Burned	**Unburned**	**None**		
Observed	Rare	1 to 3	93	41	28	**78.80**	**< 0.0001**
	Uncommon	4 to 20	49	4	41		
	Common	21 to 100	10	1	33		
	Abundant	100 and +	3	0	15		
Predicted	Rare	1 to 3	84	25	53		
	Uncommon	4 to 20	49	14	31		
	Common	21 to 100	23	6	15		
	Abundant	100 and +	9	3	6		

Table 2-4: Indicator value analysis results for all species sampled (n ≥ 10 individuals at 1st and 2nd steps; n ≥ 5 individuals at 3rd step). Only species that have an IndVal > 55% were listed.

Species	IndVal	Burned sites							Unburned sites							
		Recent		Mid-aged			Old		Slope >25%			Slope < 10%				
		2005	2004	2003	2001	1999	1997	1995	2	3	5	1	4	6	7	8
All habitats (A + B + C + D+E)																
Ubiquitous species	-							-								
Burned sites (A + B+C)																
Corticarina sp. (Sapro)	92.42				64. / 7							6. / 5				
Corticaria sp. (Sapro)	88.22				59. / 7							9. / 4				
Epuraea truncatella (Sapro)	85.65				47. / 7							9. / 7				
Triplax thoracica (Sapro)	85.60				26. / 7							5. / 4				
Silvanus bidentatus (Sapro)	82.93				102. / 7							24. / 7				
Hylobius congener (Sapro)	79.80				899. / 7							260. / 8				
Melanophtalma sp. (Sapro)	77.42				135. / 7							45. / 8				
Ptiliolum sp. (Sapro)	75.11				31. / 6							5. / 2				
Atomaria sp. (Sapro)	75.06				79. / 7							30. / 6				
Agriotes stabilis (Sapro)	74.07				80. / 7							32. / 6				
Rhaghonycha fraxini (Non-Sapro)	73.72				27. / 7							11. / 5				
Leiodes sp. (Non-Sapro)	71.76				18. / 6							4. / 4				
Acmaeops p. proteus (Sapro)	71.43				18. / 5							0. / 0				
Glischrochilus s. sanguilonentus (Sapro)	70.69				595. / 7							282. / 8				
Cerylon castaneus (Sapro)	63.16				93. / 7							62. / 8				
Dryophtorus americanus (Sapro)	57.14				15. / 4							0. / 0				
Unburned sites (D + E)																
No significant species	-				-							-				
Recent burns (A) (04-05)																
Notiophilus aeneus (Non-Sapro)	100.00	15. / 2			0. / 0		0. / 0			0. / 0				1. / 1		
Monochamus s. scutellatus (Sapro)	97.40	5. / 2			1. / 1		0. / 0			0. / 0				0. / 0		
Colon sp. (Non-Sapro)	88.24	7. / 2			2. / 1		0. / 0			0. / 0				0. / 0		
Syntomus americanus (Non-Sapro)	83.33	11. / 2			0. / 0		3. / 1			0. / 0				0. / 0		
Agonum retractum (Non-Sapro)	78.57	23. / 2			4. / 2		1. / 1			4. / 1				10. / 4		

Geotrupes hornii (Non-Sapro)	69.00	4. / 2	0. / 0	2. / 1	0. / 0	0. / 0
Mid-aged burns (B) (99-01-03)						
Rhizophagus brunneus (Sapro)	100.00	0. / 0	5. / 3	0. / 0	0. / 0	0. / 0
Dendroctonus valens (Sapro)	76.19	1. / 1	8. / 3	0. / 0	1. / 1	0. / 0
Crypturgus borealis (Sapro)	72.73	1. / 1	4. / 3	0. / 0	0. / 0	0. / 0
Hylastes opacus (Sapro)	70.97	0. / 0	11. / 3	1. / 1	3. / 1	0. / 0
Old burns (C) (95-97)						
No significant species	-	-	-	-	-	-
Controls slope > 25% (D)						
No significant species	-	-	-	-	-	-
Controls slope < 10% (E)						
No significant species	-	-	-	-	-	-

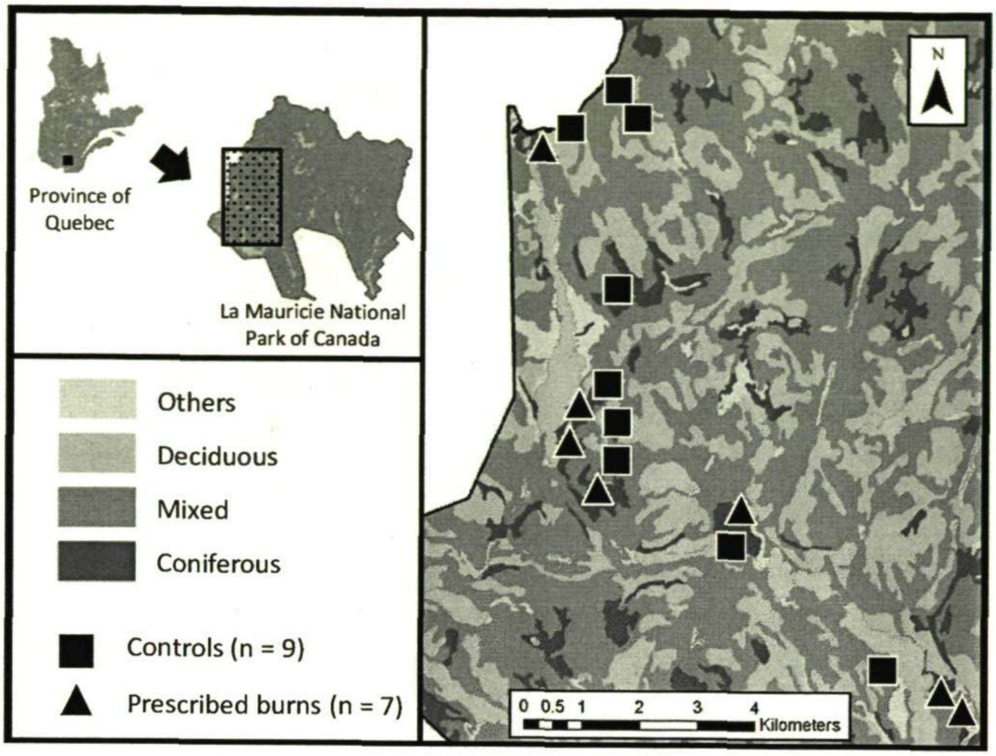


Figure 2-1: Location of the study sites in La Mauricie National Park of Canada.

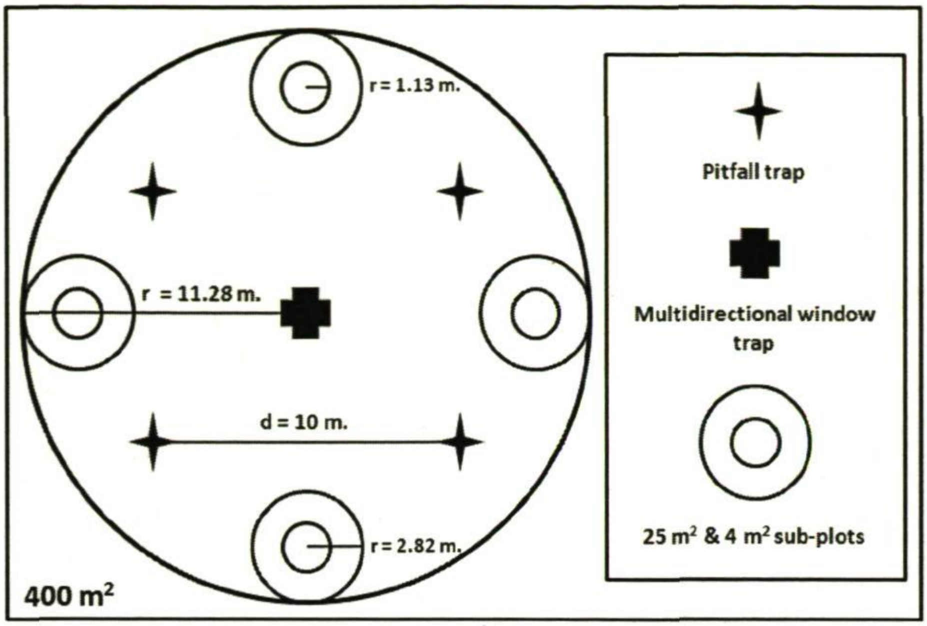


Figure 2-2: Sampling plot, sub-plots and sub-sub-plots used for the study.

Figure 2-3: Left, the pitfall trap. Right, the multidirectional flight-interception trap.

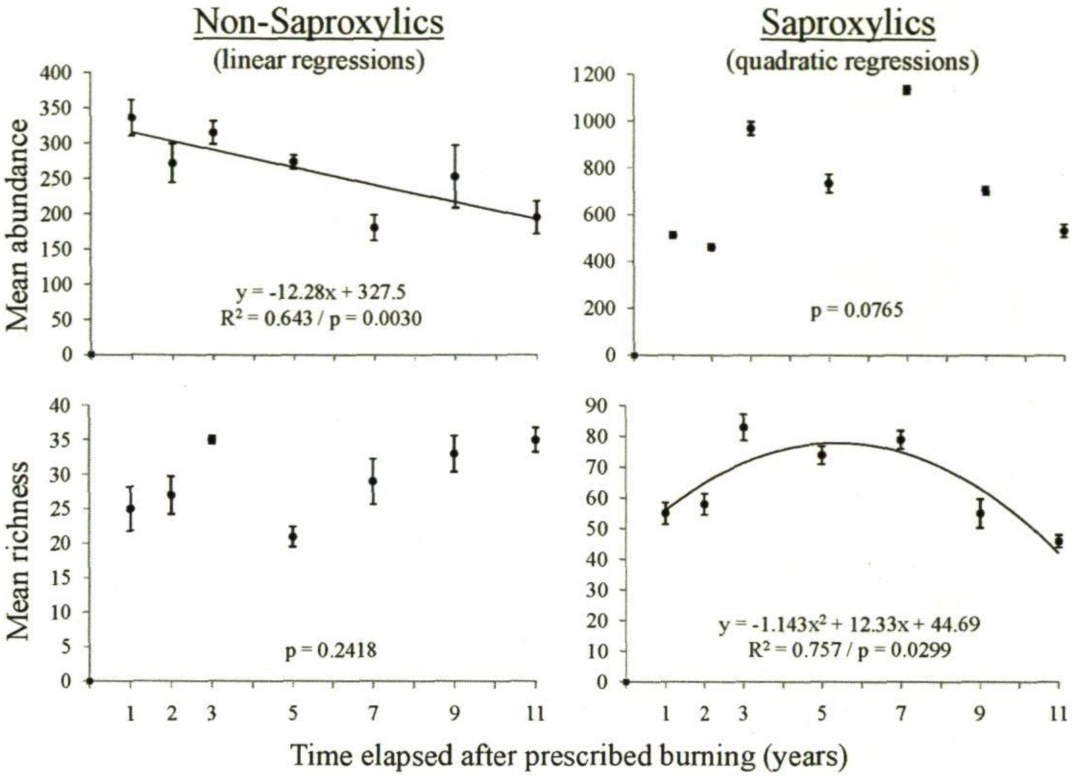


Figure 2-4: Linear (non-saproxylic) and quadratic (saproxylic) showing the relationships between the time since treatment and the mean abundance and the mean specie richness (± SE).

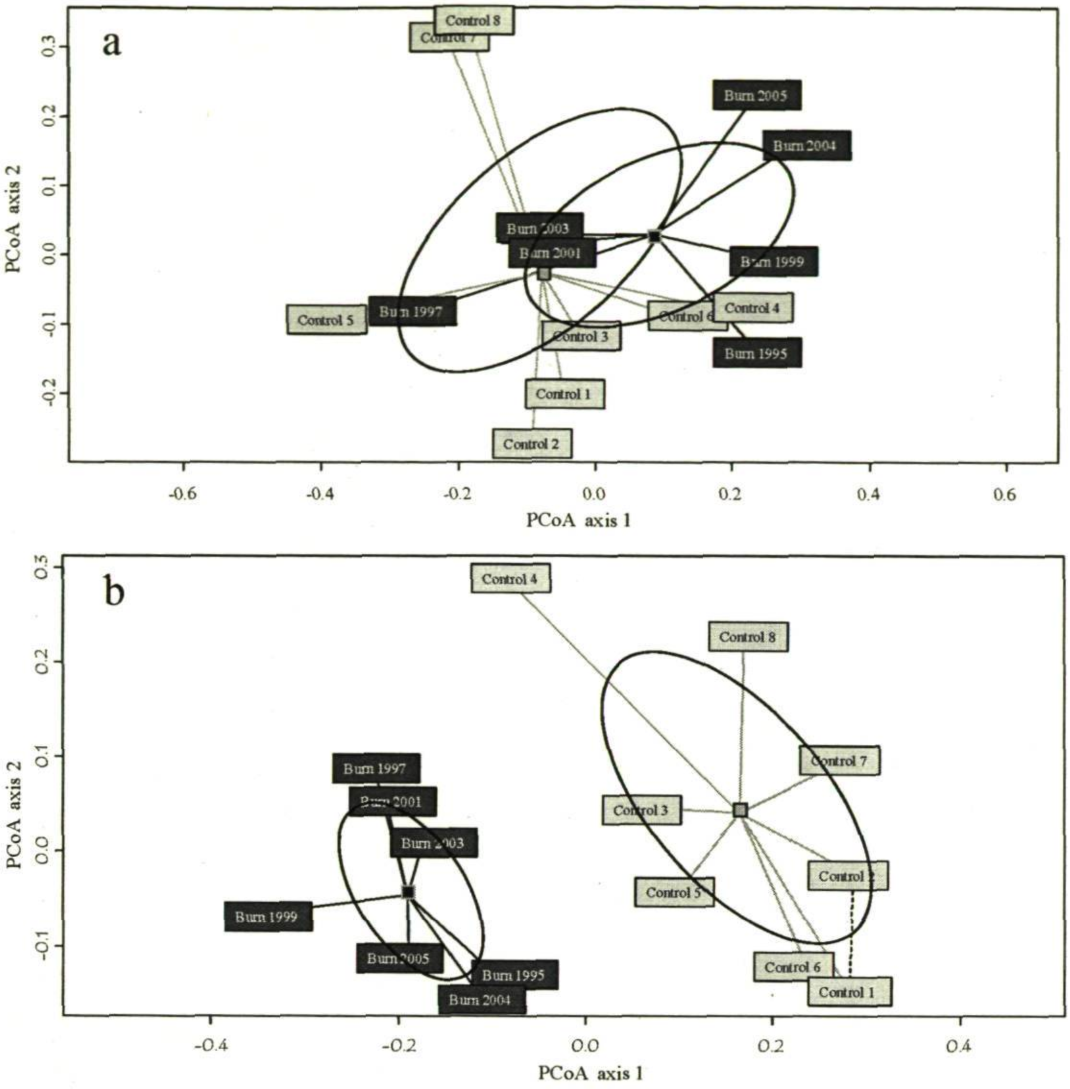


Figure 2-5: Ordination plot (a = non-saproxylic species; b = saproxylic species) of the first two axes of a principal coordinate analysis (PCoA) using the functional dissimilarity matrix for the burned and unburned forests analyzed. Ellipses are 95% confidence intervals (S.E.) around centroids

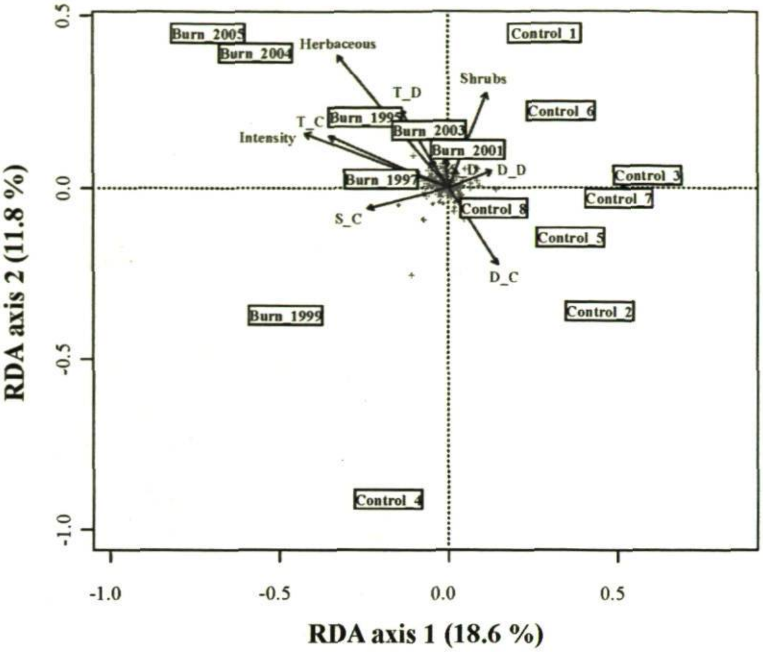


Figure 2-6: RDA (scaling 2) of saproxylic species assemblages. Environmental matrix was composed of 10 variables. Variables concerning the volume of young deadwood are described using acronyms. First letter described types of tree: D=downed woody debris, T=trees, S=saplings.

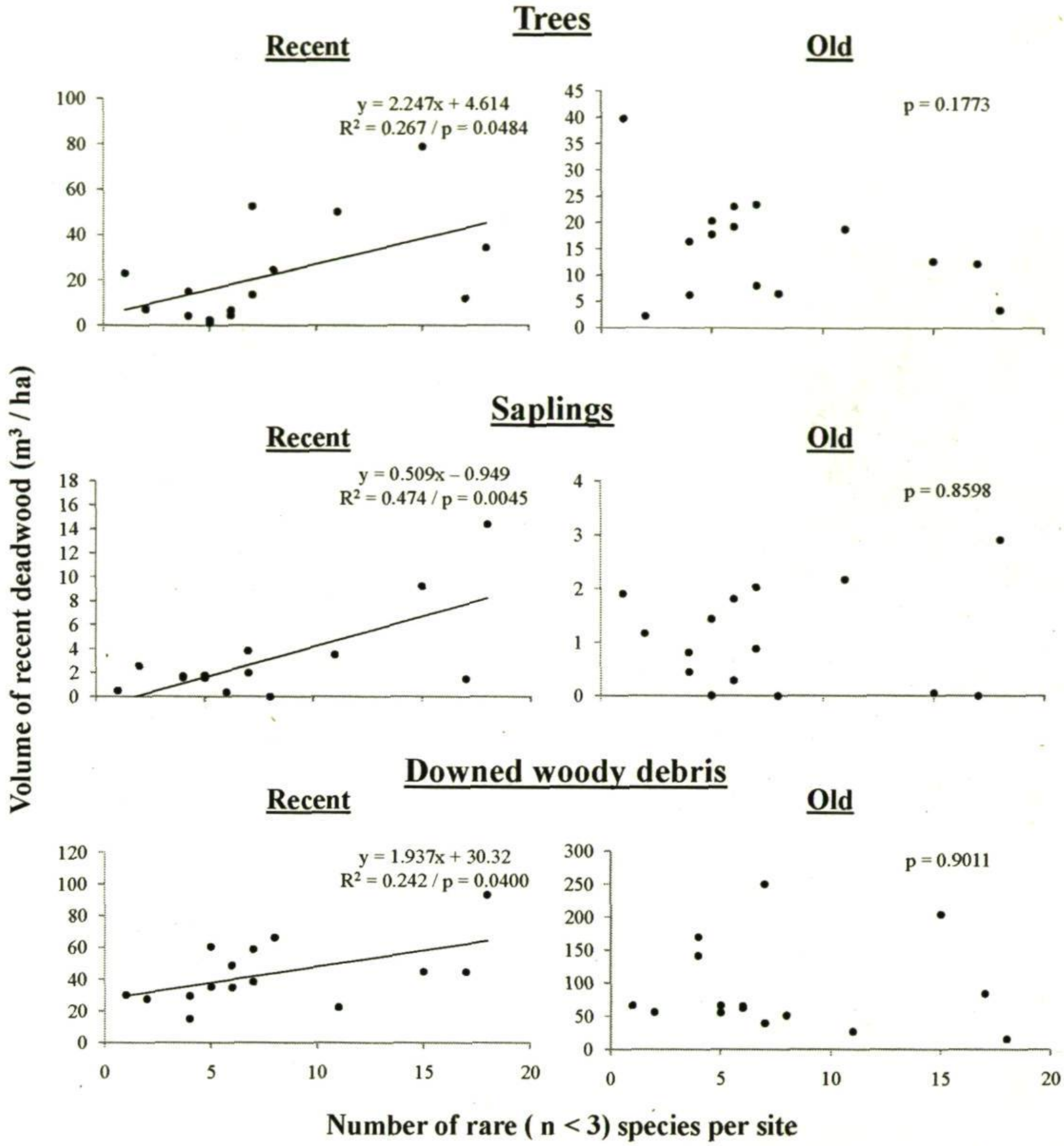


Figure 2-7: Relationships between the number of "rare" species (n min < 3) and the volume of recent (at left) and old (at right) deadwood for trees, saplings and downed woody debris.

Conclusion

La structure forestière et l'intégrité écologique des peuplements contenant du pin blanc au PNCLM a été altérée dans le passé par les coupes forestières et la suppression des incendies forestiers. A l'intérieur des sites étudiés, on retrouve de nombreuses souches de pins démontrant l'importante activité forestière passée sur ce territoire. De plus, la réduction des feux de forêt a permis au sapin baumier de dominer les communautés de sous-étage tant au niveau des semis que des gaules. Dans ces peuplements, on observe très peu de semis de pin blanc de plus de 25 cm de hauteur et les gaules de cette espèce sont quasiment absentes. En utilisant le brûlage dirigé de faible intensité comme moyen de gestion active, les gestionnaires de Parcs Canada avaient pour objectifs (1) d'améliorer les conditions de germination des graines de pin blanc, (2) d'augmenter la représentativité des semis de PIB à court terme dans les sites brûlés, (3) d'augmenter la représentativité des gaules de PIB à moyen terme dans les sites brûlés et (4) de diminuer la compétition pour la lumière faite aux semis de pin blanc par le sapin baumier. Dans les sites traités, la densité des semis de pin blanc était significativement plus élevée qu'à l'intérieur des sites non-brûlés. Le brûlage dirigé a permis d'augmenter le nombre de semis jusqu'à 21 000 / ha comparativement à une moyenne de 5 135 / ha dans les sites non-brûlés. La mortalité du sapin baumier a atteint presque 70% pour les gaules et 40% pour les arbres. Les objectifs fixés par Parcs Canada ont donc été atteints. Cependant, dans les sites brûlés les conditions de croissance des semis de pin blanc ne sont pas optimales, les plus grands semis atteignant rarement 50 cm de hauteur dans le site brûlé il y a 11 ans. Le brûlage dirigé de plus forte intensité semble être un moyen efficace de se davantage rapprocher des objectifs fixés. Dans le futur, il sera impératif de trouver des solutions innovatrices pour permettre aux jeunes semis de croître et éventuellement atteindre le stade de gaule.

Les objectifs fixés par Parcs Canada concernant la restauration des peuplements de pin blanc au PNCLM touchaient purement la structure et la composition forestière. Cependant, comme la définition de l'intégrité écologique inclue également l'ensemble des communautés animales, les coléoptères, l'ordre d'insectes le plus diversifié actuellement connu sur la planète, ont aussi été étudiés en tant que groupe animal indicateur. Les analyses portant sur l'abondance, la richesse et la rareté des coléoptères démontrent que les communautés des sites brûlés et témoins diffèrent. Ainsi, les assemblages de coléoptères des peuplements non-brûlés possèdent moins d'espèces saproxyliques que les sites brûlés. L'analyse de redondance des espèces saproxyliques a démontré des relations fortes entre plusieurs espèces saproxyliques et le bois mort sur pied récemment rendu disponible par le brûlage dirigé. Un total de 107 espèces a été capturé uniquement dans les sites brûlés comparativement à 45 dans les sites non-brûlés. La richesse spécifique et la rareté des espèces non-saproxyliques et saproxyliques a été plus élevée dans les sites brûlés. L'abondance des coléoptères non-saproxyliques diminue au fur et à mesure qu'augmente le temps depuis le traitement. La richesse spécifique et l'abondance des espèces saproxyliques a été maximale entre trois et sept ans après le traitement. Cependant, même si le nombre d'espèces dans les plus vieux brûlages ressemble sensiblement à la moyenne des sites non-brûlés, leurs assemblages d'espèces sont toujours distincts laissant entrevoir une trajectoire écologique différente des sites non-brûlés dans le futur. Dans un contexte de suppression des feux, les brûlages dirigés semblent donc générer des conditions propices pour certains insectes favorisés par ce genre perturbation. Le site brûlé le plus sévèrement, là où plusieurs arbres matures sont morts, possède des communautés de coléoptères différentes et souvent plus riches que celles des autres sites brûlés.

Le PNCLM semble atteindre ses objectifs immédiats de restauration d'un écosystème en déclin sur son territoire et se rapproche également de l'objectif de restauration de l'intégrité écologique de cet écosystème en favorisant plusieurs éléments de sa biodiversité et en réintroduisant une perturbation jadis importante dans les forêts de pin blanc. Cependant, comme il n'existe aucun peuplement d'origine de pin blanc, il est difficile de déterminer comment se structuraient les communautés végétales et animales qui prévalaient autrefois. En effet, il est difficile de caractériser les communautés historiques de coléoptères car aucune étude portant sur ce sujet n'est disponible pour la période pré-coloniale. Cependant, la capture de plusieurs espèces saproxyliques uniquement dans les sites brûlés démontre le caractère unique des habitats brûlés. Ainsi, les brûlages dirigés constituent de bons outils pour émuler les effets naturels du feu tant sur le plan de la structure végétale que des communautés de coléoptères.

Bibliographie

Abrams, M.D. 2001. Eastern white pine versatility in the pre-settlement forest. Bioscience 51: 967-979.

Attiwill, P.M. 1994. The disturbance of forest ecosystems: the ecological basis for conservative management. Forest Ecology and Management 63: 247-300.

Backer, D.M., S.E. Jensen et G.R. McPherson. 2004. Impacts of fire-suppression activities on natural communities. Conservation Biology 18: 937-946.

Baker, W.L. 1992. Effects of settlement and fire suppression on landscape structure. Ecology 73: 1879-1887.

Baker, W.L. 1994. Restoration of landscape structure altered by fire suppression. Conservation Biology 8: 763-769.

Barden, L.S. et F.W. Woods. 1976. Effects of fire on pine and pine-hardwood forests in the southern Appalachians. Forest Sciences 22: 399-403.

Barrette, M. 2004. Caractérisation du paysage primitive de la region écologique ds hautes collines du Bas-Saint-Maurice pour une gestion des écosystèmes du parc national du Canada de la Mauricie. Thèse de doctorat. Université Laval, Québec. 129 p.

Bergeron, Y., S. Gauthier, V. Kafka, P. Lefort et D. Lesieur. 2001. Natural fire frequency for the eastern Canadian boreal forest: consequences for sustainable forestry. Canadian Journal of Forest Research 31: 384-391.

Bonnicksen, T.M. et E.C. Stone. 1985. Restoring naturalness to National Parks. Environmental Management 9: 479-486.

Brown, R.T., J.K. Agee et J.F. Franklin. 2004. Forest restoration and fire: principles in the context of place. Conservation Biology 18: 903-912.

Buddle, C.M., D.W. Langor, G.R. Pohl et J.R. Spence. 2006. Arthropod responses to harvesting and wildfire: Implications for emulation of natural disturbance in forest management. Biological Conservation 128: 346-357.

Burgess, D.M., et I.R. Methven. 1977. The historical interaction of fire, logging and pine: a case study at Chalk River, Ontario. Edited by Station d'expérimentation forestière de Petawawa. Service canadien des forêts. 18 p.

Carleton, T.J., P.F. Maycock, R. Arnup, et A.M. Gordon. 1996. In Situ regeneration of *Pinus strobus* and *P. resinosa* in the Great Lakes forest communities of Canada. Journal of Vegetation Science 7: 431-444.

Carleton, T.J. 2003. Old growth in the Great Lakes forest. Environmental Reviews 11: 115-134.

Carlton, W.R. 1939. New England masts and the king's navy. The New England Quarterly 12: 4-18.

Conseil Canadien des Parcs. 2007. Principes et lignes directrices pour la restauration écologique dans les aires naturelles protégées du Canada, Ébauche pour approbation ministérielle, Approuvée par le ministère des parcs le 11 septembre 2007. Gouvernement du Canada. 74 p.

Davis, M.B. 1996. Eastern old-growth forests. Edited by Mary Byrd Davis. Foreword by John Davis. Island Press, Washington. 383 p.

Day, G.M. 1953. The indian as an ecological factor in the northeastern forest. Ecology 34: 329-346.

Département de Justice du Canada. 2000. Canada National Parks Act (2000, c. 32) Ottawa, Canada. Accessible en ligne à:http://laws.justice.gc.ca/en/N-14.01/index.html.

Dovčiak, M., L.E. Frelich et P.B. Reich. 2001. Discordance in spatial patterns of white pine (*Pinus strobus*) size-classes in a patchy near-boreal forest. Journal of Ecology 89: 280-291.

Dryade, Le Groupe. 1986. Étude de l'importance du rôle écologique du feu dans les parcs nationaux de la région de Québec. 145 p.

Elliott, K.J., J.M. Vose et B.D. Clinton. 2002. Growth of eastern white pine (*Pinus strobus* L.) related to forest floor consumption by prescribed fire in the southern Appalachians. Southern Journal of Applied Forestry 26: 18-25.

Evans, W.G. 1966. Perception of infrared radiation from forest fires by *Melanophila acuminata* de Geer (Buprestidae, Coleoptera). Ecology 47: 1061-1065.

Farrar, J.L. 1995. Les arbres du Canada, Service canadien des forêts, Ressources Naturelles Canada. Les éditions Fides, 502 p.

Forman, R.T.T. et M. Gordon. 1986. Landscape Ecology. John Wiley and Sons, New York.

Frelich, L.E. 1995. Old forest in the Lake States today and before European settlement, Natural Areas Journal 15: 157-167.

Granström, A. 2001. Fire management for biodiversity in the european boreal forest. Scandinavian Journal of Forest Research 3: 62-69.

Haeussler, S. et D. Kneeshaw. 2003. Comparing forest management to natural processes. Pages 307-368 in P. J. Burton, C. Messier, D. W. Smith, et W. L. Adamowicz, editors. Towards Sustainable Management of the Boreal Forest. NRC Research Press.

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

Horton, K.W. et W.G.E. Brown. 1960. Ecology of white and red pine in the Great lakes-St.Lawrence forest region, Government of Canada, Environment Canada, Note Technique No. 88: 22 p.

Hyvärinen, E., J. Kouki, P. Martikainen et H. Lappalainen. 2005. Short-term effects of controlled burning and green-tree retention on beetle (Coleoptera) assemblages in managed boreal forest. Forest Ecology and Management 212: 315-332.

Jonsell, M., J. Weslien et B. Ehnström. 1998. Substrate requirements of red-listed saproxylic invertebrates in Sweden. Biodiversity and Conservation 7: 749–764.

Jonsell, M., G. Nordlander et M. Jonsson. 1999. Colonization patterns of insects breeding in wood-decaying fungi. Journal of Insect Conservation 3: 145–161.

Jonsell, M., K. Nittérus et K. Stighäll. 2004. Saproxylic beetles in natural and man-made deciduous high stumps retained for conservation. Biological Conservation 118: 163–173.

Junninen, K., J. Kouki et P. Renvall. 2008. Restoration of natural legacies of fire in European boreal forests: an experimental approach to the effects on wood-decaying fungi. Canadian Journal of Forest Research 38: 202-215.

Kouki, J., S. Löfman, P. Martikainen, S. Rouvinen et A. Uuotila. 2001. Forest fragmentation in Fennoscandia: linking habitat requirements of wood-associated threatened species to landscape and habitat changes. Scandinavian Journal of Forest Research 3: 27–37.

Linder, P., P. Jonsson and M. Niklasson. 1998. Tree mortality after prescribed burning in an old-growth Scots pine forest in northern Sweden. Silva Fennica 32: 339–349.

Lorimer, C.G. 2008. Eastern white pine abundance in 19th century forests: A re-examination of evidence from land surveys and lumber statistics. Journal of Forestry 106: 253-260.

Louck, O.L. 1970. Evolution of diversity, efficiency, and community stability. American Zoologist 10: 17-25.

Maissurow, D.K. 1935. Fire as a necessary factor in the perpetuation of white pine. Journal of Forestry 33: 373-378.

Martikainen P., J. Siitonen, P. Puntilla, L. Kaila et J. Rauch. 2000. Species richness of Coleoptera in mature managed and old-growth boreal forests in southern Finland. Biological Conservation 94: 199-209.

McCullough, D.G., R.A. Werner et D. Neumann 1998. Fire and insects in northern and boreal forest ecosystems of North America. Annual Review of Entomology 43: 107-127.

McRae, D.J., T.J. Lynham et R.J. Frech. 1994. Understory prescribed burning in red pine and white pine. The Forestry Chronicle 70: 395-401.

Methven, I.R. et W.G. Murray. 1974. Using fire to eliminate understory balsam fir in pine management. The Forestry Chronicle 50: 77-79.

Mirov, N. T. et J. Hasbrouck. 1976. The story of pines. Indiana university press, Bloomington, London. 148 p.

Muona, J. et I. Rutanen. 1994. The short-term impact of fire on the beetle fauna in boreal coniferous forest. Annales Zoologici Fennici 31: 109-121.

Naylor, B.J. 1994. Managing wildlife habitat in red pine and white pine forests of central Ontario. The Forestry Chronicle 70: 411-419.

Niemelä, J., D.W. Langor et J.R. Spence. 1993. Effects of clear-cut harvesting on boreal ground-beetle assemblages (Coleoptera: Carabidae) in western Canada. Conservation Biology 7: 551-562.

Niwa, C. et R.W. Peck. 2002. Influence of prescribed fire on carabid beetle (Carabidae) and spider (Araneae) assemblages in forest litter in southwestern Oregon. Community and Ecosystem Ecology 31: 785-796.

Økland, B., A. Bakke, S. Hagvar et K. Torstein. 1996. What factors influence the diversity of saproxylic beetles? A multiscaled study from a spruce forest in southern Norway. Biodiversity and Conservation 5: 75–100.

Östlund, L., O. Zackrisson et A.L. Axelsson. 1997. The history and transformation of a Scandinavian boreal forest since the 19th century. Canadian Journal of Forestry 27: 1198-1206.

Palik, B.J., et K.S. Pregitzer. 1994. White pine seed-tree legacies in an aspen landscape: influences on post-disturbance white pine population structure. Forest Ecology and Management 67: 191-201.

Partel, M., R. Kalamees, U. Reier, E.L. Tuvi, E. Roosaluste, A. Vellak et M. Zobel. 2005. Grouping and prioritization of vascular plant species for conservation:

combining natural rarity and management need. Biological Conservation 123: 271–278.

Peattie, D.C. 1966. A natural history of trees of eastern and central North America. Houghton Mifflin Co. Boston. 606 p.

Pelletier, H. 1998. Plan de conservation des écosystèmes terrestres, Parc national de la Mauricie, Service de la conservation des ressources naturelles, Parcs Canada. 320 p.

Quenneville, R. et M. Thériault. 1998. Cadre pour la restauration écologique du pin blanc au parc national de la Mauricie. Service de la conservation des écosystèmes, 37 p.

Reich, P.B., P. Bakken, D. Carlson, L.E. Frelich, S.K. Friedman et D.F. Grigal. 2001. Influence of logging, fire, and forest type on biodiversity and productivity in southern boreal forests. Ecology 82: 2731-2748.

Richard, P. 1975. La vulgarisation des travaux paléobiogéographiques effectués dans le parc national de la Mauricie (Rapport final). Service de la recherche en analyse pollinique, Université du Québec à Chicoutimi, Chicoutimi, Canada. 132 p.

Sargent, C.S. 1947. The silva of North America: a description of the trees which grow naturally in North America exclusive of Mexico. Volume XI (Coniferae), Peter Smith. New York. 163 p.

Siitonen, J. 2001. Forest management, coarse woody debris and saproxylic organisms: Fennoscandian boreal forests as an example. Ecological Bulletins 49: 11–41.

Simberloff, D. 2001. Management of boreal forest biodiversity: a view from the outside. Scandinavian Journal of Forest Research 16: 105-118.

Similä, M., J. Kouki, A. Martikainen et A. Uotila. 2002. Conservation of beetles in boreal pine forests: the effects of forest age and naturalness on species assemblages. Biological Conservation 106: 19-27.

Speight, M.C.D. 1989. Les invertébrés saproxyliques et leur protection. Conseil de l'Europe, Collection Sauvegarde de la Nature 42: 1-78.

Toivannen, T. et J.S. Kotiaho. 2007. Mimicking natural disturbances of boreal forests: the effects of controlled burning and creating dead wood on beetle diversity. Biodiversity and Conservation 16: 3193-3211.

Turbis, C. 2005. Le retour des grands pins au Québec. Ressources Naturelles Canada. Progrès forestier, Printemps 2005 : 24-25.

Uotila, A., J. Kouki, H. Kontkanen et P. Pulkkinen. 2002. Assessing the naturalness of boreal forests in eastern Fennoscandia. Forest Ecology and Management 161: 257-277.

Väisänen, R., O. Biström, et K. Heliövaara. 1993. Sub-cortical Coleoptera in dead pines and spruces: is primeval species composition maintained in managed forests? Biodiversity and Conservation 2: 95-113.

Varner III, M.J., D.R. Gordon, F.E. Putz et K.J. Hiers. 2005. Restoring fire to long-unburned *Pinus palustris* ecosystems novel fire effects and consequences for long-unburned ecosystems. Restoration Ecology 13: 536-544.

Vlasiu, P.D., P. Nolet et F. Doyon. 2001. Le pin blanc: revue de littérature. Institut québécois d'aménagement de la forêt feuillue, Ripon, Canada.

Watson, R. 1923. Forest devastation in Michigan. Journal of Forestry 21: 425-451.

Wendel, G.W. et H.C. Smith. 1990. *Pinus strobus* L., eastern white pine. In: Burns, R.M. et Honkala, B.H. (Eds.). Silvics of North America, Vol. 1, Conifers. USDA Forest Service, Agriculture Handbook 654, Washington, D.C. pp. 476-488.

Weyenberg, S.A., L.E. Frelich et P.B. Reich. 2004. Logging versus fire: How does disturbance type influence the abundance of *Pinus strobus* regeneration? Silvia Fennica 38: 179-194.

White, M.A. et D.J. Mladenoff. 1994. Old-growth forest landscape transitions from pre-european settlement to present landscape. Ecology 9: 191-205.

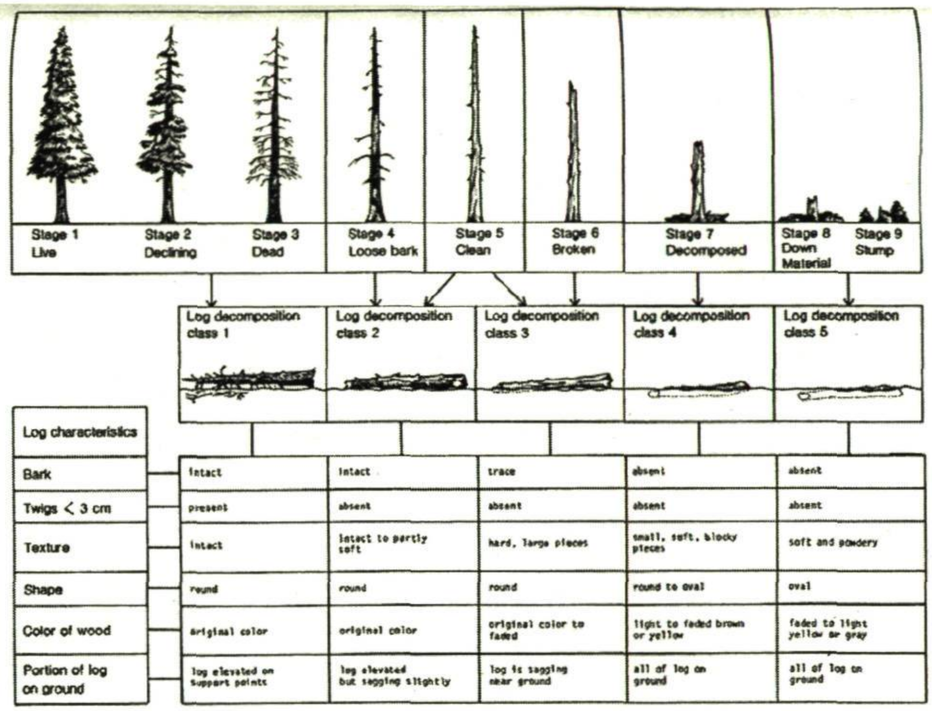
Wikars, L.O. 1997. Effects of forest fire and the ecology of fire-adaptated insects. Department of zoology, Uppsala University, Uppsala. 35p.

Wikars, L.-O. 2002. Dependance on fire in wood-living insects: An experiment with burned and unburned spruce and birch logs. Journal of Insect Conservation 6: 1-12.

Wilkins, C. et L. Kiceluk. 1994. The mythic white pine is in trouble. Canadian Geographic 114: 58-67.

Ziegler, S.S. 1995. Relict eastern white pine (*Pinus strobus* L.) stands in southwestern Wisconsin. American Midland Naturalist 133: 88-100.

Annexe 1: Hunter's decay classes.



Log characteristics	Log decomposition class 1	Log decomposition class 2	Log decomposition class 3	Log decomposition class 4	Log decomposition class 5
Bark	intact	intact	trace	absent	absent
Twigs < 3 cm	present	absent	absent	absent	absent
Texture	intact	intact to partly soft	hard, large pieces	small, soft, blocky pieces	soft and powdery
Shape	round	round	round	round to oval	oval
Color of wood	original color	original color	original color to faded	light to faded brown or yellow	faded to light yellow or gray
Portion of log on ground	log elevated on support points	log elevated but sagging slightly	log is sagging near ground	all of log on ground	all of log on ground

Annexe 2: List of Coleoptera captured.

Family	Name	Burn	Unburn	Total	p-val	Trophic
Aderidae	*Vanonus sp.*	6		6	-	Sapro
Anobiidae	*Hadrobregmus notatus* (Say)	2	1	3	-	Sapro
	Hemicoelus carinatus Say	1		1	-	Sapro
	Microbregma e. emarginatum (Duftschmid)	3		3	-	Sapro
Anthicidae	*Ischalia costata* (LeConte)	13	13	26	0.6746	Sapro
Anthribidae	*Euparius marmoreus* (Olivier)	2		2	-	Sapro
Brentidae	*Podapion gallicola* Riley	1		1	-	Sapro
Buprestidae	*Agrilus anxius* Gory	1		1	-	Sapro
	Anthaxia inornata (Randall)	1		1	-	Sapro
	Chrysobothris femorata (Olivier)	1		1	-	Sapro
	Chrysobothris scabripennis Gory and Laporte	1		1	-	Sapro
Byrrhidae	*Byrrhus americanus* LeConte	2		2	-	Non-Sap
	Curimopsis sp.	1		1	-	Non-Sap
Cantharidae	*Cantharis rotundicollis* Say	1	1	2	-	Non-Sap
	Malthodes fragilis (LeConte)	9	5	14	-	Sapro

	Podabrus diadema (Fabricius)	2	1	3	-	Non-Sap
	Podabrus puncticollis (Kirby)		2	2	-	Non-Sap
	Podabrus punctulatus LeConte	7		7	-	Non-Sap
	Podabrus rugulosus LeConte		1	1	-	Non-Sap
	Rhagonycha fraxini (Say)	27	11	38	0.0327	Non-Sap
	Rhagonycha sp. près imbecillis	2		2	-	Non-Sap
Carabidae	*Agonum retractum* LeConte	28	14	42	0.5301	Non-Sap
	Amara otiosa Casey	2		2	-	Non-Sap
	Bembidion wingatei Bland		1	1	-	Non-Sap
	Bradycellus lugubris (LeConte)		1	1	-	Non-Sap
	Calathus ingratus Dejean	32	58	90	0.5823	Non-Sap
	Cymindis cribricollis Dejean	4		4	-	Non-Sap
	Dromius piceus Dejean	4	4	8	-	Non-Sap
	Mioptachys flavicauda Say	1		1	-	Non-Sap
	Notiophilus aeneus (Herbst)	15	1	16	-	Non-Sap
	Platynus decentis (Say)	2		2	-	Non-Sap
	Pterostichus adoxus (Say)	15	18	33	0.9801	Non-Sap
	Pterostichus adstrictus Eschscholtz	200	328	528	0.6064	Non-Sap
	Pterostichus coracinus (Newman)	229	534	763	0.3280	Non-Sap
	Pterostichus melanarius (Illiger)	1		1	-	Non-Sap
	Pterostichus pensylvanicus LeConte	527	804	1331	0.7354	Non-Sap
	Pterostichus punctatissimus (Randall)	2	13	15	-	Non-Sap
	Pterostichus tristis (Dejean)	7	29	36	0.1559	Non-Sap
	Sphaeroderus c. canadensis Chaudoir	9	20	29	0.3975	Non-Sap
	Sphaeroderus l. lecontei Dejean	16	27	43	0.5227	Non-Sap
	Sphaeroderus nitidicollis brevoorti LeConte	2	1	3	-	Non-Sap
	Syntomus americanus (Dejean)	14		14	-	Non-Sap

	Synuchus impunctatus (Say)	410	341	751	0.2562	Non-Sap
	Tachyta angulata Casey	1		1	-	Sapro
Cerambycidae	*Acmaeops p. proteus* (Kirby)	18		18	-	Sapro
	Anthophylax attenuatus (Haldeman)	26	36	62	0.8948	Sapro
	Anthophylax cyaneus (Haldeman)		1	1	-	Sapro
	Anthophylax viridis LeConte	1		1	-	Sapro
	Asemum striatum (Linnaeus)	4		4	-	Sapro
	Astylopsis macula (Say)	2	2	4	-	Sapro
	Bellamira scalaris (Say)	1		1	-	Sapro
	Clytus ruricola (Olivier)	72	79	151	0.9627	Sapro
	Cosmosalia chrysocoma (Kirby)		1	1	-	Sapro
	Evodinus m. monticola (Randall)	8	5	13	-	Sapro
	Gaurotes cyanipennis (Say)	10	10	20	0.8232	Sapro
	Idiopidonia pedalis (LeConte)	1		1	-	Sapro
	Leptura subhamata Randall	1		1	-	Sapro
	Lepturopsis biforis (Newman)	1		1	-	Sapro
	Microclytus compressicollis (Castleneau et Gory)		2	2	-	Sapro
	Microgoes oculatus (LeConte)	4	1	5	-	Sapro
	Monochamus mutator LeConte		1	1	-	Sapro
	Monochamus notatus (Drury)	2		2	-	Sapro
	Monochamus s. scutellatus (Say)	6		6	-	Sapro
	Phymatodes maculicollis LeConte		1	1	-	Sapro
	Pogonocherus penicillatus LeConte	1		1	-	Sapro
	Pogonocherus sp.	1		1	-	Sapro
	Priognathus molinicornis (Randall)	1		1	-	Sapro
	Psenocerus supernotatus (Say)	2		2	-	Sapro
	Rhagium inquisitor (Linnaeus)	5	2	7	-	Sapro

	Sachalinobia r. rugipennis (Newman)		1	1	-	Sapro
	Stictoleptura c. canadensis (Olivier)	1	3	4	-	Sapro
	Tetropium cinnamopterum Kirby	1	2	3	-	Sapro
	Trachysida mutabilis (Newman)	3	1	4	-	Sapro
	Urgleptes querci (Fitch)	6	1	7	-	Sapro
	Urographis fasciatus (DeGeer)	1		1	-	Sapro
	Xestoleptura tibialis (LeConte)	3		3	-	Sapro
	Xylotrechus quadrimaculatus (Haldeman)	1		1	-	Sapro
	Xylotrechus undulatus (Say)		1	1	-	Sapro
Cerylonidae	*Cerylon castaneus* Say	93	62	155	0.0189	Sapro
Chrysomelidae	*Calligrapha sp.*		1	1	-	Non-Sap
	Capraita sp.	2		2	-	Non-Sap
	Donacia fulgens LeConte	1		1	-	Non-Sap
	Pachybrachys peccans Suffrian	1		1	-	Non-Sap
	Phratora americana canadensis Brown	1		1	-	Non-Sap
	Pyrrhalta cavicollis (LeConte)		2	2	-	Non-Sap
	Syneta extorris borealis W.J. Brown		1	1	-	Non-Sap
Ciidae	*Octotemnus laevis* Casey		1	1	-	Sapro
	Orthocis punctatus (Mellié)	1	2	3	-	Sapro
Clambidae	*Clambus sp.*	7	5	12	-	Sapro
Cleridae	*Enoclerus nigripes rufiventris* Say		1	1	-	Sapro
	Madoniella dislocata (Say)	1		1	-	Sapro
	Phlogistosternus dislocatus (Say)	1	1	2	-	Sapro

	Thanasimus dubius (Fabricius)	2		2	-	Sapro
	Thanasimus undulatus (Say)	1	1	2	-	Sapro
	Thanasimus undulatus nubilus (Say)	4		4	-	Sapro
	Zenodosus sanguineus (Say)	15	16	31	0.7980	Sapro
Coccinellidae	*Anatis mali* (Say)	1		1	-	Non-Sap
	Chilochorus stigma Say		1	1	-	Non-Sap
	Coccinella trifasciata perplexa Mulsant	1		1	-	Non-Sap
	Harmonia axyridis Pallas	4		4	-	Non-Sap
	Myzia pullata (Say)	1		1	-	Non-Sap
	Psyllobora vigintimaculata (Say)	2	1	3	-	Non-Sap
Corylophidae	*Molamba fasciata* (Say)	3	1	4	-	Sapro
Cryptophagidae	*Atomaria sp.*	79	30	109	0.0243	Sapro
	Cryptophagus sp.	5	2	7	-	Sapro
	Henoticus sp.	1		1	-	Sapro
Cucujidae	*Cucujus clavipes clavipes* Fabricius	1	1	2	-	Sapro
Curculionidae	*Carphonotus testaceus* Casey	3	1	4	-	Sapro
	Conotrachelus nenuphar (Herbst)		1	1	-	Non-Sap
	Crypturgus borealis Swaine	5		5	-	Sapro
	Dendroctonus rufipennis (Kirby)	4		4	-	Sapro
	Dendroctonus valens LeConte	9	1	10	-	Sapro
	Dryocoetes affaber (Mannerheim)	7	2	9	-	Sapro
	Dryocoetes autographus (Ratzeburg)	23	37	60	0.3300	Sapro
	Dryocoetes betulae Hopkins	3	2	5	-	Sapro

Dryophtorus americanus Bedel	15		15	-	Sapro
Gnathotrichus materiarius (Fitch)	1		1	-	Sapro
Hormorus undulatus (Uhler)	7		7	-	Sapro
Hylastes opacus Erichson	12	3	15	-	Sapro
Hylastes porculus Erichson	3		3	-	Sapro
Hylobius congener Dalla Torre	899	260	1159	<0.0001	Sapro
Hylobius pinicola (Couper)		1	1	-	Sapro
Hylobius warreni Wood	2	4	6	-	Sapro
Hylurgopinus rufipes (Eichhoff)		1	1	-	Sapro
Hylurgops rugipennis pinifex (Fitch)		1	1	-	Sapro
Magdalis picea Buchanan	2		2	-	Sapro
Monarthrum mali (Fitch)	5	1	6	-	Sapro
Nemocestes horni Van Dyke	7	5	12	-	Non-Sap
Orthotomicus caelatus (Eichhoff)	1		1	-	Sapro
Otiorhynchus ovatus (Linné)	2		2	-	Non-Sap
Pachyrhinus elegans (Couper)		1	1	-	Non-Sap
Phyllobius oblongus (Linné)	4	2	6	-	Non-Sap
Pissodes affinis Randall	3	1	4	-	Sapro
Pissodes fiskei Hopkins	1	1	2	-	Sapro
Pissodes similis Hopkins		2	2	-	Sapro
Pissodes strobi (Peck)	1		1	-	Sapro
Pityogenes hopkinsi Swaine	3	4	7	-	Sapro
Pityokteines sparsus (LeConte)	5	2	7	-	Sapro
Pityophtorus paberulus (LeConte)	1		1	-	Sapro
Polygraphus rufipennis (Kirby)	42	22	64	0.0456	Sapro
Prorutidosoma decipiens (LeConte)	1		1	-	Non-Sap
Rhyncolus brunneus Mannerheim	3	2	5	-	Sapro
Rhyncolus macrops Buchanan		2	2	-	Sapro

	Trypodendron lineatum (Olivier)	61	55	116	0.5224	Sapro
	Xyleborus obesus LeConte	46	11	57	0.1539	Sapro
	Xyleborus saxeseni Ratzeburg	1		1	-	Sapro
	Xyleborus sayi (Hopkins)	758	1018	1776	0.7672	Sapro
	Xyloterinus politus (Say)	5	3	8	-	Sapro
Dermestidae	*Anthrenus castanaea* Casey	1		1	-	Sapro
Dysticidae	*Neoscutopteris hornii* (Crotch)	1		1	-	Non-Sap
Elateridae	*Agriotella debilis* (LeConte)	2	11	13	-	Sapro
	Agriotes collaris (LeConte)	19	28	47	0.8348	Sapro
	Agriotes fucosus (LeConte)	52	3	55	0.3409	Sapro
	Agriotes limosus (LeConte)	9	1	10	-	Sapro
	Agriotes stabilis (LeConte)	80	32	112	0.0290	Sapro
	Ampedus apicatus (Say)	6	1	7	-	Sapro
	Ampedus deletus (LeConte)		1	1	-	Sapro
	Ampedus evansi W.J. Brown	2		2	-	Sapro
	Ampedus fusculus (LeConte)	1	5	6	-	Sapro
	Ampedus laurentinus W.J. Brown	1		1	-	Sapro
	Ampedus luctuosus (LeConte)	9	8	17	-	Sapro
	Ampedus mixtus (Herbst)		1	1	-	Sapro
	Ampedus nigrinus (Herbst)	4		4	-	Sapro
	Ampedus pullus Germar	3	1	4	-	Sapro
	Ampedus sp.	10	6	16	-	Sapro
	Ampedus sp1 (non-décrite)	1		1	-	Sapro
	Ampedus sp2 (non-décrite)		1	1	-	Sapro
	Athous rufifrons (Randall)	1		1	-	Sapro

	Ctenicera resplendens (Eschsholtz)		1	1	-	Sapro
	Ctenicera sp.	1		1	-	Sapro
	Dalopius vagans W.J. Brown	2		2	-	Sapro
	Danosoma brevicornis (LeConte)	3	5	8	-	Sapro
	Denticollis denticornis (Kirby)	4	1	5	-	Sapro
	Lacon auroratus (Say)	1		1	-	Sapro
	Limonius aeger LeConte	9	10	19	-	Sapro
	Liotrichus falsificus (LeConte)		2	2	-	Sapro
	Liotrichus spinosus (LeConte)	4	9	13	-	Sapro
	Melanotus castanipes (Paykull)	48	34	82	0.0315	Sapro
	Neohypdonus tumescens (LeConte)	2		2	-	Sapro
	Netanomus insidiosus (LeConte)		1	1	-	Sapro
	Paractenicera fulvipes Bland		1	1	-	Sapro
	Pseudanostirus hamatus (Say)	1		1	-	Sapro
	Pseudanostirus hieroglyphica (Say)	3	3	6	-	Sapro
	Pseudanostirus p. propola (LeConte)	3	1	4	-	Sapro
	Pseudanostirus triundulatus (Randall)	54	22	76	0.9309	Sapro
	Selatosomus cruciata pulcher (LeConte)	3	5	8	-	Sapro
	Sericus honestus (Randall)	1	1	2	-	Sapro
	Sericus incongruus (LeConte)	8	8	16	-	Sapro
	Setasomus aratus (LeConte)	2	1	3	-	Sapro
Endomychidae	*Endomychus biguttatus* Say	3	3	6	-	Sapro
	Hadromychus chandleri Bosquet	1		1	-	Sapro
	Lycoperdina ferruginea LeConte	2	1	3	-	Sapro
	Mycetina perpulchra (Newman)		1	1	-	Sapro
	Phymaphora pulchella Newman	17	13	30	0.3339	Sapro

Erotylidae	*Triplax dissimulator* (Crotch)	28	7	35	0.0418	Sapro
	Triplax thoracica Say	26	5	31	0.0003	Sapro
	Tritoma pulcra Say	2	1	3	-	Sapro
Eucinetidae	*Eucinetus sp.*	4	1	5	-	Sapro
	Eucinetus strigosus LeConte	2	1	3	-	Sapro
	Eucinetus terminalis LeConte	6	1	7	-	Sapro
Eucnemidae	*Isorhipis obliqua* (Say)	5	6	11	-	Sapro
Geotrupidae	*Geotrupes balyi* Jekel	7	4	11	-	Non-Sap
	Geotrupes hornii Blanchard	6		6	-	Non-Sap
Histeridae	*Cylistus deficiens* (Casey)	1	1	2	-	Sapro
	Hister furtivus LeConte	6		6	-	Non-Sap
	Margarinotus brunneus Fabricius		1	1	-	Non-Sap
	Margarinotus lecontei Wenzal	2	1	3	-	Non-Sap
	Paromalus teres LeConte	4	2	6	-	Sapro
	Platysoma lecontei Marseul	1		1	-	Sapro
Hydrophilidae	*Cercyon assecla* Smetana		2	2	-	Non-Sap
	Cercyon minusculus Melsheimer	5		5	-	Non-Sap
	Hydrobius fuscipes LeConte	1		1	-	Non-Sap
Laemophloedidae	*Laemophloeus biguttatus* (Say)	11	10	21	0.6500	Sapro
Lampyridae	*Ellychnia corrusca* (Linné)	95	75	170	0.0498	Sapro
	Lucidota atra (Oliv.)		1	1	-	Sapro

	Pyractomena sp.	3		3	-	Non-Sap
Lathridiidae	*Cartodere sp.*	2		2	-	Sapro
	Corticaria sp.	59	9	68	0.0017	Sapro
	Corticarina sp.	64	6	70	0.0006	Sapro
	Cortinicara sp.	22	10	32	0.0144	Sapro
	Eunicmus sp.	17	25	42	0.7277	Sapro
	Lathridius sp.	19	13	32	0.1597	Sapro
	Melanophtalma sp.	135	45	180	0.0018	Sapro
Leiodidae	*Agathidium sp.*	28	23	51	0.1600	Sapro
	Anisotoma sp.	4	3	7	-	Sapro
	Catops sp.	13	9	22	0.5325	Non-Sap
	Colon sp.	9		9	-	Non-Sap
	Hydnobius sp.	2		2	-	Non-Sap
	Leiodes sp.	18	4	22	0.0038	Non-Sap
	Sciodrepoides sp.		1	1	-	Non-Sap
Lucanidae	*Ceruchus piceus* (Weber)	1		1	-	Sapro
Lycidae	*Dictyopterus aurora* Herbst	3	4	7	-	Sapro
	Plateros sp.	1	2	3	-	Non-Sap
Lymexylidae	*Hylecoetus lugubris* Say	80	47	127	0.2335	Sapro
Melandryidae	*Dircaea liturata* (LeConte)	4	2	6	-	Sapro
	Emmesa connectens Newman	1	4	5	-	Sapro
	Eustrophus tomentosus Say	9	3	12	-	Sapro

	Orchesia sp.	4	1	5	-	Sapro
	Phryganophilus collaris LeConte	1	1	2	-	Sapro
	Serropalpus coxalis Mank	1		1	-	Sapro
	Serropalpus substriatus Haldeman	4	4	8	-	Sapro
	Xylita sp.	1		1	-	Sapro
Meloidae	*Meloe sp.*		1	1	-	Non-Sap
Monotomidae	*Rhizophagus brunneus* Horn	5		5	-	Sapro
	Rhizophagus dimidiatus Mannerheim	21	13	34	0.2220	Sapro
	Rhizophagus remotus LeConte	2	4	6	-	Sapro
Mordellidae	*Mordellaria lineella* LeConte	1		1	-	Sapro
	Mordellaria serval (Say)	8	9	17	-	Sapro
	Mordellistena scapularis Say		2	2	-	Non-Sap
	Mordellistena tosta LeConte	1		1	-	Non-Sap
Mycetophagidae	*Litargus tetraspilotus* LeConte	1		1	-	Sapro
Nemonychidae	*Cimberis elongata* (LeConte)	1	1	2	-	Non-Sap
Nitidulidae	*Carpophilus brachypterus* (Say)	1		1	-	Sapro
	Carpophilus hemicrepidius (Linné)	2		2	-	Sapro
	Colopterus truncatus (Randall)	4	1	5	-	Sapro
	Epuraea avara (Randall)	19	11	30	0.2358	Sapro
	Epuraea helvola Erichson	28	68	96	0.5804	Sapro
	Epuraea labilis Erichson	1		1	-	Sapro
	Epuraea linearis Maklin	1	1	2	-	Sapro

	Epuraea obliquus Hatch		1	1	-	Sapro
	Epuraea planulata Erichson	497	339	836	0.2312	Sapro
	Epuraea terminalis Mannerheim	31	31	62	0.7632	Sapro
	Epuraea truncatella Mannerheim	47	9	56	0.0053	Sapro
	Glischrochilus fasciatus (Olivier)	3	1	4	-	Sapro
	Glischrochilus quadrisignatus (Say)	10	2	12	-	Sapro
	Glischrochilus s. sanguilonentus (Olivier)	595	282	877	0.0127	Sapro
	Glischrochilus siepmani W.J. Brown	21	11	32	0.3226	Sapro
	Glischrochilus vittatus (Say)	7		7	-	Sapro
Oedemeridae	*Asclera ruficollis* (Say)	1		1	-	Sapro
Orsodacnidae	*Orsodacne atra* (Ahrens)	1		1	-	Non-Sap
Ptilidae	*Acrotrichis sp.*	7	1	8	-	Non-Sap
	Pteryx sp.	7	2	9	-	Sapro
	Ptiliolum sp.	31	5	36	0.0041	Sapro
	Smicrus sp.	1		1	-	Non-Sap
Pythidae	*Priognathus molinicornis* (Randall)	3	2	5	-	Sapro
	Pytho planus (Olivier)	1		1	-	Sapro
Salpingidae	*Rhinosimus viridiaeneus* Randall	24	31	55	0.9430	Sapro
	Sphaeriestes viridescens (LeConte)	1		1	-	Sapro
Scarabaeidae	*Aphodius lentus* Horn	1	1	2	-	Non-Sap
	Aphodius leopardus Horn	1		1	-	Non-Sap
	Dichelonyx albicollis (Burmeister)	2		2	-	Non-Sap

	Dichelonyx canadensis (Horn)	74	12	86	0.1154	Non-Sap
	Dichelonyx linearis (Gyllenhal)	8	13	21	0.9117	Non-Sap
	Dichelonyx subvittata (LeConte)	3	8	11	-	Non-Sap
	Serica atracapilla (Kirby)	28	20	48	0.2738	Non-Sap
	Trichiotinus assimilis (Kirby)	1		1	-	Non-Sap
Scirtidae	*Prionocyphon limbalus* LeConte	1		1	-	Non-Sap
Scraptiidae	*Anaspis flavipennis* Haldeman	13	4	17	-	Sapro
	Anaspis rufa Say	17	11	28	0.6041	Sapro
	Canifa sp.	10	3	13	-	Sapro
Scydmaenidae	*Brachysepsis sp.*		2	2	-	Non-Sap
	Euconnus (Napoconnus) sp.	1		1	-	Non-Sap
	Euconnus (Napocus) sp.	2		2	-	Non-Sap
	Parascydmus sp.	3	4	7	-	Non-Sap
	Scydmaenus sp.	1	1	2	-	Non-Sap
	Stenichnus sp.	5	4	9	-	Sapro
Silphidae	*Nicrophurus defodiens* Mannerheim	8	13	21	0.5504	Non-Sap
	Nicrophurus pustulatus Herschel	1		1	-	Non-Sap
	Nicrophurus sayi Laporte de Castelnau	3	6	9	-	Non-Sap
	Nicrophurus surinamensis Fabricius	1		1	-	Non-Sap
	Oiceptoma noveboracense (Forst.)	1		1	-	Non-Sap
Silvanidae	*Dendrophagus cygnaei* Mannerheim	17	3	20	-	Sapro
	Silvanus bidentatus (Fabricius)	102	24	126	0.0014	Sapro

Staphylinidae	Staphylinidae	926	749	1675	0.0110	Unclassified
Stenotrachelidae	*Cephaloon lepturides* Newman	1		1	-	Sapro
Tenebrionidae	*Arthromacra aenea* (Say)	1		1	-	Sapro
	Bolitotherus cornutus Panzer	3		3	-	Sapro
	Isomira quadristriata (Couper)	99	91	190	0.5713	Sapro
	Mycetochara bicolor Couper		1	1	-	Sapro
	Paratenetus sp.	1	2	3	-	Non-Sap
	Platydema americanus Laporte & Castleneau	1	1	2	-	Sapro
	Upis ceramboides Linné	2		2	-	Sapro
Tetratomidae	*Penthe obliquata* Fabricius	1	2	3	-	Sapro
	Penthe pimelia Fabricius	28	40	68	0.7709	Sapro
Throscidae	*Aulonothroscus punctatus* (Bonvouloir)	5	11	16	-	Non-Sap
	Trixagus sp.	4		4	-	Non-Sap
Trogidae	*Trox sp.*	1	1	2	-	Non-Sap
Trogossitidae	*Grynocharis quadrilineata* (Melsheimer)	1		1	-	Sapro
	Ostoma ferruginea (Linné)	1		1	-	Sapro
	Thymalus marginicollis Chevrolat	7	16	23	0.2725	Sapro
Total général		**7821**	**6382**	**14203**	-	-