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HISTORIQUE ET CARACTÉRISTIQUES ÉCOLOGIQUES DES ÎLOTS RÉSIDUELS APRÈS FEU EN FORÊT BORÉALE MIXTE

THÈSE

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AVANT-PROPOS

En plus de l'introduction générale et de la conclusion générale, cette thèse est composée de quatre chapitres principaux rédigés sous forme d'articles scientifiques. Le style d'écriture varie légèrement d'un chapitre à l'autre puisqu'ils ont été soumis ou sont en préparation pour des revues différentes et les répétitions d'un chapitre à l'autre sont inévitables. Trois des chapitres présentés ont été soumis et le dernier chapitre est en cours de finalisation.

Chapitre 2 – Ouarmim, S., Ali, A.A., Asselin, H., Hély, C. et Bergeron, Y. (accepté) *Evaluating the persistence of post-fire residual patches in the eastern Canadian boreal mixedwood forest*. Boreas.

Chapitre 3 – Ouarmim, S., Asselin, H., Hély, C., Bergeron, Y. et Ali, A.A. (2014) *Long term dynamics of fire refuges in boreal mixedwood forests.* Journal of Quaternary Science 29: 123-129.

Chapitre 4 – Ouarmim, S., Asselin, H., Bergeron, Y., Ali, A.A. et Hély, C. (accepté) *Stand characteristics of fire refuges in the eastern Canadian boreal mixedwood forest.* Forest Ecology and Management.

Chapitre 5 – Ouarmim, S., Hély, C., Paradis, L., Asselin, H., Bergeron, Y. et Ali, A.A. (en préparation) *Burning potential of fire refuges in the mixedwood boreal forest.*

Je suis la première auteure de chacun des chapitres de cette thèse, ayant réalisé chaque partie depuis la collecte des données jusqu'à la rédaction. Mes directeurs, Hugo Asselin et Adam Ali, et mes codirecteurs, Christelle Hély et Yves Bergeron, ont toutefois suivi chaque étape de cette thèse et ont contribué à la réalisation des chapitres. Pour le chapitre 5, Laure Paradis a participé activement à générer les fichiers de base, essentiels à la réalisation des simulations.

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RÉSUMÉ

Le feu est la principale perturbation en forêt boréale mixte. La sévérité des feux n'est pas spatialement homogène et épargne souvent partiellement ou entièrement des parties de la forêt appelées îlots résiduels. Ces îlots forestiers résiduels sont étudiés depuis de nombreuses années, et ces études se sont surtout intéressées aux facteurs déterminant leur occurrence à l'échelle du paysage. Cependant, des travaux réalisés en Fennoscandinavie et aux États-Unis ont révélé la présence de peuplements forestiers (appelés refuges) ayant la capacité de se maintenir dans le territoire pendant plusieurs millénaires. L'objectif principal de cette thèse était de caractériser la dynamique temporelle et la structuration d'îlots forestiers résiduels localisés au sein de la forêt boréale mixte de l'est du Canada. Les travaux ont porté sur la reconstitution de l'historique des feux et de la dynamique de la végétation de ces îlots au cours de l'Holocène, et de leurs caractéristiques stationnelles. Cette recherche s'inscrivait dans une perspective d'aménagement forestier écosystémique des massifs forestiers, avec comme point de mire la préservation de la diversité biologique des différentes mosaïques paysagères.

Treize îlots forestiers qui ont échappé au dernier feu ont été échantillonnés. Des carottes de sol ont été extraites dans chacun des sites pour réaliser des analyses paléoécologiques. Les reconstitutions de l'historique des feux et des dynamiques de végétation ont respectivement été fondées sur l'analyse des charbons de bois macroscopiques (> 250 µm) et des macrorestes végétaux. Les caractéristiques stationnelles de chaque site ont été échantillonnées (composition spécifique, diamètre et hauteur des arbres et des chicots, épaisseur de la matière organique, densité et volume des arbres et des chicots, volume de bois mort au sol). La charge en combustible des îlots a aussi été mesurée. Les données ont également servi à alimenter des modèles numériques de comportement du feu (Fire Behavior Prediction System, BehavePlus, FlamMap3) qui ont été utilisés afin de déterminer les caractéristiques stationnelles qui pourraient permettre à certains îlots d'échapper à plusieurs feux successifs.

Les résultats ont mis en évidence l'existence de deux types d'îlots résiduels en forêt boréale mixte : les refuges et les îlots résiduels transitoires. Les refuges sont moins susceptibles au feu comparativement aux îlots transitoires qui ont échappé uniquement au dernier feu, probablement de façon fortuite. Les refuges ont en revanche la capacité de persister dans le paysage forestier durant plusieurs millénaires, ne brûlant que lors de feux particulièrement sévères. Les analyses macrofossiles des refuges soulignent des changements majeurs au sein de la végétation locale, avec notamment le passage de formations dominées par *Larix* *laricina*/*Picea* spp. vers des formations dominées par *Abies balsamea*/*Thuja occidentalis*. Ce changement de végétation s'est produit à différentes périodes selon les sites, soulignant un processus endogène. Le développement de *Larix laricina* s'est accompagné dans certains assemblages macrofossiles de taxons typiques de milieux humides (tels que les characées). Les espèces de fin de succession (*Abies balsamea*/*Thuja occidentalis*) se sont maintenues dans le paysage forestier pendant plusieurs siècles, même après des feux sévères, probablement en raison de l'humidité des sites. L'épaisse couche de matière organique qui caractérise les refuges semble entraver le développement d'espèces de début de succession telles que *Betula papyrifera* et *Populus tremuloides*.

Certains facteurs biotiques ou abiotiques pourraient limiter la propagation du feu dans les îlots refuges, ce qui expliquerait leur caractère persistant. Les résultats des simulations du comportement du feu suggèrent un rôle mineur des coupe-feu (lacs, tourbières et affleurements rocheux), de la charge en combustible et de la topographie dans l'occurrence des refuges. L'humidité semble être le seul facteur déterminant leur développement au sein de la mosaïque paysagère. Les refuges se mettent en place au sein de faibles dépressions humides qui favorisent l'accumulation de la matière organique.

La structure des refuges et des autres îlots résiduels révèle deux principales caractéristiques permettant de les distinguer sur le terrain : le diamètre moyen des arbres et l'épaisseur de la matière organique. Les arbres des refuges ont un plus petit diamètre que ceux des autres îlots résiduels. Ceci peut s'expliquer par l'importante épaisseur de matière organique des refuges, qui affecte négativement la croissance des arbres. La facilité de détection des îlots refuges permettra leur prise en compte dans les stratégies d'aménagement forestier, notamment en assurant leur conservation à des fins de préservation de la biodiversité. Les recherches futures consacrées aux îlots forestiers résiduels après feu pourront se focaliser sur la mise en évidence de leurs éventuelles spécificités biologiques (surtout les refuges) et sur une caractérisation plus fine des paramètres biotiques et abiotiques déterminant leur développement.

Mots clés : forêt boréale mixte, feux de forêt, charbons de bois, macrorestes végétaux, îlots transitoires, refuges, structure forestière, humidité.

CHAPITRE 1 INTRODUCTION GÉNÉRALE

La forêt boréale est un vaste biome à l'échelle planétaire (Bonan et Shugart 1989), et elle constitue le principal domaine de végétation au Québec (Hare et Ritchie 1972, Rowe 1972, Payette 1983). La forêt boréale mixte, qui couvre environ 11,5% du territoire québécois, correspond au domaine bioclimatique de la sapinière à bouleau blanc. Il s'agit d'une zone de transition entre la pessière noire à mousses au nord et la forêt tempérée au sud (Ordre des ingénieurs forestiers du Québec 2009). La forêt boréale mixte apparaît à l'échelle du paysage comme une mosaïque naturelle constituée d'une juxtaposition de peuplements feuillus, résineux et mélangés, agencés selon le type de dépôt de surface ainsi que les effets des perturbations naturelles.

Les perturbations en forêt boréale influencent la régénération et la répartition des espèces arborescentes au sein de chaque zone de végétation. Ces perturbations comprennent principalement le feu, les épidémies d'insectes, les maladies, les chablis ainsi que les inondations (Weber et Flannigan 1997, Pothier 2001). Le feu joue un rôle primordial dans la structuration de la végétation et est donc un facteur écologique important dans la dynamique des écosystèmes forestiers (Heinselman 1981, Johnson 1992). Le feu exerce en effet un contrôle sur la composition floristique, la structure de la végétation et la répartition de la mosaïque végétale (Van Wagner 1978, Heinselman 1981, Johnson 1992). En l'absence de feux récurrents dans la partie orientale de son aire de répartition, la sapinière est principalement perturbée par des épidémies de la tordeuse des bourgeons de l'épinette (*Choristoneura fumiferana* Clem.) (Morin et Laprise 1990).

Le régime des feux pour une région donnée peut être documenté par différents paramètres, à savoir le cycle de feu, l'intervalle moyen entre les feux, la fréquence, la sévérité, l'intensité et la taille du feu (e.g. Johnson 1992, Gauthier et al. 2001, Keeley 2009). De façon générale, plusieurs facteurs agissent sur le comportement et l'impact des incendies forestiers : les conditions climatiques et météorologiques, la végétation (qualité du combustible), la topographie (relief et disposition du réseau hydrographique ou de tout autre coupe-feu, naturel ou anthropique) et les activités humaines qui contribuent à l'allumage et à la suppression des feux. Cependant, en forêt boréale, le régime des feux semble principalement contrôlé par le climat et les conditions météorologiques, et ce, depuis la fin de la dernière période glaciaire (Flannigan et al. 1998, Girardin et al. 2008, Hély et al. 2010, Ali et al. 2012), quoique la composition de la végétation puisse moduler l'occurrence, la propagation, la sévérité et la taille des feux (Hély et al. 2010, Girardin et al. 2013).

La fréquence des feux n'est pas spatialement homogène dans le paysage forestier. Cette variabilité du régime des feux est à l'origine d'une mosaïque complexe de peuplements d'âges, de compositions et de structures variables, en partie responsable de la diversité à l'échelle du paysage (Payette 1992, Cyr et al. 2009). Cette variabilité de fréquence serait due en partie aux conditions météorologiques au moment du feu et à une différence de susceptibilité du milieu forestier à cette perturbation, en lien avec l'hétérogénéité des conditions stationnelles en mesure d'influencer le comportement du feu (Turner et al. 1994, Hély et al. 2000a). Les feux ont ainsi la particularité de laisser intacte une partie des peuplements forestiers affectés, sous forme d'arbres groupés en îlots, contribuant à l'hétérogénéité du paysage forestier (Fig. 1.1) (Gasaway et Dubois 1985, Hörnberg et al. 1998, Delong et Tanner 1996, Wallenius et al. 2004, Cyr et al. 2005). Certains de ces îlots pourraient avoir été épargnés par le feu depuis des siècles, voire même des millénaires (Hemstrom et Franklin 1982, Hörnberg et al. 1998, Cyr et al. 2005, Bergeron et Harper 2009). Dans la forêt boréale canadienne, les études concernant ces îlots épargnés par les feux sont fragmentaires et ne rendent pas compte de toutes les caractéristiques historiques, physiques et biologiques de ces milieux. La problématique générale de cette thèse est fondée sur une stratégie de recherche visant à mieux comprendre la dynamique pluriséculaire de ces îlots, dans une perspective d'aménagement forestier écosystémique des massifs de la forêt boréale mixte. Nous émettons comme hypothèse qu'il existe deux types d’îlots forestiers en forêt boréale mixte : (1) des îlots qui ont échappé uniquement au dernier feu, probablement en raison de conditions météorologiques particulières, comme par exemple un changement dans la direction du vent ou des précipitations inopinées (îlots transitoires), et (2) des îlots plus persistants (refuges), qui auraient échappé à plusieurs feux successifs du fait de leur position dans le territoire forestier ou en raison de caractéristiques stationnelles défavorables à l'ignition et à la propagation du feu.

Figure 1.1: Îlot forestier résiduel après feu (photographie : Sandrine Picq).

1.1 Caractéristiques des îlots résiduels après feu

La mise en évidence et l'étude des îlots résiduels après feu remonte au moins à une trentaine d'années (Hemstrom et Franklin 1982, Eberhart et Woodard 1987, Camp et al. 1997). La proportion du territoire incendié occupée par ces îlots est bien documentée, les différentes études rapportant des valeurs entre 1 et 25 % (Eberhart et Woodard 1987, Delong et Tanner 1996, Madoui et al. 2011, Dragotescu et Kneeshaw 2012). Cette proportion varie cependant d'une région à l'autre au Canada : entre 3 et 5 % du territoire incendié en Colombie-Britannique (Delong et Tanner 1996), entre 1 et 25 % pour le centre-ouest de la Colombie-Britannique (Stuart-Smith et Hendry 1998), entre 0 et 20 % pour l'Alberta (Andison 2003), entre 2 et 22% dans le domaine bioclimatique de la pessière à mousses au Québec (Madoui et al. 2011), entre 6 et 7 % pour le Nord de l'Alberta (Eberhart et Woodwad 1987) et entre 7 et 19 % pour le Témiscamingue et la Mauricie au Québec (Dragotescu et Kneeshaw 2012). Ces données montrent que l'occurrence des îlots résiduels après feu est loin d'être un phénomène marginal.

La superficie des îlots résiduels après feu est variable et pourrait dépendre de la superficie du feu (Delong et Tanner 1996, Eberhart et Woodwad 1987, Smyth et al. 2005). Ainsi, 50 % des feux produisent des îlots de superficie inférieure à 2 ha; les feux les plus importants (plus de 1000 ha) produisent des îlots pouvant atteindre 10 ha, alors que les petits feux ne renferment souvent aucun îlot (Delong et Tanner 1996, Eberhart et Woodward 1987). La corrélation entre la superficie du feu et la taille et le nombre d'îlots pourrait s'expliquer par le fait que les grands feux ont une probabilité plus élevée de rencontrer des obstacles à la combustion laissant une proportion plus élevée de zones résiduelles. Cependant cette corrélation ne semble pas être une vérité absolue (Bergeron et al. 2002, Andison 2004, Fortin et Payette 2002, Madoui et al. 2011, Dragotescu et Kneeshaw 2012) et la présence d'îlots paraît plutôt dépendre du territoire considéré (relief, proportion de coupe-feu) et de l'intensité du feu (Kafka et al. 2001, Madoui et al. 2011).

1.2 Rôles des îlots résiduels après feu

Les îlots résiduels après feu ont un rôle important à jouer dans le fonctionnement à long terme de la matrice perturbée (Amaranthus et al. 1994, Gasaway et Dubois 1985, Gandhi et al. 2001). En effet, les arbres résiduels agissent comme semenciers et facilitent la recolonisation forestière du milieu perturbé, diversifiant par conséquent la structure, la composition et la fonctionnalité de peuplements en cours de régénération (Zenner et al. 2000, Asselin et al. 2001, Kafka et al. 2001). Ces îlots jouent également le rôle de refuge pour la faune sauvage en mesure de repeupler le milieu incendié après le retour de la végétation (Gasaway et Dubois 1985, Amaranthus et al. 1994, Gandhi et al. 2001). En plus d'un rôle écologique primordial dans le paysage forestier, les îlots refuges (qui peuvent échapper à plusieurs feux successifs), pourraient servir de refuges pour des espèces sensibles aux perturbations et constituer de véritables « *hotspots* » de biodiversité. Des travaux menés dans la forêt boréale fennoscandinave ont ainsi rapporté que les îlots résiduels pouvaient renfermer plus de 30% des espèces de bryophytes connues (Ohlson et al. 1997). Ces milieux serviraient aussi de refuges à des espèces de coléoptères, incluant les espèces de carabidés reliques de la dernière glaciation (Gandhi et al. 2001, 2004). L'évaluation du potentiel de ces îlots à abriter une biodiversité importante, requiert une reconstitution de leur histoire et une compréhension de leur structuration, notamment au regard des perturbations naturelles. Il est également essentiel de caractériser les spécificités stationnelles responsables de leur éventuelle rémanence.

1.3 Facteurs influençant la création des îlots résiduels après feu

Les facteurs responsables de la persistance de certains îlots résiduels après feu dans le paysage forestier ont été peu étudiés. En effet, les facteurs environnementaux contrôlant l'hétérogénéité spatiale du régime des feux sont nombreux et varient selon l'écosystème et l'échelle spatiale considérés (Cyr et al. 2007). À l'échelle régionale, le climat et la végétation sont les facteurs les plus souvent invoqués (Johnson 1992). À une échelle plus fine, les facteurs environnementaux contrôlant le régime des feux sont principalement la topographie, l'humidité du sol et la qualité du combustible (Cyr et al. 2007, Hély et al. 2000a). La distance à un coupe-feu peut également jouer un rôle important, mettant un terme au feu dans une partie du peuplement par manque de combustible (Larsen 1997, Cyr et al. 2005). Dragotescu et Kneeshaw (2012) ont révélé que près de 50 % des îlots sont situés à moins de 200 m d'un plan d'eau, alors que Stuart-Smith et Hendry (1998) ont rapporté des valeurs atteignant 66 %. Madoui et al. (2011) ont également révélé une corrélation positive entre l'occurrence d'îlots et la présence d'obstacles naturels aux feux.

La topographie exerce un effet direct et indirect sur le comportement des incendies, avec la mise en place de conditions microclimatiques et d'humidité du sol (Whelan 1995) qui sont défavorables au déclenchement et à la propagation du feu. L'importance de la topographie sur l'occurrence des îlots est avérée dans les régions où les variations topographiques sont importantes (Keeton et Franklin 2004, Romàn-Cuesta et al. 2009). Néanmoins, Delong et Tanner (1996) ont révélé que la position topographique des îlots épargnés par le feu reste aléatoire et dépendrait surtout d'un ensemble de facteurs liés entre eux. La forêt boréale mixte que nous avons étudiée étant une région relativement plane, l'effet de la topographie dans le développement des îlots résiduels serait donc *a priori* minime.

L'humidité est un facteur important dans l'ignition et la propagation du feu. Les sites à fort drainage brûlent plus souvent que les sites mésiques ou humides (Zackrisson 1977, Suffling et al. 1982). Des études réalisées en Fennoscandinavie, ont mis en évidence que l'historique des feux pouvait différer entre deux sites localisés à quelques centaines de mètres l'un de l'autre du seul fait de l'humidité locale (Wallenius et al. 2002).

Avec le climat et la topographie, le combustible fait partie des paramètres importants de l'environnement du feu (Agee 1997). La qualité du combustible est un facteur primordial dans l'ignition et la propagation du feu (Brown et Davis 1973). La mosaïque forestière est constituée de peuplements d'âge et de composition divers qui fournissent des environnements variés aux feux (Bergeron 2000). Le comportement du feu est fonction des combustibles tels que les débris ligneux (rameaux et branches de moins de 7,6 cm de diamètre), la couche de litière, les herbes mortes et des arbustes de petits diamètres (Brown et Davis 1973, Hély et al. 2000b). La charge, la composition, ainsi que l'arrangement spatial des débris ligneux auront des influences différentes sur la disponibilité du combustible (susceptibilité au feu d'un peuplement) et sur le comportement du feu (McRae et al. 1979, Schimmel et Granström 1997). De ce fait, la présence de peuplements moins inflammables jouerait un rôle majeur dans la rémanence des îlots forestiers (Hély et al. 2000b). Une meilleure compréhension des propriétés structurelles des combustibles est donc nécessaire pour bien comprendre le comportement d'un feu de forêt menant au développement d'îlots résiduels.

1.4 Importance des îlots résiduels pour l'aménagement forestier

L'exploitation forestière est un moteur social et économique important au Québec et au Canada. De plus en plus d'acteurs du milieu prônent une gestion durable des écosystèmes forestiers, qui tient compte du maintien d'une activité économique viable, mais aussi de la pérennité des processus écologiques et de la biodiversité. De ce fait, les aires protégées à elles seules ne suffisent pas à garantir la persistance des espèces et les efforts de protection devraient s'étendre aux aires de récolte. Afin de préserver la biodiversité, l'une des techniques les plus souvent proposées est l'émulation des effets du feu avec la rétention dans les chantiers de coupe d'éléments structuraux (arbres vivants et morts, débris ligneux) de l'habitat forestier (Doyon et Sougavinski 2003, Work et al. 2003, Gauthier et al. 2008). Cependant, la rétention est souvent réalisée selon des critères arbitraires, en fonction de l'accessibilité du terrain, de la présence de plans d'eau, etc. La présence dans le paysage forestier d'îlots résiduels pourrait être prise en considération dans les plans de gestion de la biodiversité. La protection de ces îlots permettrait notamment d'intégrer les objectifs de protection des vieux peuplements qui sont en régression du fait de la coupe forestière.

1.5 Objectifs de l'étude et structure de la thèse

Bien que l'on reconnaisse la présence d'îlots résiduels après feu dans les paysages forestiers boréaux, très peu d'études se sont intéressées aux facteurs contribuant à leur émergence et à leurs spécificités (structuration, composition et historique des feux) en comparaison avec la matrice forestière. L'objectif principal de cette thèse est de mieux comprendre les interactions entre le climat, les incendies forestiers, les conditions stationnelles et la végétation qui ont mené à la création d'îlots résiduels après feu. Plus spécifiquement, notre étude s'articule autour des objectifs suivants :

- Retracer l'historique des feux dans les îlots résiduels après feu, pour évaluer leur persistance dans le paysage forestier au cours de l'Holocène (Chapitre 2). Des études dendrochronologiques ont permis de retracer l'historique des feux des trois derniers siècles dans la région d'étude (Dansereau et Bergeron 1993, Bergeron 2000). Ces études sont toutefois limitées dans le temps par l'âge des arbres échantillonnés. Pour éviter ce verrou temporel, nous avons reconstitué l'historique des feux à l'échelle pluriséculaire ou millénaire par l'analyse d'assemblages de macrocharbons de bois conservés dans des humus forestiers (Jasinski et Payette 2005, Ali et al. 2008). Ces charbons de bois ont l'avantage de se préserver de façon durable dans les sols forestiers (de Lafontaine et Asselin 2011). Ils sont par conséquent considérés comme une source d'information sur les feux locaux passés (Gagnon et Payette 1985, Gavin et al. 2003a, Asselin et Payette 2005b).
- Retracer l'évolution temporelle de la végétation dans les refuges (Chapitre 3). Nous avons voulu vérifier que le régime de feux différent dans les îlots, comparativement à la matrice forestière environnante, pourrait conduire à une dynamique végétale singulière, avec notamment la persistance au cours du temps d'espèces sensibles au feu. Pour ce faire, nous avons analysé et identifié les macrorestes végétaux (aiguilles, feuilles, écailles de cônes, graines, etc.) préservés dans les humus forestiers pour les sites possédant les séquences de matière organique les plus longues.
- Caractériser et comparer les caractéristiques stationnelles (composition spécifique, diamètre et hauteur des arbres et des chicots, épaisseur de la matière organique, densité et volume des arbres et des chicots, volume de

bois mort au sol) permettant de différencier les îlots ayant échappé à plusieurs feux successifs au cours du temps de ceux ayant échappé seulement au dernier feu (chapitre 4).

- Identifier les caractéristiques stationnelles qui expliquent la persistance des refuges dans le paysage forestier (chapitre 5). Les facteurs les plus souvent invoqués sont : la topographie, la distance à une barrière naturelle au feu, l'humidité du sol et le combustible. L'originalité de cette étude vient du choix de l'outil utilisé pour mettre en évidence les rôles respectifs de chacun des facteurs. En effet, nous avons mené des simulations du comportement du feu à l'échelle du paysage de la zone d'étude grâce à trois systèmes utilisés en Amérique du Nord : le système canadien du comportement du feu FBP (Van Wagner 1968) pour fournir une « réalité terrain », le système BehavePlus (Andrews 2008) pour calibrer des modèles de combustibles sur la base de la réalité terrain et le système FlamMap (Stratton 2004) afin de spatialiser le comportement du feu dans le paysage étudié et déterminer le rôle de chaque facteur.

1.6 Zone d'étude

Le territoire d'étude est situé dans le domaine bioclimatique de la sapinière à bouleau blanc, dans les plaines de l'Abitibi. Il s'agit plus précisément de la Forêt d'enseignement et de recherche du Lac Duparquet (FERLD), un territoire de 8045 ha situé dans le canton d'Hébécourt, dans l'ouest de l'Abitibi (de 48°25'80" à 48°32'00" N et de 79°17'00" à 79°28'00" O). Les espèces les plus abondantes y sont le sapin baumier (*Abies balsamea* (L.) Mill.), le bouleau à papier (*Betula papyrifera* Marsh.), l'épinette blanche (*Picea glauca* (Moench) Voss.), le peuplier faux-tremble (*Populus tremuloides* Michx.) et le thuya occidental (*Thuja occidentalis* L.) (Dansereau and Bergeron 1993, Bergeron 2000). Les dépôts glaciolacustres sont caractéristiques de la ceinture d'argile du Nord du Québec et de l'Ontario et ont été déposés par les lacs pro-glaciaires Barlow et Ojibway (Vincent et Hardy 1977). Les peuplements forestiers présents sur le territoire sont issus de plusieurs feux datant de 1717 à 1944 (Dansereau et Bergeron 1993). La forêt a été affectée par trois grandes épidémies de la tordeuse des bourgeons de l'épinette au cours du XX^{e} siècle, soit durant les périodes de 1919 à 1929, de 1930 à 1950 et de 1970 à 1987 (Morin et al. 1993). Le climat est frais et la température moyenne est de 0,7 °C et la moyenne annuelle des précipitations est de 889,8 mm (Environnement Canada 2011).

CHAPITRE 2 EVALUATING THE PERSISTENCE OF POST-FIRE RESIDUAL PATCHES IN THE EASTERN CANADIAN BOREAL MIXEDWOOD FOREST

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2.1 Abstract

In boreal forest ecosystems, wildfire severity (i.e., the extent of fire-related tree mortality), is affected by environmental conditions and fire intensity. A burned area usually includes tree patches that partially or entirely escaped fire, called “residual patches”. Although the occurrence of residual patches has been extensively documented, their persistence through time, and thus their capacity to escape *several consecutive* fires, has not yet been investigated. Macroscopic charcoal particles embedded in organic soils were used to reconstruct the fire history of 13 residual patches of the eastern Canadian boreal mixedwood forest. Our results display the existence of two types of residual patches: (1) patches that only escaped fire by chance, maybe due to local site or meteorological conditions unsuitable for fire spread (random patches), and (2) patches with lower fire susceptibility, also called “fire refuges” that escaped at least two consecutive fires, likely due to particular site characteristics. Fire refuges can escape fire for more than 500 years, up to several thousand years, and likely burn only during exceptionally severe fire events. Special conservation efforts could target fire refuges owing to their old age, long ecological continuity, and potential specific biological diversity associated to different microhabitats.

2.2 Résumé

Dans les écosystèmes forestiers boréaux, la sévérité des feux (i.e. la proportion d'arbres tués), est influencée par les conditions environnementales et par l'intensité du feu. Le feu n'affecte pas le paysage de façon homogène et laisse des îlots forestiers épargnés dans les zones incendiées, appelés « îlots résiduels après feu ». Bien que la présence de ces îlots ait été largement rapportée dans la littérature, leur persistance dans le temps et leur capacité à échapper à plusieurs feux successifs n'ont pas encore été documentées en forêt boréale mixte. Des charbons de bois macroscopiques présents dans les sols forestiers de 13 îlots résiduels ont été analysés pour reconstituer leur historique de feux. Les résultats font état de deux types d'îlots résiduels : (1) des îlots qui ont échappé uniquement au dernier feu, par hasard, probablement en raison de conditions météorologiques ou stationnelles défavorables à la propagation du feu (îlots transitoires), et (2) des îlots forestiers qui présentent une susceptibilité moindre au feu, qui peuvent être qualifiés de refuges. Ces refuges ont échappé à au moins deux feux consécutifs et ont persisté dans le paysage forestier jusqu'à plusieurs milliers d'années. Ces refuges échappent de façon récurrente au feu du fait de caractéristiques stationnelles défavorables à l'ignition et à la propagation du feu, mais brûlent tout de même lors de feux particulièrement sévères. Ces îlots pourraient faire l'objet d'une protection particulière liée à leur âge avancé et à leur continuité écologique, qui pourraient se traduire par une biodiversité particulière.

2.3 Introduction

Fire is the main natural disturbance shaping boreal forest landscapes (Zackrisson 1977, Payette 1992). In North American boreal ecosystems, wildfires contribute to the creation of a complex mosaic of stands of varying age, composition, and structure, within which other disturbances and processes can interact (Payette 1992). The boreal forest is characterized by intense crown wildfires covering large areas (Kafka et al. 2001). Fire severity, i.e., the extent of fire-induced tree mortality, depends on environmental conditions, forest structure, and fire intensity. A burned area usually includes tree patches that partially or entirely escaped fire, called post-fire residual forests (Gluck and Rempel 1996, Wallenius et al. 2004, 2005, Burton et al. 2008). Residual patches have so far been largely ignored in forest management planning in the North American boreal forest (Gauthier et al. 2009).

The proportion of post-fire residual boreal forest can vary between 1 and 25% of the area burned (Delong and Tanner 1996, Dragotescu and Kneeshaw 2012). The maximum size of residual patches is usually less than 10 ha (Eberhart and Woodard 1987, Gluck and Rempel 1996). Their number may vary from 0 to 10.4 patches per 100 ha of area burned (Eberhart and Woodard 1987, Delong and Tanner 1996, Gluck and Rempel 1996, Kafka et al. 2001). It is still unclear whether the number and size of residual patches varies with fire size (Eberhart and Woodard 1987, Fortin and Payette 2002).

Although residual patches represent a small proportion of the area burned, they could represent significant and unique habitats in post-fire successional landscapes (Burton et al. 2008). Such patches can be refuges for disturbance-sensitive species, and can thus constitute biodiversity hotspots (Amaranthus et al. 1994, Segerström 1997, Hörnberg et al.1998, Gandhi et al. 2001). Residual patches also constitute seed banks providing propagules for recolonization of burned areas (Asselin et al. 2001). Furthermore, being older than the surrounding landscape, residual patches can include 'biological legacies' such as large diameter trees, snags, and coarse woody debris, which are important in the long term ecological functioning of forest ecosystems (Amaranthus et al. 1994).

Although the occurrence of post-fire residual patches has been extensively described, their persistence through time, and thus their capacity to escape several consecutive fires has not yet been investigated in North America. The presence of fire refuges has been mostly documented in Fennoscandia, where so-called swamp forests can escape fire for several millennia (Hörnberg et al. 1997, Segerström 1997, Wallenius et al. 2004). However, there is a lack of detailed data on ecosystem continuity in North American boreal forests. Potential long-term ecological continuity in post-fire residual patches could provide refuges for species with specific biodiversity signatures associated with older successional stages (Selva et al. 2003, Rivas Plata et al. 2008) that could be taken into account in biological conservation strategies in boreal ecosystems (Angelstam 1998). Hence, the objective of this study was to assess the persistence through time of post-fire residual patches in the eastern Canadian boreal mixedwood forest. To test the hypothesis that some post-fire residual forest patches can display long continuity, we reconstructed the fire histories of 13 such patches using macroscopic wood charcoal particles (>250 μm) embedded in the organic soil layer.

2.4 Material and methods

2.4.1 Study area

The study area is located within the Lake Duparquet Research and Teaching Forest (Fig. 2.1), in the eastern Canadian boreal mixedwood forest characterized by *Abies balsamea* (L.) Mill. (balsam fir), *Betula papyrifera* Marsh. (paper birch), *Picea glauca* (Moench) Voss. (white spruce), *Populus tremuloides* Michx. (trembling aspen), and *Thuja occidentalis* L. (eastern white cedar) as the main tree species (Dansereau and Bergeron 1993, Bergeron 2000). *Abies balsamea, Thuja occidentalis* and *Picea glauca* are late-successional species, whereas *Populus tremuloides* and *Betula papyrifera* initiate forest succession after stand-replacing disturbances (Bergeron 2000). The local geomorphology is characterized by a massive glaciolacustrine clay deposit left by pro-glacial lake

Ojibway, which covers most of the area below 300 m elevation (Vincent & Hardy 1977). Hills with partially reworked or eroded morainic deposits are interspersed in the landscape (Bergeron et al. 1982). The study site is characteristic of this pattern as the lakeshore topography alternates between flat clay plains and steep hills. The climate is cold with a mean annual temperature of 0.7°C (1971-2000) and mean annual precipitation of 889.8 mm (Environment Canada 2011). The closest meteorological station is located at La Sarre, 42 km north of the study area.

2.4.2 Identifying residual patches

The post-fire residual forest patches were selected within young matrix forest burned for the last time in AD 1944 or 1923, as revealed by previously-published fire history based on dendrochronological research (Dansereau and Bergeron 1993, Bergeron 2000) (Fig. 2.1). Areas affected by the 1944 and 1923 fires had previously burned in AD 1717 and 1760, respectively (Dansereau and Bergeron 1993, Bergeron 2000). Post-fire residual patches were distinguished from the surrounding forest matrix based on forest structure and composition retrieved from ecoforestry maps (Ministère des Ressources naturelles http://www.mrn.gouv.qc.ca/forets/inventaire/fiches/couches-peuplements-ecoforestiers.jsp). These patches were identified as old-growth coniferous patches (with *Abies balsamea* or *Thuja occidentalis*) embedded in a matrix of younger deciduous forests (with *Populus tremuloides* or *Betula papyrifera*). Thirteen post-fire residual forest patches with thick organic matter layers (mean: 39 cm; range 8-149 cm) were sampled (Fig. 2.1). A Russian corer was used to sample organic matter when it was more than ~ 50 cm thick (5 patches, Table 2-1), otherwise organic matter monoliths were extracted using a shovel and a knife (8 patches, Table 2-1). All the organic matter was sampled at each site, down to the mineral soil.

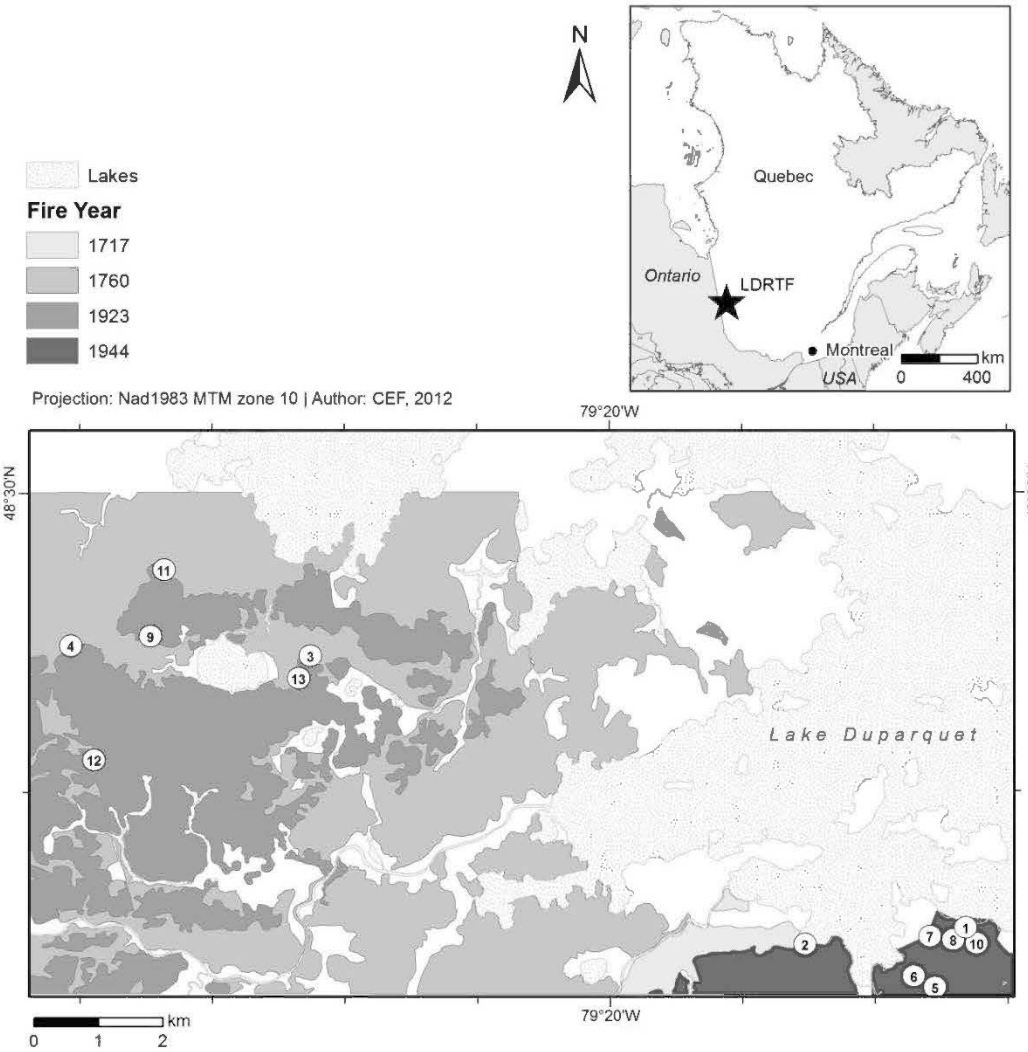

Figure 2.1: Location of the studied post-fire residual patches in the eastern Canadian boreal mixedwood forest (Lake Duparquet Research and Teaching Forest: LDRTF): 1= Georges; 2= Limite; 3= Mosquito1; 4= Surprise; 5= Venteux; 6= Cadeau; 7= Lauriane; 8= Jennifer; 9= Expérience; 10= Falaise; 11= Barrage; 12= Monsabrais; and 13= Mosquito2. Areas burned by the 1717, 1760, 1923 and 1944 fires are shown in different shades of gray.

Table 2-1 : Characteristics of the 13 sampled post-fire residual patches.

Name	Site number (as in Fig. 2.1)	Density (trees ha^{-1})	Organic matter thickness (cm)	Slope (°)
Georges	1	476	49	0
Limite	2	437	22	0
Mosquito1	3	1238	8	0
Surprise	4	331	9	3
Venteux	5	668	50.5	0
Cadeau	6	1173	98	0
Lauriane	7	254	9	5
Jennifer	8	272	14	7
Expérience	9	645	9	3
Falaise	10	294	11	4
Barrage	11	665	59	1
Monsabrais	12	617	149	2
Mosquito2	13	219	25	0

2.4.3 Dating and age-depth models

Radiocarbon (^{14}C) dating by accelerator mass spectrometry (AMS) was conducted on plant macroremains and charcoal fragments by Beta Analytic Inc. (Miami, FLA, USA), Poznań Radiocarbon Laboratory (Poznań, Poland), and Laboratoire de mesure du Carbone 14 (LMC14) (Saclay, France). Profiles with less organic matter accumulation were poor in plant macroremains, and thus AMS ^{14}C dates were obtained from macroscopic charcoal fragments sampled from the charcoal layer representing the last fire (see below). Radiocarbon age determinations of wood charcoal are commonly used to date past forest fire events, even though such fire ages can be overestimated because of the phenomenon of inbuilt age resulting from dating wood material that could have been dead for a long time before it burned (Gavin 2001). However, dead trees usually decompose rapidly in wet boreal forests (Naesset 1999), and thus the inbuilt age effect was likely restricted to a few decades at most. A total of 26 AMS ^{14}C dates were obtained (9 from charcoal, 17 from macroremains; Table 2-2). We developed age-depth models for the five sites with the thickest organic matter accumulations. Age-depth models were based on calibrated ages and the age of the surface was established at −61calibrated years before present (cal. a BP, i.e., AD 2011; present = AD 1950 by convention). All ^{14}C age determinations were converted to cal. a BP using version 6.1 of the CALIB software (http://calib.qub.ac.uk/calib/), and reported as intercepts with 2σ ranges (Table 2-2). Age-depth models were constructed assuming vertical accumulation as a continuous monotonic process applying linear interpolation between dated levels. Only one date was available for site Venteux, but linear interpolation using this date and the surface (present time) yielded a realistic sedimentation rate (see Results).

2.4.4 Laboratory analyses

Contiguous 1-cm and 0.5-cm thick slices were cut from the sampled organic soil profiles. A 1-cm^3 subsample was retrieved from each slice and left for at least 1 hour in a 3% $(NaPO_3)_6$ dispersing solution, before gentle wet-sieving through 2 mm and 0.25 mm meshes. Macroscopic charcoal fragments from each subsample were counted and sorted under a dissecting microscope.

Determining the distance of the charcoal source is not a trivial issue because dispersal and deposition mechanisms are spatially and temporally variable (Clark et al. 1998, Ohlson and Tryterud 2000, Lynch et al. 2004). Charcoal fragments larger than 2 mm are a good proxy of *in situ* fire events because they usually do not travel more than a few meters from the flame front (Ohlson and Tryterud 2000, Asselin and Payette 2005) and resist fragmentation for millennia in soil deposits (de Lafontaine and Asselin 2011). Moreover, 94% of the charcoal mass produced in an *in situ* fire consists of particles ≥2.0 mm (Ohlson and Tryterud 2000). Charcoal deposition can vary substantially within a burned area – with some samples even being devoid of charcoal – when tree density is low, such as in a stand following partial logging (Ohlson and Tryterud 2000) or in the forest tundra (Asselin and Payette 2005). However, we sampled stands in the closed-crown boreal mixedwood forest, where tree density was high enough that charcoal would have been deposited more evenly on the ground after fire. Charcoal fragments larger than 0.25 mm, but smaller than 2 mm were used to identify extra-local fires, i.e., wildfires that occurred in the surrounding forest matrix. Such particles can travel several hundred meters from the flame front (Ohlson and Tryterud 2000).

Table 2-2 : Radiocarbon dates obtained from organic matter profiles from the 13 sampled post-fire residual patches.

Site	Sample depth (cm)	Dated material	Age (a BP)	Age (cal. BP, median probability)	Sample number
Limite	7-8	Charcoal	190±30	180	Beta321200
Jennifer	13-14	Charcoal	350±30	395	Beta321198
Mosquito2	18-19	Charcoal	1880±30	1830	Beta321199
Expérience	5-6	Charcoal	680±30	650	Beta326011
Mosquito1	5-6	Charcoal	190±30	180	Beta326012
Surprise	5-6	Charcoal	190±30	180	Beta326013
Falaise	6-7	Charcoal	750±30	685	Beta326008
Lauriane	8-9	Charcoal	250±30	295	Beta326012
Monsabrais	24.5-25	Macroremains	810±30	720	SacA 25579
	50-50.5	Macroremains	4975±45	5695	SacA 25578
	75-75.5	Macroremains	5790±45	6590	SacA 25577
	100-100.5	Macroremains	6090±45	6960	SacA 25576
	124.5-125.5	Macroremains	6275±45	7210	SacA 25575
	148-149	Macroremains	7265±50	8090	SacA 25574
Cadeau	10-10.5	Macroremains	530±30	540	Beta318903
	25.5-26	Macroremains	2160±35	2180	Poz43088
	50-50.5	Macroremains	2820±35	2925	Poz43087
	75-75.5	Macroremains	3695±35	4035	Poz43086
	97-98	Macroremains	5470±40	6275	Poz43085
Georges	14-14.5	Macroremains	140±30	140	Beta318904
	30-30.5	Macroremains	1240±30	1185	Beta318905
	47-47.5	Macroremains	4325±35	4890	Poz43091
Barrage	29-29.5	Macroremains	260±30	305	Beta321197
	57-57.5	Macroremains	900±30	825	Poz43090
Venteux	50-50.5	Macroremains	800±30	715	Poz43089

2.4.5 Fire history reconstructions

For the five sites having the thickest organic matter accumulation (>50 cm: Monsabrais, Cadeau, Georges, Barrage, Venteux), we used numerical treatments commonly employed to detect fire events from lacustrine deposits (e.g. Higuera et al. 2007, Ali et al. 2009). Because *in situ* fires generally produce both large and small charcoal particles (Ohlson and Tryterud 2000), we considered the detected fire events had affected the patches (*in situ* fire events) only if small (0.25-2 mm) and large (>2 mm) charcoal particles were simultaneously associated to the detected fire event. In other words, detected fire events based only on small charcoal particles were interpreted as extra-local (Clark 1988), i.e., fires that burned outside the residual patches.

The extra-local fire history was reconstructed using the CharAnalysis software (http://code.google.com/p/charanalysis/). Total charcoal concentrations (# cm^{-3}; sum of small and large particles), were converted into charcoal accumulation rates (CHAR; # cm^{-2} $year^{-1}$) using sediment accumulation rates as determined by radiocarbon dating. The CHAR series were decomposed into peak (C_{peak}) and background ($C_{background}$) components in order to identify fire events. C_{peak} represents the inferred fire events (a charcoal peak can correspond to one or more fires) (Long et al. 1998), whereas $C_{background}$ represents the slowly varying charcoal trend attributed to various factors, including long-term changes in fuel biomass and area burned. To separate fire-related (i.e., signal) from non-fire related variability (i.e., noise) in the C_{peak} component, a locally determined threshold value was set as the 99th percentile of a Gaussian distribution model of the noise in the C_{peak} time series. C_{peak} was screened and peaks were eliminated if the maximum charcoal count from a peak had a >1% chance of coming from the same Poisson-distributed population as the minimum count within the preceding 75 years (Gavin et al. 2006).

To optimize the identification of *in situ* fire events we used an approach based on large charcoal particles. However, high variability in the record prevented us from using the CharAnalysis procedure. Instead we followed the method developed by Higuera et al. (2005). Total large charcoal concentrations (#cm^{-3}), were converted into charcoal accumulation rates (CHAR; # cm^{-2} $year^{-1}$) using sediment accumulation rates as determined by radiocarbon dating. Median CHAR (hereafter mCHAR) was used to fix the threshold to separate peaks from background noise and thus identify potential fire events. Using mCHAR allows minimizing the effect of extreme CHAR values (Gavin et al. 2003). Because the peak component still encloses noise, varying multiples of the mCHAR have to be tested to identify the value that minimizes the detection of peaks not associated with known *in situ* fires (as recorded using historical records and dendrochronology (see Dansereau and Bergeron 1993, Bergeron 2000)). In other words, peaks more recent than AD 1717/1760 were interpreted as "false positive". Still following the Higuera et al. (2005) method, to be identified as a fire event, a CHAR peak had to exceed the threshold for three consecutive samples representing more than 10 consecutive years. Similarly, CHAR had to drop below the threshold for three samples and more than 10 consecutive years before one peak was considered finished and another could begin.

For the eight sites having less organic matter accumulation (<30 cm: Limite, Jennifer, Mosquito1, Mosquito2, Falaise, Expérience, Surprise, Lauriane), statistical analysis as described above was not possible and we only aimed to identify the most recent fire event by dating the topmost charcoal layer (including both small and large fragments) detected by visual inspection of the sequences.

2.5 Results

2.5.1 Chronological setting and accumulation rates

Organic matter accumulation began at least 8090 cal. a BP at the Monsabrais site, although most sequences covered shorter periods (Table 2-2). Core lengths were variable and in some cases did not appear to be correlated with the date of organic matter inception. For example, Mosquito 2 (25-cm accumulation) had an older basal date than Barrage (60-cm accumulation). Age-depth models showed variable shapes and the mean sedimentation rate was 55·cm a^{-1} (range: 10-218·a cm^{-1}). Lower accumulation rates were noted at Monsabrais between 720 and 5695 cal. a BP, at Georges between 1185 cal. a BP and 4890 cal. a BP and at Cadeau between 540 and 2180 cal. a BP (Fig. 2.2). These sudden leaps in ^{14}C ages were interpreted as potential sedimentary hiatuses, likely caused by consumption of organic matter during severe fire events (see Discussion). The linear interpolation for site Venteux (only two points: 50 cm and surface) yielded a sedimentation rate of 15.5·a cm^{-1}, in the lower part of the observed range, comparable to rates of sites Barrage (15.5) and George (14.4).

2.5.2 Fire history reconstruction

The presence of charcoal layers at all sites indicates that all residual patches sampled in this study experienced fire at least once in the past (Figs. 2.3, 2.4). For the patches with thicker organic matter accumulation (Monsabrais, Cadeau, Georges, Barrage, Venteux), and using small charcoal particles, C_{fire} was effectively separated from C_{noise}, as median SNIs were >4.3 (Table 2-3; Kelly et al. 2011). The resulting total number of fire events detected per core was 5 at Barrage and Monsabrais, 9 at Georges, 18 at Cadeau and 3 at Venteux (Fig. 2.3). The mean fire-free interval was 144 years at Barrage (range 42-239 years), 222 years at Venteux (range 171-256 years), 291 years at Cadeau (range 44-924 years), 362 years at Monsabrais (range 48-1152 years), and 455 years at Georges (range 5-1980 years). The 1717/1760 fire was detected at all patches except Monsabrais, but the 1923/1944 fire was only detected at Georges.

From the above-mentioned fire events detected in the charcoal records, only one (Monsabrais and Venteux) or two (Cadeau, Georges, Barrage) fires were also detected using large charcoal particles, and could thus be qualified as *in situ* fires (Fig. 2.3). The remaining fire events were thus extra-local and likely did not burn the sampled patches.

Taking into account all 13 sites, the time since the last *in situ* fire ranged from 160 to 1830 years (Figs. 2.3, 2.4). Eight sites burned during the AD 1717/1760 fire (i.e., between ~ 160 and 295 cal. a BP) (Figs. 2.3, 2.4). The remaining sites burned for the last time before AD 1717/1760 and thus escaped at least two consecutive fires (Figs. 2.3, 2.4).

The long-term fire history reconstructed at the five sites with thicker organic matter accumulation (>50 cm) revealed that site Cadeau remained fire-free for at least 4095 years during the middle Holocene (6275-2180 cal. a BP). Long fire-free periods were also recorded at site Monsabrais during the early to middle Holocene (2395 years, between 8090 and 5695 cal. a BP) and at site Venteux during the late Holocene (520 years, between 715 and 195 cal. a BP). Site Georges, with two sedimentary hiatuses, shows a more complicated history, but at least 1470 years elapsed between the two recorded fire events (excluding hiatuses). Site Barrage was affected by two fire events separated by 250 years, but nevertheless escaped the last two fires.

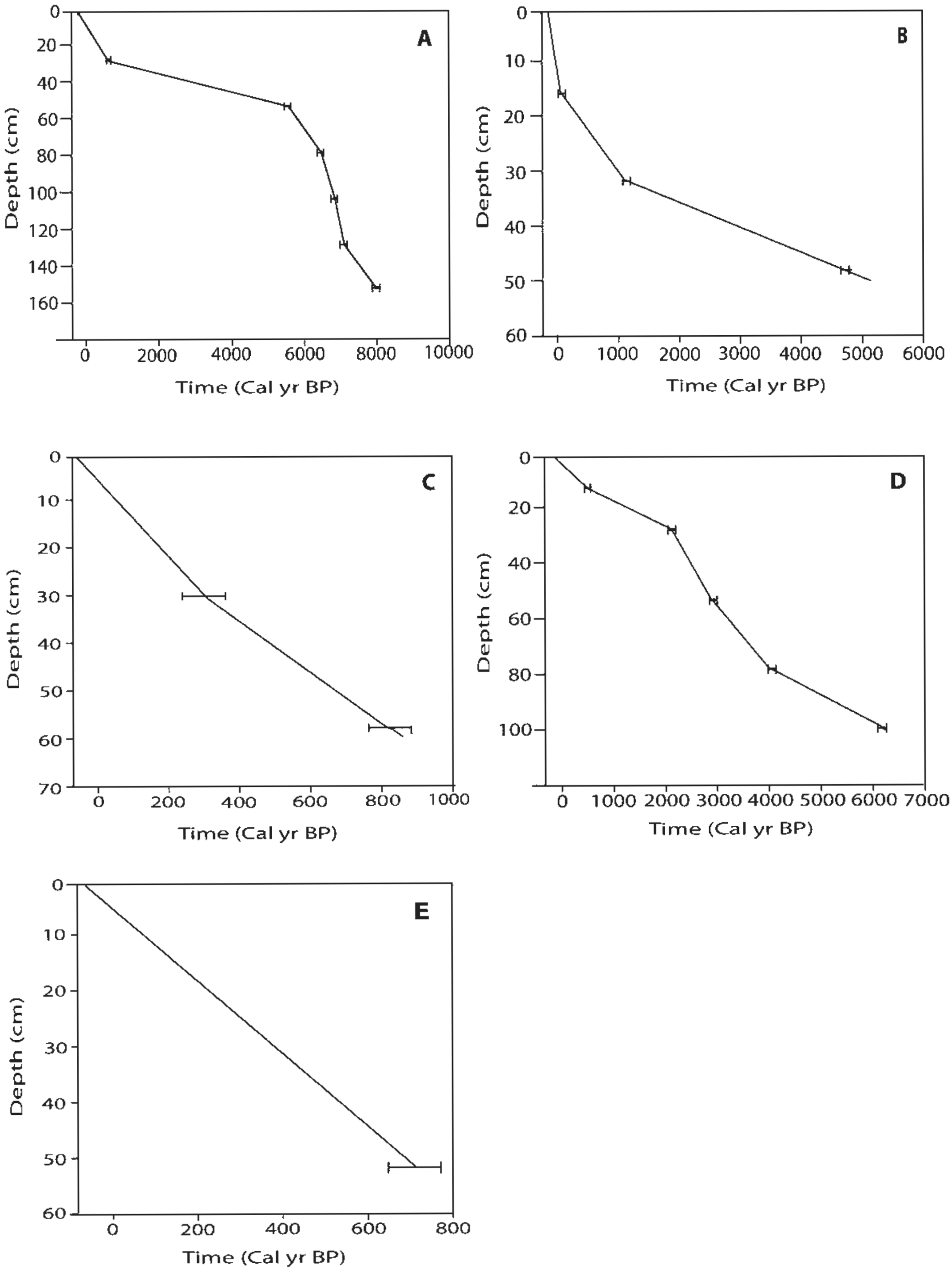

Figure 2.2: Age-depth models for the five sites with > 50 cm organic matter accumulation (A= Monsabrais, B= Georges, C= Barrage, D= Cadeau, E= Venteux).

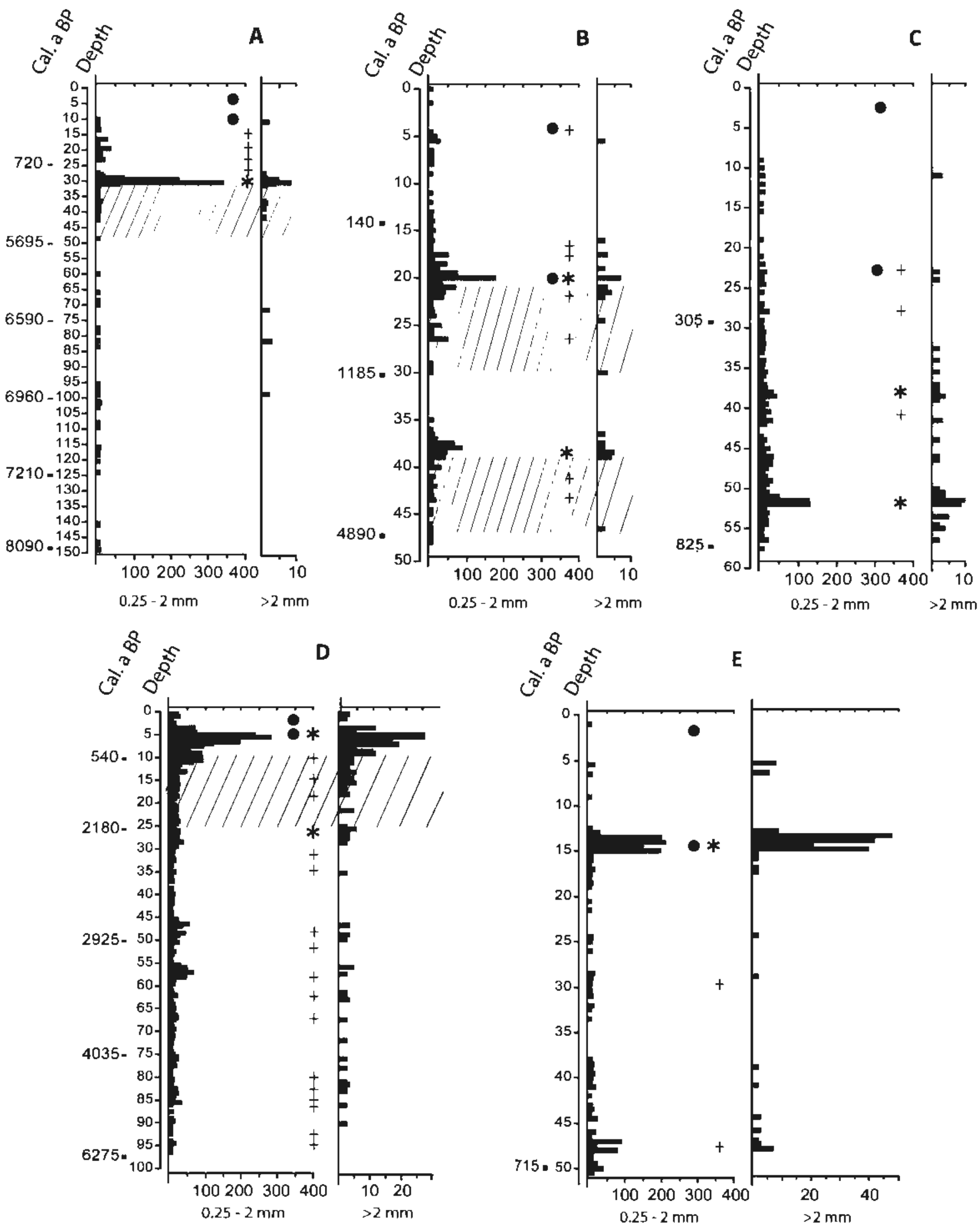

Figure 2.3: Holocene charcoal accumulation records according to depth in the organic matter profile for the five sites with > 50 cm organic matter accumulation (A= Monsabrais, B= Georges, C= Barrage, D= Cadeau, E= Venteux). Small (> 0.25 mm) and large (> 2mm) charcoal particles are shown separately. *In situ* fire events are indicated by an asterisk and extra-local fire events are indicated by a cross. Black dots indicate the 1923/1944 and 1717/1760 fires. Hatched areas represent sedimentary hiatuses. Calibrated ages (radiocarbon dates) are indicated beside corresponding depths.

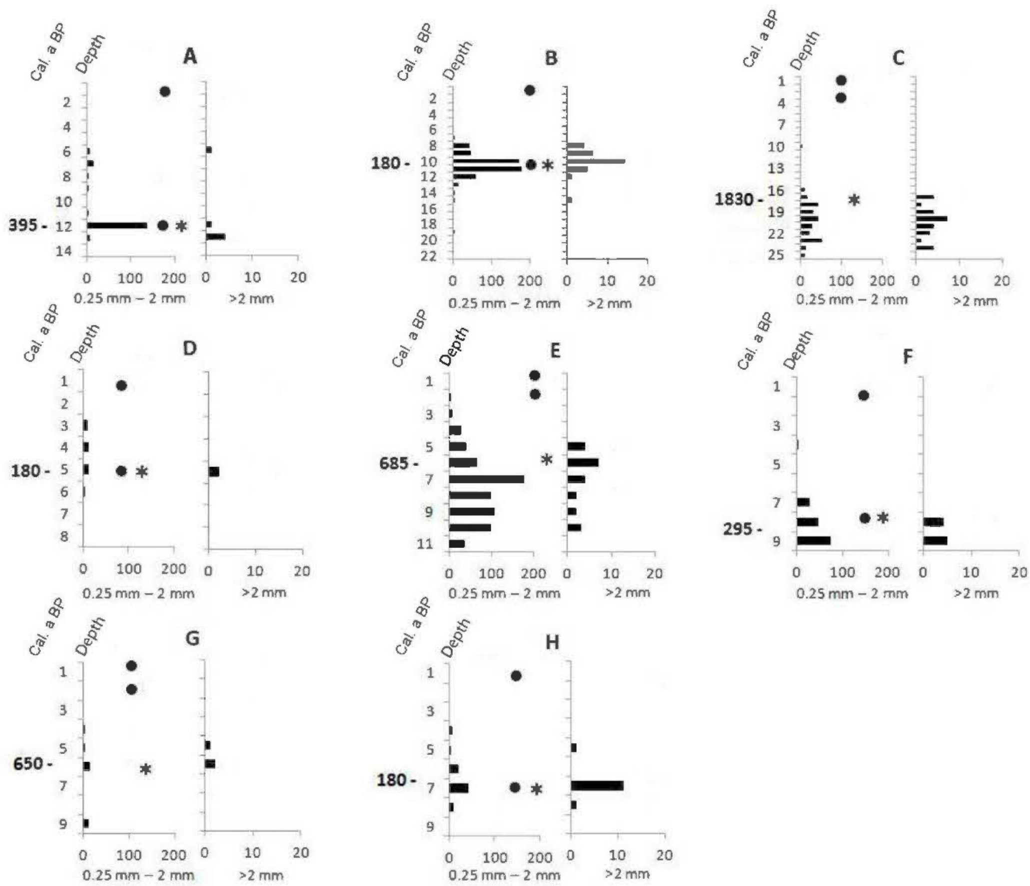

Figure 2.4: Charcoal concentration (# fragments/cm^3) according to depth in the organic matter profile for the eight sites with < 30 cm organic matter accumulation (A= Jennifer, B= Limite, C= Mosquito2, D= Mosquito1, E= Falaise, F= Lauriane, G= Experience, H= Surprise). Asterisks represent *in situ* fire events, and black dots indicate the 1923/1944 and 1717/1760 fires. Calibrated ages (radiocarbon dates) are indicated beside corresponding depths.

Table 2-3 : Output from CharAnalysis for the five sites with thick organic matter accumulation.

Site	Median sample resolution (year sample^{-1})	C_{back} smoothing windows (year)	Median SNI	Mean FRI	Fires (#)
Monsabrais	16	700	41.30	362	5
Cadeau	22	900	5.81	291	18
Georges	33	900	4.37	455	9
Barrage	6	300	4.74	144	5
Venteux	8	300	18.76	222	3

2.6 Discussion

The long-term regional fire history based on fire events recorded from the longest sequences shows fire-free intervals similar to mean or median fire-free intervals recorded in lacustrine sediments in the same area (Carcaillet et al. 2001, Cyr et al. 2009), i.e., between 144 and 455 years for this study (Table 2-3) compared to ~ 100-500 years for lacustrine studies.

The reconstruction of the *in situ* fire events showed that five of the 13 sampled post-fire residual patches escaped at least two consecutive fires (the 1923/1944 fire and the 1717/1760 fire) (Barrage, Expérience, Falaise, Monsabrais, Mosquito2) and thus displayed long ecological continuity and could be considered fire refuges. Their low susceptibility to fire could be due to particular microsite characteristics. Previous studies indeed have shown that topography, soil moisture, vegetation structure, or fuel characteristics could contribute to decrease fire severity (Eberhart and Woodard 1987, Román-Cuesta et al. 2009, Madoui et al. 2010). Peatlands, rock outcrops, lakes or rivers have also previously been shown to act as barriers to fire propagation (Eberhart and Woodard 1987, Madoui et al. 2011). The other eight sites (Cadeau, Georges, Jennifer, Lauriane, Limite, Mosquito1, Surprise, and Venteux) burned in the 1717/1760 fire and only escaped the most recent fire (1923/1944). These patches could have escaped fire due to stochastic processes, possibly involving the presence of fire breaks (e.g., peatlands, rock outcrops, lakes, rivers) or changes in meteorological conditions (e.g., sudden rain, change in wind speed or direction) that limited fire spread (Shroeder and Buck 1970). They can thus be considered random residual patches.

The long-term fire history reconstructed from the five sites with thicker organic matter accumulation (>50 cm) revealed that four of them (Cadeau, Georges, Monsabrais, Venteux) remained fire-free for very long periods during the Holocene (520-4095 years) and only burned during what appeared to have been exceptionally severe fires, as deduced by dendrochronological studies (Dansereau and Bergeron 1993, Bergeron 2000) or according to the sedimentary hiatuses created by the fire consumption of some part of the organic matter layer

(Pitkänen et al. 1999, Ali et al. 2008). Such low fire susceptibility and long ecological continuity is comparable to that of fire refuges in Fennoscandian and Russian boreal forests, where fire-free periods were shown to be as long as 3600 years (Hörnberg et al. 1998, Wallenius et al. 2004, 2005). Hence, three of the patches that burned in 1717/1760, first leading us to classify them as random residual patches (Cadeau, Georgees and Venteux; see above), have been fire refuges in the past.

2.7 Conclusion

Identifying fire events from charcoal particles embedded in soil deposits is not an easy task, and the combination of several methods was necessary to obtain a satisfactory reconstruction of *in situ* fire history of the sampled post-fire residual forest patches. Although the presence of fire refuges had already been documented in Fennoscandian and Russian boreal forests, this study is the first to describe their occurrence in the eastern Canadian boreal mixedwood forest. Furthermore, post-fire residual patches with longer ecological continuity (either recently or in the past), having escaped at least two consecutive fires, were differentiated from other sites having escaped only one fire, likely by chance. Fire refuges can persist in the landscape for several centuries, up to a few millennia, and could serve as refuges for plant and animal species associated with ancient forests and key structural factors dependent on ecological continuity. Special conservation efforts could thus target fire refuges owing to their old age, long ecological continuity and potential specific biological diversity associated to different microhabitats.

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CHAPITRE 3 LONG-TERM DYNAMICS OF FIRE REFUGES IN BOREAL MIXEDWOOD FORESTS

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3.1 Abstract

Burned areas in boreal mixedwood forests usually include tree patches that partially or entirely escaped fire. Some of these post-fire residual stands – called fire refuges – can escape several consecutive fires due to particular microsite conditions. Despite their potential importance as biodiversity hotspots, the long-term forest dynamics of fire refuges is unknown. High-resolution analysis of plant macroremains retrieved from forest organic matter profiles sampled in five fire refuges allowed us to describe up to 8000 years of forest dynamics. Our results display the importance of local conditions in forest dynamics. Wildfire was probably prevented by high moisture, as indicated by the presence of aquatic taxa and moisture-tolerant tree species. Lack of stand-replacing fire, coupled with organic matter accumulation, favored the millennial persistence of late-successional tree species. Shifts from spruce/larch dominance to fir/cedar dominance were noted at different occasions during the Holocene, probably resulting from endogenous processes.

3.2 Résumé

Les aires incendiées en forêt boréale mixte renferment souvent des îlots forestiers qui ont été partiellement ou entièrement épargnés par le feu. Certains de ces îlots – appelés refuges – ont la capacité d'échapper à plusieurs feux et de persister dans le paysage forestier pendant plusieurs siècles, probablement en raison de conditions stationnelles particulières défavorables à la propagation du feu. Malgré leur importance potentielle pour la biodiversité, la dynamique à long terme de la végétation des refuges n'a pas encore été documentée en forêt boréale mixte. Une analyse des macrorestes végétaux a été réalisée sur la matière organique des sols forestiers de cinq de ces refuges, permettant ainsi de reconstituer la dynamique de la végétation durant les 8000 dernières années. Nos résultats mettent en évidence l'importance des conditions locales dans les dynamiques forestières. La faible susceptibilité au feu des refuges est probablement liée à l'humidité de ces milieux, comme en atteste la présence d'espèces aquatiques (telles que les characées) et d'espèces arborescentes tolérantes à l'humidité (p.ex. : *Larix laricina*). Un changement majeur de végétation a été observé à la majorité des sites étudiés, à partir du couple *Larix laricina*/*Picea* spp. vers le couple *Abies balsamea*/*Thuja occidentalis*. Ce changement est probablement lié à des processus endogènes rythmés par les fluctuations de la nappe phréatique. L'absence d'espèces de début de succession après feu, associée à une forte accumulation de la matière organique, favorise le maintien d'espèces de fin de succession pendant des millénaires.

3.3 Introduction

Ecosystem-based forest management aims at preserving biodiversity and forest functions by reproducing the spatiotemporal patterns created by natural disturbances (Bergeron et al. 2002, Gauthier et al. 2008). Wildfire is one of the main natural disturbances shaping boreal forest landscapes (Zackrisson 1977, Payette 1992) and burned areas usually include tree patches that partially or entirely escaped fire – called post-fire residual stands (Gluck and Rempel 1996, Burton et al. 2008). Some of those post-fire residual stands – called fire refuges – can escape two or more consecutive fires and might remain unburned for up to several thousand years due to particular microsite conditions (Ouarmim et al. accepted). Many boreal forest attributes are related to the time elapsed since the last fire, including tree species composition, stand structure, abundance of woody debris and thickness of the soil organic matter layer (Hély et al. 2000, Cyr et al. 2009). Long-term ecological continuity in fire refuges could provide habitat for species associated with older successional stages (Selva 2003, Rivas Plata et al. 2008), as was observed in several Fennoscandian swamp forests (Zackrisson 1977, Esseen et al. 1992, Segerström 1997, Hörnberg et al. 1998). Despite their potential importance as biodiversity hotspots, the long-term forest dynamics of fire refuges has yet to be documented (Segerström 1997), and such stands have so far been largely ignored in conservation policies in North American boreal forests (Cyr et al. 2005, Gauthier et al. 2008).

Following wildfire in the Eastern Canadian boreal mixedwood forest, there generally is a gradual change over time from stands dominated by shade-intolerant species (mostly broadleaved species but also pines on drier sites) to shadetolerant species (mostly conifer species). Stand dynamics can broadly be divided into three stages: (i) the post-fire stage dominated by broad-leaved tree species, such as trembling aspen (Populus tremuloides) and paper birch (Betula papyrifera); (ii) the development of a mixedwood stand as coniferous species reach the canopy, such as balsam fir (Abies balsamea), eastern white cedar (Thuja occidentalis) and white spruce (Picea glauca); and (iii) the decline of broad-leaved species and the shift to dominance by coniferous species, some being characteristic of old-growth stands, such as eastern white cedar (Bergeron 2000). The third stage is generally reached 150–200 years after a stand-replacing fire (Bergeron and Dubuc 1989, Bergeron 2000) and it is generally assumed that gap dynamics maintain the stand in a relative steady state until the next fire (Kneeshaw and Gauthier 2003).

The species that currently characterize the Eastern Canadian boreal mixedwood forest have been present on the territory for several millennia (Richard 1980). During periods characterized by high fire frequencies (e.g. early and late Holocene) and low fire frequencies (e.g. middle Holocene), landscapes have typically been dominated by species adapted to fire [e.g. jack pine (Pinus banksiana) and black spruce (Picea mariana)] or not (e.g. balsam fir and eastern white cedar), respectively (Bergeron 1998).

The long-term vegetation dynamics of boreal and temperate forests are mostly controlled by wildfire (Bergeron et al. 2004). However, stand dynamics in the prolonged absence of fire (e.g. from several centuries to millennia) remain to be documented. The main objective of this study was to describe long-term vegetation history in fire refuges of the Eastern Canadian boreal mixedwood forest using highresolution sedimentary records of plant macroremains.

3.4 Materials and methods

3.4.1 Study area

The study area is located within the Lake Duparquet Research and Teaching Forest (Fig. 3.1), in the Eastern Canadian boreal mixedwood forest characterized by balsam fir, paper birch, white spruce, trembling aspen and eastern white cedar as the main tree species (Dansereau and Bergeron 1993, Bergeron 2000). Geomorphology is characterized by the presence of a massive clay deposit left by pro-glacial lakes Barlow and Ojibway (Vincent and Hardy 1977). The climate is cold temperate with a mean annual temperature of 0.7 °C and mean annual precipitation of 889.8mm (Environment Canada 2011). The closest meteorological station is located at La Sarre, 42 km north of the study area.

In the Eastern Canadian mixedwood boreal forests, the two principal causes of natural disturbances, wildfire and spruce budworm [Choristoneura fumiferana (Clem.)], have been widely studied (e.g. Dansereau and Bergeron 1993, Morin et al. 1993). The fire cycle for the Lake Duparquet area has been estimated at 63 years before 1870 and more than 99 years afterwards (Bergeron 1991). Spruce budworm outbreaks followed a 30-year cycle during the 20th century (Morin et al. 1993), and the 1972–1987 outbreak resulted in the death of most of the mature balsam fir trees (Bergeron et al. 1995).

3.4.2 Site selection and sampling

Typical post-fire succession in the Eastern Canadian boreal mixedwood forest involves a gradual change from pioneering stands dominated by broad-leaved tree species (trembling aspen and paper birch), to mid-successional mixed stands, and to late-successional coniferous stands dominated by balsam fir and eastern white cedar (Bergeron 2000). Post-fire residual stands were thus distinguished from the surrounding forest matrix based on forest structure and composition retrieved from ecoforestry maps. Thirteen accessible post-fire residual stands were identified in areas where the last known fire occurred in 1944 or 1923, depending on site location (Dansereau and Bergeron 1993), and the second-to-last fire occurred in 1717 or 1760. These stands were coniferous oldgrowth forest patches (with balsam fir or eastern white cedar) embedded in a matrix of younger deciduous forests (with trembling aspen or paper birch) (Fig. 3.2).

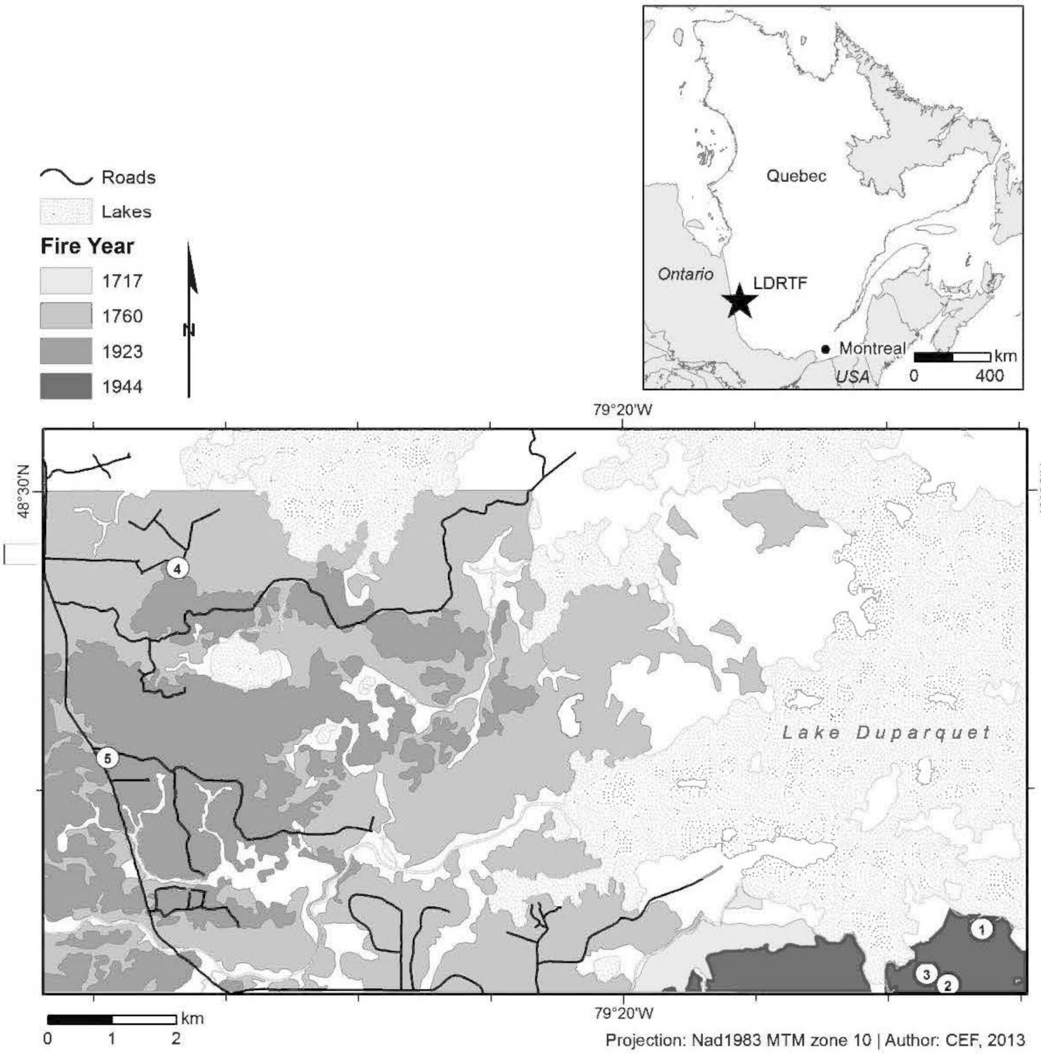

Figure 3.1: Location of the studied fire refuges in the eastern Canadian boreal mixedwood forest (Lake Duparquet Research and Teaching Forest): (1) Georges; (2) Venteux, (3) Cadeau, (4) Barrage, (5) Monsabrais. Areas burned by the 1717, 1760, 1923 and 1944 fires are shown in different shades of gray.

Long-term fire reconstruction based on macroscopic soil charcoal analyses revealed that eight stands currently are fire refuges, or have been refuges in the past, before burning during an exceptionally severe fire (Ouarmimet al. accepted). The other stands only escaped the most recent fire, and thus displayed shorter ecological continuity (Ouarmim et al. accepted). From the eight fire refuges, the five sites with the thickest organic matter accumulation (>50 cm, Monsabrais, Cadeau, Georges, Barrage and Venteux; see Table 3-1) were selected to maximize the potential for paleoecological analysis (Fig. 3.1). A Russian corer was used to sample one complete organic matter profile (i.e. down to the mineral soil) in a micro-depression located in the center of each refuge.

3.4.3 Laboratory analyses

A previous analysis of macroscopic charcoal was carried out to detect fire events (Ouarmim et al. accepted). To reconstruct forest dynamics, contiguous 0.5-cm-thick slices were cut from the sampled organic matter profiles. A 1-cm3 subsample was retrieved from each slice and gently wet sieved through a 0.25-mm mesh. Plant macroremains (twigs, seeds, needles, leaves and macroscopic charcoal) from each subsample were sorted and counted under a dissecting microscope. Knowing that the production of macroremains differs among species, for each taxon, counts per level were divided by the maximum value recorded, resulting in data having a maximum range between zero and 1. Radiocarbon dating (14C) by accelerator mass spectrometry (AMS) was conducted on 17 plant macroremain samples by Beta Analytic, Inc. (Miami, FL, USA), Poznan Radiocarbon Laboratory (Poznan, Poland) and Laboratoire de mesure du Carbone 14 (LMC14) (Saclay, France). All 14C age determinations were converted to calendar years before present (cal a BP; present¼1950AD) using version 6.1 of the Calib software (Stuiver and Reimer 2005), and reported as intercepts with 2 sigma ranges (Table 3-2).

Figure 3.2: Transition between a fire refuge (right) dominated by eastern white cedar and the surrounding matrix (left) dominated by paper birch.

Table 3-1 : Characteristics of the five sampled fire refuges.

Name	Site number (as in Fig. 3.1)	Dominant species	Stand density (trees/ha)	Organic matter thickness (cm)	Number of *in situ* fires
Georges	1	*Abies balsamea*	3373	49	2
Venteux	2	*Thuja occidentalis*	1211	50.5	1
Cadeau	3	*Thuja occidentalis*	2354	98	2
Barrage	4	*Thuja occidentalis*	1271	59	1
Monsabrais	5	*Abies balsamea*	1551	149	1

Sudden leaps in 14C ages observed at Monsabrais between 720 and 5695 cal a BP, at Georges between 1185 and 4890 cal a BP, and at Cadeau between 540 and 2180 cal a BP (Table 3-2) were interpreted as sedimentary hiatuses, i.e. loss of organic matter, probably due to combustion during severe fire events (Ali et al. 2008). The TILIA and CONISS programs were used, respectively, to plot macroremains data and to identify vegetation periods by cluster analysis (Grimm, 1987).

Table 3-2 : Radiocarbon dates obtained from macroremains sampled in organic matter profiles from the five studied fire refuges.

Site	Sample depth (cm)	^{14}C age (yr BP)	Cal yr BP (Median probability)	Reference
Monsabrais	24.5-25	810±30	720	SacA 25579
	50-50.5	4975±45	5695	SacA 25578
	75-75.5	5790±45	6590	SacA 25577
	100-100.5	6090±45	6960	SacA 25576
	124.5-125.5	6275±45	7210	SacA 25575
	148-149	7265±50	8090	SacA 25574
Cadeau	10-10.5	530±30	540	Beta318903
	25.5-26	2160±35	2180	Poz43088
	50-50.5	2820±35	2925	Poz43087
	75-75.5	3695±35	4035	Poz43086
	97-98	5470±40	6275	Poz43085
Georges	14-14.5	140± 30	140	Beta318904
	30-30.5	1240±30	1185	Beta318905
	47-47.5	4325±35	4890	Poz43091
Barrage	29-29.5	260±30	305	Beta321197
	57-57.5	900±30	825	Poz43090
Venteux	50-50.5	800±30	715	Poz43089

3.5 Results

The same four taxa dominated tree assemblages at all sites during the Holocene, although their respective abundances varied with time: eastern larch (Larix laricina), spruce (black and/or white), balsam fir and eastern white cedar. The presence of sedimentary hiatuses prevented a complete Holocene history to be reconstructed at all sites. Nevertheless, each of the three main periods of the Holocene (i.e. early, middle and late) was recorded at least at one site.

3.5.1 *Early Holocene (ca. 8090-5000 cal a BP)*

At site Monsabrais, the early Holocene can be subdivided into three periods (Fig. 3.3A). The first period corresponds to an aquatic environment (between 8090 and 7695 years) characterized by relatively high percentages of aquatic taxa, including macrofossils of algae (Chara, blue–green algae), Potamogeton sp., Typha sp. and punctual presence of herbaceous species, predominantly Carex sp. and Rumex sp. Abundance of tree taxa was very low during this period. The second period corresponds to the afforestation process, with the arrival of eastern larch ca. 7695 cal a BP, and spruce ca. 7055 cal a BP. Even though balsam fir and eastern white cedar established soon after spruce ca. 6965 cal a BP, larch and spruce remained dominant until ca. 6750 cal a BP. The third period records a major dominance shift, from spruce/ larch to fir/cedar. Nevertheless, spruce abundance increased again at the end of the third period (between ca. 6250 and 5770 cal a BP) coincident with a decrease of fir and cedar. At site Cadeau (Fig. 3.3B) the beginning of the first period was assigned to the early Holocene. Plant assemblages were dominated by larch, spruce and cedar, and their relative abundance fluctuated through time. Fir was not as dominant here as it was at the Monsabrais site.

3.5.2 *Mid-Holocene (ca. 5000-3000 cal a BP)*

Sites Monsabrais and Georges presented sedimentary hiatuses for the mid-Holocene period (Fig. 3.3A and C). At site Cadeau, the start of the mid-Holocene (period 1) was characterized by the continuation of the larch–spruce–cedar period (fir abundance remained low) (Fig. 3.3B). Then, starting from ca. 3325 cal a BP (period 2), the abundance of tree taxa was considerably lower and mostly dominated by spruce. This decrease in local tree abundance coincided with a slight increase in charcoal concentration.

3.5.3 *Late Holocence (ca. 3000-0 cal a BP)*

At sites Cadeau (periods 3 and 4) and Monsabrais (period 4), all tree species abundances were very low in the late Holocene, compared with the earlier periods (Fig. 3.3A and B). Although eastern white cedar is currently present at the

Monsabrais site, no macroremains of this species were found in the topmost part of the organic matter profile. Similarly, no fir or spruce macroremains were recorded in the topmost part of the Cadeau profile, despite these species being currently present at the site.

At site Georges, two fires occurred during the late Holocene (Fig. 3.3C), causing sedimentary hiatuses that complicated data interpretations. Consequently, we have limited our interpretation to the last 20 cm, which could be divided into two periods. A post-fire cohort dominated by spruce and larch dominated the stand between 160 and 60 cal a BP, before a rapid shift towards fir/cedar, which still dominate the stand today.

At site Barrage, the late Holocene period can be subdivided into five periods (Fig. 3.3D). The first was dominated by aquatic taxa with some balsam fir from the bottom of the sequence, ca. 825 cal a BP. The second period started at ca. 750 cal a BP with a dominance shift from aquatic taxa to fir and spruce. The third one, from ca. 280 to 160 cal a BP, was dominated by larch, although fir and spruce remained present. The fourth period, from 160 to 80 cal a BP, showed a sharp decrease of larch, whereas fir and spruce abundances remained high. Then, dominance shifted to fir/cedar in the last period, from 80 cal a BP to the present.

At site Venteux (Fig. 3.3E), the late Holocene can be subdivided into three periods. The first period was characterized by low abundances of eastern white cedar and balsam fir. Then, between ca. 590 and 200 cal a BP, the second period showed the co-occurrence of spruce, larch and fir. A fire prompted the switch from the second to the third period, characterized by the dominance of balsam fir and eastern white cedar.

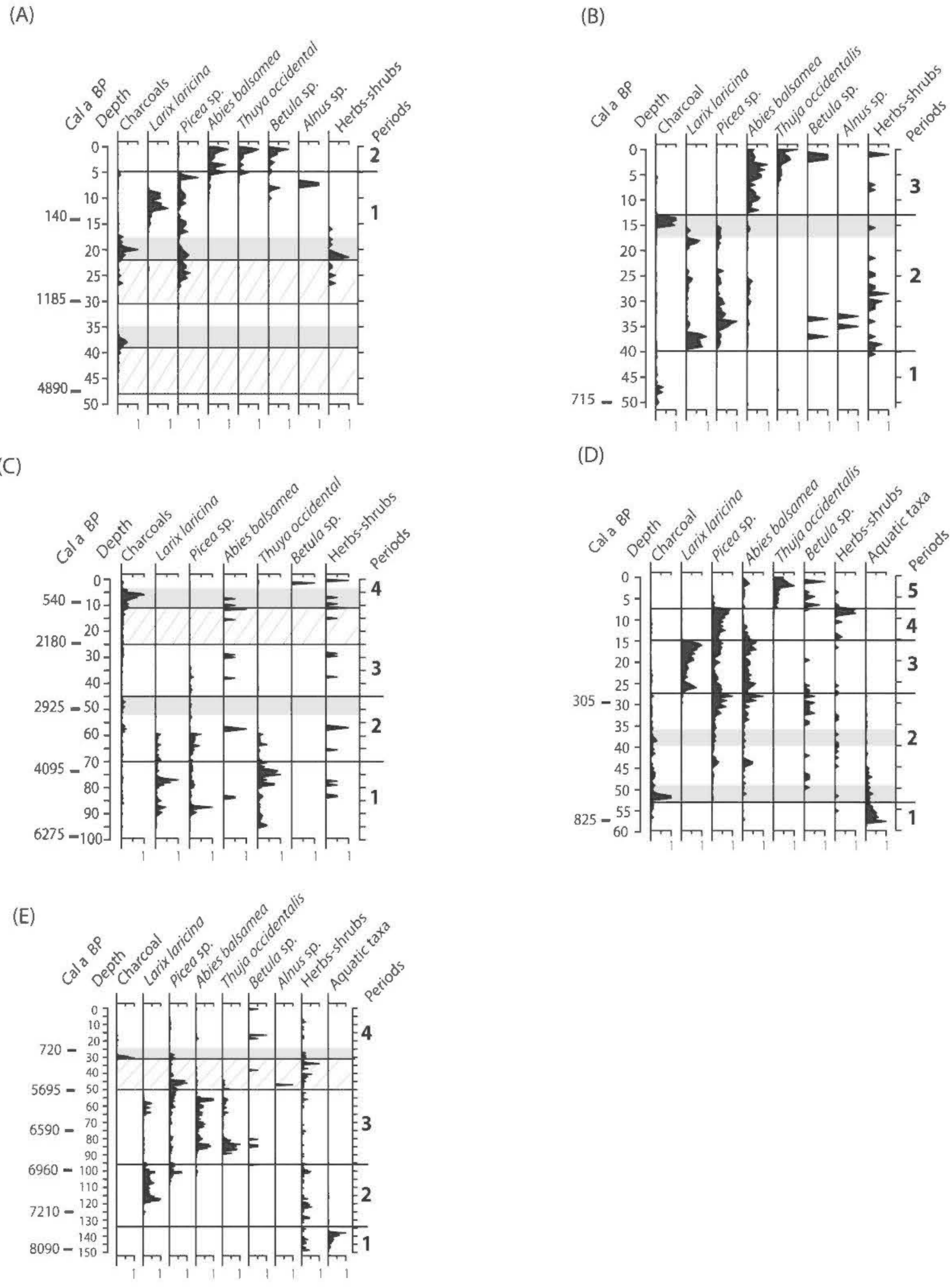

Figure 3.3: Charcoal and plant macroremain records (rescaled between 0 and 1) for sites Georges (A), Venteux (B), Cadeau (C), Barrage (D), and Monsabrais (E). Horizontal lines separate the periods identified by cluster analysis. Grey bars indicate in situ fire events and hatched bars indicate sedimentary hiatuses.

3.6 Discussion

Four tree taxa were present in various abundances throughout the Holocene at all sites: eastern white cedar, spruce, balsam fir and eastern larch. These species are fire-sensitive (except white spruce) and common in lowland sites, bogs and hydric sites (Eyre 1980, Bergeron and Dubuc 1989, Burns and Honkala 1990). The occurrence of these species near or at the bottom of the profiles indicates that organic matter accumulation is not only attributable to time since fire (Heinselman 1973) or climate (Charman 2002), but also to endogenic factors, especially hydrological conditions (Payette 2001). The accumulation of organic matter at a site is influenced by allogenic and autogenic factors, which reduce soil temperature, rate of organic matter decomposition, microbial activity, thickness of the aerated soil layer and nutrient availability (Taylor et al. 1989, Payette 2001). Two different processes could explain the initiation of organic matter accumulation in this study: (i) terrestrialization at sites Monsabrais and Barrage, as shown by the presence of aquatic taxa at the bottom of the sequences; and (ii) paludification at sites Venteux, Cadeau and Georges, explained by the absence of aquatic taxa at the bottom of the sequences (Gorham 1957, Payette 2001).

3.6.1 Successional pathways

The early Holocene composition at the Monsabrais site, dominated by aquatic and herbaceous taxa, probably corresponds to a eutrophic pond community with floating aquatic macrophytes, surrounded by an emergent shore-marsh (Kuhry et al. 1993). The creation of this pond could have resulted from the infilling of a relictual lake following the retreat of post-glacial lake Ojibway ca. 8200 cal a BP (Vincent and Hardy 1977). The aquatic community was progressively replaced by a forest community (spruce and larch) as eutrophication continued. The spruce/larch association is currently observed in peatlands, or in wet, lowland sites (Rudolf 1966, Rowe 1972).

A period dominated by aquatic taxa was also recorded in the late Holocene at site Barrage. Here, this could be explained by a flash flood as tree taxa were present concurrently, which excludes the possibility of the site having been a lake or a pond progressively colonized by trees through eutrophication. Flash floods were previously recorded in other boreal sites (Payette and Delwaide 2004, Asselin and Payette 2006, Ali et al. 2008). Alternatively, the site could have been subject to periods of exceptionally wet conditions, flooding parts of the forested area (Denneler et al. 2008). All sites, except Cadeau, recorded a dominance shift from spruce/larch to fir/cedar. However, the shifts occurred at different periods, thus excluding a regional climatic forcing and pointing instead to internal processes. Spruce and larch are considered pioneer species on humid, organic sites (Tilton 1977, Eyre 1980, Harvey et al. 2002), and larch is generally the first tree species to invade filled-lake bogs (Elliott 1979). The spruce/larch period varied in duration from 100 years at site Georges to 305 years at sites Venteux and Monsabrais. These differences in residence time could be related to differential proximity of balsam fir and eastern white cedar seed sources (Asselin et al. 2001).

Although particular local conditions explained the initiation of forest succession, their effect decreased with time elapsed since disturbance, allowing for directional succession to take place and for late-successional species to establish (Bergeron and Dubuc 1989, De Grandpré et al. 1993). The association of eastern white cedar and balsam fir can be found on richer hydric soils and on mesic to subhydric sites (Harvey et al. 2002). This is evidence that conditions remained somewhat wet in fire refuges, even several hundred years after the initiation of organic matter accumulation. Nevertheless, the dominance shift from spruce/larch to fir/cedar could indicate a lowering of the water table (Bergeron et al. 1983). The fir/cedar period can last up to 1680 years (site Monsabrais).

The low abundance of balsam fir at site Cadeau is hard to explain, although the nearby presence of black ash (Fraxinus nigra) and alder (Alnus sp.) (seen during fieldwork but not recorded in the organic matter profile) suggests a possible role of periodical flooding (Denneler et al. 2008). The other coniferous species (larch, spruce, cedar) would sustain such stress, but not balsam fir (Ahlgren and Hansen 1957). Some species were not recorded in the topmost organic sediments, although they are currently present at the sites: cedar at Monsabrais, as well as fir and spruce at Cadeau. Macroremains are deposited a short distance (<20 m) from their origin (Bhiry and Filion 2001), and thus species that were not dominant at the sites could have been missed if they were not present within a few tens of meters of the sampling point.

3.6.2 Post-fire succession

Sediment charcoal records (Ouarmim et al. accepted) indicated that sites Monsabrais and Venteux each burned once during the Holocene, whereas sites Cadeau, Barrage and Georges recorded two fire events (Table 3-1; Fig. 3.3). Some of these fire events were probably quite severe, as they created sedimentary hiatuses in the records. Such high-severity fires would be needed to burn fire refuges, that usually escape fire due to humid soil conditions (Ouarmim et al. accepted).

Different assemblages of tree species were recorded following fire: spruce/larch (Georges), spruce/fir (Barrage, Monsabrais), cedar/spruce (Cadeau) and fir/cedar (Venteux). Larch or spruce (black spruce) can establish after fire on hydric soils (Harvey et al. 2002), but the presence of fir and cedar in early successional stages is more surprising. The low occurrence of broad-leaved species in early successional stages is also unusual in boreal mixedwood forests (Harvey and Bergeron 1989, Bergeron and Charron 1994, Bergeron 2000) and could be explained by the thick humus layer preventing the recruitment of trembling aspen and paper birch (Lavertu et al. 1994), coupled with low occurrence of fire disturbances through the post-fire residual stands. Proximity of coniferous seed sources is important, as seeds of balsam fir, white spruce and eastern white cedar are generally dispersed <100m from parent trees (Asselin et al. 2001).

3.7 Conclusion

Post-fire forest dynamics in fire refuges does not appear to follow the traditional successional pathway observed in boreal mixedwood forests. Humid site conditions favor species associated with moist areas like eastern larch, and a thick organic matter layer prevents the establishment of early successional broad-leaved species. In humid forest ecosystems, variations in water supply play an important role in determining ecosystem structure and function (Schuur and Matson 2001). The characteristics of the studied sites are not only less prone to fire, but they also favor the long-term persistence of late-successional tree species. Such ecological continuity might be crucial for species closely associated with old-growth forests (Harper et al. 2003), especially for species with low dispersal capacity (Martikainen et al. 2000, Gandhi et al. 2004). Fire refuges have conservation value as ecosystem types and they should thus be protected to meet the objectives of biodiversity maintenance central to ecosystem- based forest management.

3.8 Acknowledgments

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CHAPITRE 4 STAND STRUCTURE IN FIRE REFUGES OF THE EASTERN CANADIAN BOREAL MIXEDWOOD FOREST

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4.1 Abstract

Wildfires in boreal forest ecosystems usually spare tree stands called post-fire residual patches. There are two types of post-fire residual patches: (1) patches that only escaped fire by chance, probably due to local meteorological conditions unsuitable for fire spread at the moment fire reached their surroundings (random post-fire residual patches), and (2) patches with lower fire susceptibility, that escaped several consecutive fires, likely due to particular site characteristics (fire refuges). Special conservation efforts could target fire refuges owing to their old age, long ecological continuity, and potential specific biological diversity. Here we compared the stand characteristics of 13 post-fire residual patches from the eastern Canadian boreal mixedwood forest to develop guidelines and information for forest managers to differentiate fire refuges from random post-fire residual patches. Two main structural characteristics differentiated fire refuges from random post-fire residual patches: mean tree diameter and thickness of the soil organic matter layer. Thick organic matter accumulation in fire refuges is likely linked to a paludification process, which in turn reduces stand productivity, and thus, mean tree diameter.

4.2 Résumé

Les feux en forêt boréale mixte laissent souvent derrière eux des îlots épargnés appelés « îlots résiduels ». On peut distinguer deux types d'îlots : (1) des îlots qui ont échappé uniquement au dernier feu, par hasard, en raison de conditions météorologiques défavorables à la propagation du feu (îlots transitoires), et (2) des îlots qui ont échappé à plusieurs feux successifs en raison de caractéristiques stationnelles particulières, et qui sont qualifiés de refuges. Du fait de leur âge et de la continuité écologique qui les caractérisent, les refuges ont un potentiel de biodiversité important et devraient faire l'objet d'une protection particulière. Pour ce faire, il est important de pouvoir distinguer les deux types d'îlots résiduels. Nous avons donc comparé les caractéristiques de 13 îlots résiduels après feu de la forêt boréale mixte du Canada pour identifier des critères facilement mesurables sur le terrain permettant aux forestiers de les différentier. Deux principales caractéristiques structurales différencient les refuges des autres îlots résiduels : le diamètre moyen des arbres et l'épaisseur de la matière organique du sol. En d'autres termes, les refuges présentent une forte accumulation de matière organique associée à des diamètres moyens plus faibles en comparaison avec les autres îlots résiduels. L'épaisse couche de matière organique des refuges est probablement liée à un processus de paludification qui a pour effet de réduire la productivité des sites, expliquant le faible diamètre moyen des arbres.

4.3 Introduction

Preservation of biological diversity and consideration of natural processes are two issues that are increasingly seen as being of importance to forestry in the boreal zone (Franklin 1993, Weber and Stocks 1998). At the landscape level, fire suppression practices have led to major changes in species composition and stand structure (Esseen et al. 1997, Haeussler and Kneeshaw 2003, Kardynal et al. 2011). Large-scale clearcuts over the past 50 years have homogenized the landscapes and considerably reduced the proportion of old boreal forests (Östlund et al. 1997, Cyr et al. 2009). Species associated with old forests have thus declined in abundance (Archambault et al. 1998, Martikainen et al. 2000). To prevent biodiversity loss, new forest harvesting practices have been developed that aim to reproduce the spatiotemporal patterns created by natural disturbances (Hansen et al. 1991, Franklin 1993, Hunter 1993, Gauthier et al. 2008).

To use natural disturbance dynamics to guide forest management decisions calls for a precise understanding of their spatial and temporal dynamics. Wildfire is the main natural disturbance in boreal forests (Zackrisson 1977, Payette 1992) and burned areas usually include tree patches, so-called "residual patches" that partially or entirely escaped fire (Gluck and Rempel 1996, Burton et al. 2008). Residual patches are habitat islands with diverse structural legacies and unique environmental conditions (Foster et al. 1998, Keeton 2000). They can serve as sources for the recolonization of burned areas (Keeton 2000, Asselin et al. 2001), as refuges for disturbance-sensitive species (Gasaway and Dubois 1985, Gandhi et al. 2001), and they can increase structural complexity in the forest landscape (Zenner 2000).

In North American boreal mixedwood forests, two types of post-fire residual patches have been distinguished: (1) patches that only escaped the last fire, probably due to local meteorological conditions unsuitable for fire spread occurring at the moment fire reached their surroundings (random post-fire residual patches), and (2) patches that escaped several consecutive fires, also called fire refuges, likely due to particular site characteristics (Ouarmim et al. accepted). Fire refuges can escape fire for several centuries, up to a few millennia, i.e., much longer than the fire frequency recorded in the surrounding landscape (Ouarmim et al. accepted). These patches are characterized by long ecological continuity and specific biological diversity (Selva et al. 2003). Hence, they should be subjected to special conservation efforts. Recent forest management approaches include structural retention and active creation of structural and spatial complexity (e.g., Bergeron et al. 2002, Gauthier et al. 2008). However, the difference between the two types of post-fire residual patches has so far been largely ignored in conservation policies in the North American boreal forest and should be included in future forest management planning (Gasaway and DuBois 1985, Bergeron et al. 2002, Cyr et al. 2005, Gauthier et al. 2008).

The aim of the present study was to compare the stand characteristics of post-fire residual patches from the eastern Canadian boreal mixedwood forest. Our specific objectives were to (1) establish which stand characteristics most accurately discriminate between fire refuges and random post-fire residual patches; and (2) evaluate the effects of environmental conditions and disturbance history on the characteristics of post-fire residual patches.

4.4 Material and methods

4.4.1 Study area

The study area is located within the Lake Duparquet Research and Teaching Forest (Fig.4.1), in the eastern Canadian boreal mixedwood forest characterized by balsam fir (*Abies balsamea* (L.) Mill.), paper birch (*Betula papyrifera* Marsh.), white spruce (*Picea glauca* (Moench) Voss.), trembling aspen (*Populus tremuloides* Michx.), and eastern white cedar (*Thuja occidentalis* L.) as the main tree species (Dansereau and Bergeron 1993, Bergeron 2000). Geomorphology is characterized by the presence of a massive clay deposit left by pro-glacial lakes Barlow and Ojibway (Vincent and Hardy 1977). The climate is cold temperate with a mean annual temperature of 0.7 °C and mean annual precipitation of 889.8 mm (Environment Canada 2011). The fire cycle for the Lake Duparquet area has been estimated at 63 years prior to 1870 and more than 99 years afterwards (Bergeron 1991). Spruce budworm outbreaks occur at approximately 40-year intervals (Boulanger and Arseneault 2004), and the last one (1972-1987) killed most of the mature balsam fir trees in the study area (Morin et al. 1993, Bergeron et al. 1995).

4.4.2 Identification of residual patches

Typical post-fire succession in the eastern Canadian boreal mixedwood forest involves a gradual change from pioneering stands dominated by deciduous tree species (trembling aspen and paper birch) during the first *ca.* 75 years, to mixed stands with an important white spruce component in the next *ca.* 75 years, to coniferous stands dominated by balsam fir and eastern white cedar after *ca.* 150 years (Bergeron 2000). Thirteen post-fire residual patches were selected in young forests that burned for the last time in 1944 or 1923 AD (Dansereau and Bergeron 1993, Bergeron 2000) (Fig. 4.1). Areas affected by the 1944 and 1923 fires had previously burned in 1717 and 1760 AD, respectively (Dansereau and Bergeron 1993, Bergeron 2000). Post-fire residual patches were thus distinguished from the surrounding forest matrix based on forest structure and composition retrieved from ecoforestry maps (scale: 1/15 000) (Ministère des Ressources naturelles http://www.mrn.gouv.qc.ca/forets/inventaire/fiches/couches-peuplements-ecoforestiers.jsp).

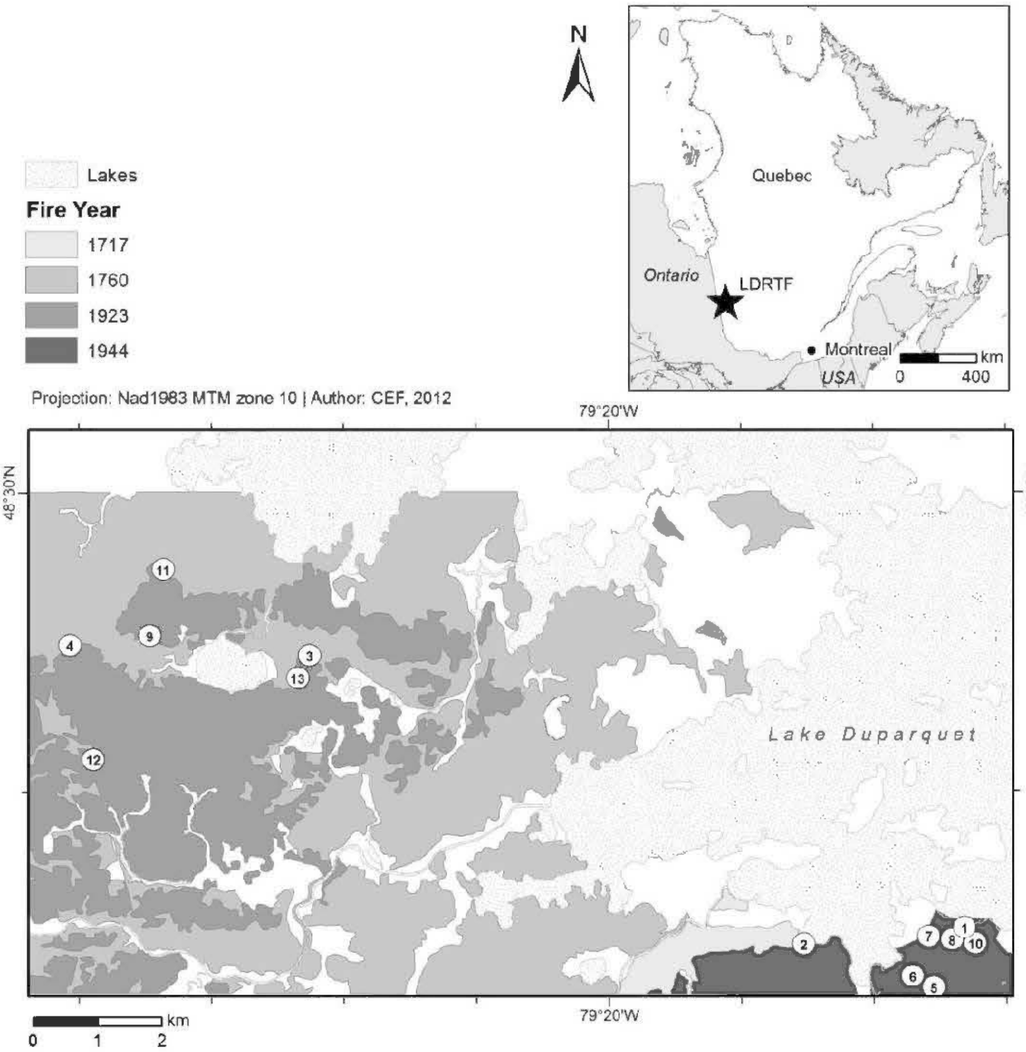

Figure 4.1: Location of the studied post-fire residual forest patches in the eastern Canadian boreal mixedwood forest (Lake Duparquet Research and Teaching Forest: LDRTF): (1) Georges; (2) Limite; (3) Mosquito1; (4) Surprise; (5) Venteux; (6) Cadeau; (7) Lauriane; (8) Jennifer; (9) Expérience; (10) Falaise; (11) Barrage; (12) Monsabrais; and (13) Mosquito2. Areas burned by the 1717, 1760, 1923 and 1944 fires are shown in different shades of gray.

These patches were identified as old-growth coniferous polygons (with balsam fir or eastern white cedar) embedded in a matrix of younger deciduous forests (with trembling aspen or paper birch). The polygons on ecoforestry maps are between 1 and 8 ha in size, and thus it is possible that smaller post-fire residual patches were not identified.

Long-term fire reconstruction based on radiocarbon dating of macroscopic soil charcoal peaks identified in soil organic matter profiles revealed that 8 patches could be classified as fire refuges, although some of them burned recently (in 1717 or 1760) during severe fires (Ouarmim et al. accepted). Random residual patches only escaped the most recent fire, and thus displayed shorter ecological continuity (Ouarmim et al. accepted).

4.4.3 Data collection

Between 3 and 9 sampling points were randomly located in each of the 13 sampled residual patches, depending on their area. Sampling points were distant from each other by at least 30 m. Trees and snags were inventoried using the point centered quadrant method (Mueller-Dombois and Ellenberg 1974). At each sampling point, four dominant trees, four suppressed trees and four snags were identified to the species level and measured (height and diameter at breast height (DBH)). Distance between trees or snags and quadrant center was measured to calculate densities per species (McRae et al. 1979). Percent occurrence was calculated for each tree species. The thickness of the soil organic matter layer was measured at six points with a meter stick for the stands with thinner organic matter layers (< 30 cm), while only one measure was taken at the five sites with thicker organic matter layers (> 50 cm).

Presence of coarse woody debris were sampled (CWD; diameter > 7.6 cm) in each patch, along 20-m sided equilateral triangles following the line intersect method (Van Wagner 1968, 1980, McRae et al. 1979). The diameter and length of logs were measured and the volume of logs was calculated (m^3 per triangle).

4.4.4 Analyses

To examine differences between patch types, multiple median comparison tests (Mann-Whitney non-parametric test) were computed on mean stand characteristics. The significant variables identified through these comparisons were used in a partitioning around medoids (PAM) analysis, which uses principal component analysis to display a predefined number of clusters in reduced space, i.e., on a two-dimensional graph (Pison et al. 1999). The value of *k* (number of clusters) was fixed to 2, corresponding to patch classification as either fire refuges or random post-fire residual patches. Diameter-frequency distributions of fire refuges and random post-fire residual patches were compared using a Chi-square test run on absolute frequencies of ten diameter classes.

Stand characteristics can be influenced by time since the last fire (e.g., Bergeron 2000, Simard et al. 2007, Brassard et al. 2008). Linear regressions were used to evaluate the effect of time since the last fire (Table 4-2, Fig. 4.3) on significant stand characteristics.

All statistical analyses were conducted using the R software (R Development Core Team 2012).

4.5 Results

Four stand characteristics showed significant differences between fire refuges and random post-fire residual patches: mean diameter of living trees, mean diameter of balsam fir trees, mean diameter of white spruce trees (Var 14, 16, and 17), and mean thickness of the soil organic matter layer (Var 36) (Table 4-1). Mean tree diameter perfectly discriminated the two types of post-fire residual patches, with lower values in fire refuges (30.9 ± 2.1 cm *vs.* 24.1 ± 1.2 cm), although diameter frequency distributions did not significantly differ between patch types ($\chi^2 = 0.18$). The mean thickness of the soil organic matter layer also differed between fire refuges (56.9 ± 47.9 cm) and random post-fire residual patches (12.4 ± 5.8 cm), although the values partly overlapped.

The four significant variables together explained 80.04% of the variability between sites, as revealed by PAM analysis (Fig. 4.2). Principal components 1 and 2 respectively show the influence of mean tree diameter and mean thickness of the soil organic matter layer. Refuges and random post-fire residual patches are clearly separated on the plot.

Table 4-1 : Mean and standard deviation of stand characteristics of the fire refuges and random post-fire residual patches and results of Mann-Whitney comparison tests.

Variable	Code	Fire refuges	Random patches	*p*
Tree species composition				
Thuja occidentalis	Var1	44.8 ± 20.9 %	23.9 ± 16.1	0.1238
Abies balsamea	Var2	21.8 ± 12.9 %	23.3 ± 18.1	0.6579
Picea spp.	Var3	12.3 ± 3.9 %	25.0 ± 18.0	0.2413
Betula papyrifera	Var4	25.2 ± 19.3%	29.4 ± 7.2	0.1630
Populus tremuloides	Var5	6.3 ± 3.0 %	8.3 ± 0.0	0.3329
Number of tree species	Var6	4.0 ± 1.0	4.0 ± 0.0	0.6331
Living trees				
Total density	Var7	1404.3 ± 923.4 trees/ha	772.4 ± 419.9	0.4507
Mean height	Var8	13.5 ± 2.7 m	16.2 ± 3.2	0.1421
Height *Thuja occidentalis*	Var9	11.5 ± 2.3 m	14.0 ± 2.9	0.1232
Height *Abies balsamea*	Var10	12.5 ± 3.4 m	15.5 ± 3.5	0.2222
Height *Picea* spp.	Var11	17.1 ± 5.9 m	18.8 ± 6.3	1.0000
Height *Betula papyrifera*	Var12	15.7 ± 2.9 m	17.6 ± 2.8	0.2224
Height *Populus tremuloides*	Var13	16.5 ± 10.6 m	22.3 ± 8.5	0.4000
Mean diameter	Var14	24.1 ± 1.2 cm	30.9 ± 2.1	0.0016**
Diameter *Thuja occidentalis*	Var15	29.7 ± 5.3 cm	30.7 ± 6.4	0.2844
Diameter *Abies balsamea*	Var16	16.0 ± 3.5 cm	23.6 ± 2.9	0.0147*
Diameter *Picea* spp.	Var17	28.1 ± 6.3 cm	42.3 ± 6.4	0.0242*
Diameter *Betula papyrifera*	Var18	22.1 ± 3.8 cm	23.6 ± 5.1	0.5152
Diameter *Populus tremuloides*	Var19	31.0 ± 14.9 cm	46.8 ± 3.1	0.4000
Mean total volume	Var20	1755.5 ± 1129.7 m^3/ha	938.8 ± 437.6	0.1274
Volume *Thuja occidentalis*	Var21	1007.7 ± 1097.5 m^3/ha	375.6 ± 303.1	0.3543
Volume *Abies balsamea*	Var22	128.6 ± 111.3 m^3/ha	51.2 ± 26.3	0.1490
Volume *Picea* spp.	Var23	279.8 ± 105.7 m^3/ha	217 ± 151.5	0.5556
Volume *Betula papyrifera*	Var24	482.6 ± 469.7 m^3/ha	365.0 ± 176.3	0.9095
Volume *Populus tremuloides*	Var25	59.0 ± 9.9 m^3/ha	180.5 ± 128.0	0.3333
Dead trees				
Total density (snags)	Var26	370.6 ± 289.7 snags/ha	288.6 ± 140.0	0.9433
Thuja occidentalis	Var27	20.3 ± 4.3 %	12.9 ± 5.4	0.1555
Abies balsamea	Var28	68.5 ± 23 %	68.7 ± 11.9	0.7136
Betula papyrifera	Var29	23.5 ± 25.2 %	26.1 ± 10.1	0.2903
Mean diameter (snags)	Var30	14.3 ± 3.9 cm	20.8 ± 10.3	0.2844
Diameter *Thuja occidentalis*	Var31	15.9 ± 6.5 cm	23.7 ± 11.3	0.4127
Diameter *Abies balsamea*	Var32	12.7 ± 2.0 cm	15.1 ± 2.8	0.1427
Diameter *Picea* spp.	Var33	28.2 ± 16.3 cm	28.2 ± 0.0	0.1658
Diameter *Betula papyrifera*	Var34	15.2 ± 7.1 cm	30.5 ± 19.8	0.1905
Mean total volume (logs)	Var35	1.2 ± 0.97 m^3	1.9 ± 1.38	0.2222
Soil properties				
Thickness of the soil organic matter layer	Var36	56.9 ± 47.9 cm	12.4 ± 5.9	0.0326*

Linear regressions showed no significant relationship between time since the last local fire and either mean tree diameter or mean thickness of the soil organic matter layer (Fig. 4.3).

Table 4-2 : Time since the last local fire at the 13 sampled patches and identification as fire refuge or not (after Ouarmim et al. (accepted)).

Site name	Site number (as in Fig. 4.1)	Time since last local fire (years)	Fire refuge?
Georges	1	160	Yes
Limite	2	180	No
Mosquito 1	3	180	No
Surprise	4	180	No
Venteux	5	195	Yes
Cadeau	6	295	Yes
Lauriane	7	295	No
Jennifer	8	395	No
Expérience	9	650	Yes
Falaise	10	685	Yes
Barrage	11	467	Yes
Monsabrais	12	880	Yes
Mosquito 2	13	1830	Yes

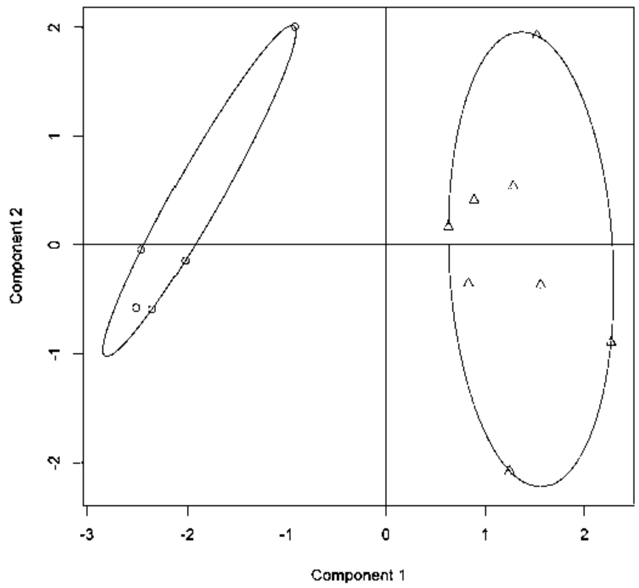

Figure 4.2: Partitioning around medoids (PAM) of the 13 sampled patches using characteristics with significant differences between refuges (triangles) and random patches (circles). The two components together explain 80.04 % of the variability between sites.

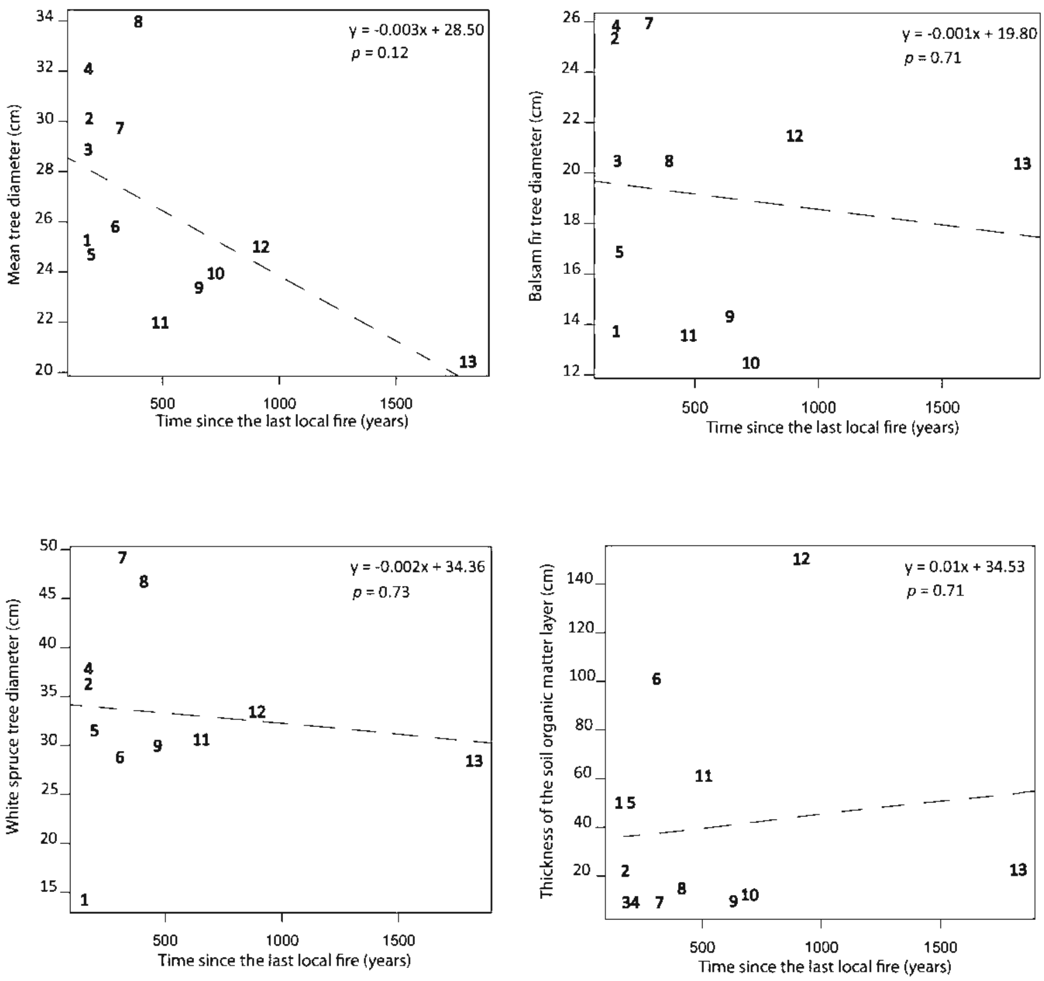

Figure 4.3: Linear regressions of stand characteristics discriminating post-fire residual patches according to time since the last local fire.

4.6 Discussion

Structural attributes of forest stands are increasingly recognized as being of importance in understanding and managing forest ecosystems (Franklin et al. 2002). Forest managers need a comprehensive understanding of natural stand development processes when designing silvicultural systems that integrate ecological and economic objectives. The long ecological continuity displayed by some post-fire residual patches should be taken into account in the development of silvicultural systems that emulate natural processes. These patches maintain critical structural elements sustaining particular organisms and ecological processes (Franklin et al. 2000). For example, fire refuges are wet and dominated by coniferous tree species, with few if any broadleaved species, at all successional stages (Ouarmim et al. 2014).

Our results showed that most of the structural and compositional characteristics of post-fire residual patches were highly variable (Table 4-1). Tree species composition did not differ between fire refuges and random post-fire residual patches, likely because post-fire succession rapidly reaches a stable state in old-growth forests (Bergeron and Dubuc 1989). Most structural changes in old-growth boreal forests occur as a result of tree replacement processes including secondary disturbances (spruce budworm outbreaks, windthrow) and gap dynamics. Such small-scale disturbances create favorable microsites for pioneer species (trembling aspen and paper birch) explaining their presence in old stands (Kuuluvainen 1994, Frelich and Reich 1995, Kneeshaw and Bergeron 1998, Bergeron 2000).

Coarse woody debris (CWD) is an important functional and structural component of forested ecosystems and it is related to the standing forest structure, as well as to stem growth and mortality (Harmon et al. 1986). Studies of CWD within forest chronosequences generally report a U-shaped temporal pattern (Lambert et al. 1980, Spies et al. 1988), with more dead wood in young and old forests. However, coarse woody debris accumulation models in the mixedwood boreal forest show a different pattern characterized by a period of load increase until stand maturity, followed by a period of load decrease during late successional stages (Hély et al. 2000). The key factors explaining this different pattern in boreal mixedwood forests are the species replacement occurring during succession (Bergeron and Dubuc 1989, Bergeron and Charron 1994), differences in species productivity (Paré and Bergeron 1995), rapid decay rates (Lambert et al. 1980, Harmon et al. 1986), and disturbances such as cyclic spruce budworm outbreaks killing mature balsam firs and favoring paper birch and/or balsam fir regeneration (Kneeshaw and Bergeron 1998). The absence of a difference between the two types of post-fire residual patches with respect to dead wood can likely be attributed to similar forest composition, to the propensity of eastern white cedar to produce small-diameter logs (Hély et al. 2000), as well as to the effect of the last spruce budworm outbreak (1972-1987) that killed most of the mature balsam fir trees (Bergeron et al. 1995).

Two stand characteristics allowed us to discriminate the two types of post-fire residual patches, explaining 80 % of the variability between sites: mean tree diameter, and mean thickness of the soil organic matter layer. Future studies could help identify additional variables that would increase discriminating efficiency. Interestingly, although some fire refuges burned during severe fires and thus had time since the last fire comparable to random post-fire residual patches, they still were identified as refuges. This finding bolsters the assertion that fire refuges harbor particular site characteristics (see below). Even though they might burn during exceptionally severe fires, they still show lower fire susceptibility compared to the surrounding forest matrix.

Tree diameter and height are closely related, and they vary according to environmental conditions (Wang et al. 2006). However, only mean diameter was significantly different between fire refuges and random post-fire residual patches, probably because height is more variable due to higher sensibility to site quality, small-scale disturbances, temperature, and water supply (Aiba and Kitayama 1999, Parish et al. 1999, Martinez and Lopez-Portillo 2003, Zenner 2000, Druckenbrod et al. 2005). While it might seem counterintuitive that trees are smaller in fire refuges, it can be partly explained by gap-phase dynamics where the oldest trees are replaced by younger ones (Kneeshaw and Bergeron 1998), and thus, mean tree age is lower than time since the last fire.

The soil organic matter layer was generally thicker in fire refuges than in random post-fire residual patches. The absence of a correlation between mean thickness of the soil organic matter layer and time since the last fire could be explained by the presence of sedimentary hiatuses, likely due to consumption of part of the organic matter layer during severe fire events (Ali et al. 2008, Ouarmim et al. 2014). Excessive accumulation of soil organic matter, called paludification, could be due to a higher position of the water table in topographic lows, which slows the decomposition rate (Heinselman 1970, Payette 2001).

Paludification appears to be a key factor preventing fire spread in refuges. While the studied refuges showed a rather flat topography at ground surface, their thicker soil organic matter layer compared to that of the surrounding matrix indicates they are located in small depressions favoring the persistence of wet conditions (Ouarmim et al. 2014). Decreased stand productivity due to paludification could also explain the smaller mean tree diameters measured in fire refuges (Paré and Bergeron 1995, Boudreault et al. 2002). Paludification can indeed cause structural changes, including decreases in tree basal area, canopy height, canopy cover, and abundance of deadwood (Harper et al. 2003). Interestingly, our results show that these effects persist even after a fire refuge burns during an exceptionally severe fire. Indeed, we found no correlation between time since the last local fire and mean tree diameter; although diameter still discriminated between refuges and random post-fire residual patches.

4.7 Conclusion

This study revealed that it is possible to discriminate fire refuges from random post-fire residual forest patches by using mean tree diameter and mean thickness of the soil organic matter layer. Paludification leads to organic matter accumulation, in turn reducing stand productivity, resulting in smaller mean tree diameter. These structural features can be measured easily and can help forest managers distinguish fire refuges from random residual patches. Knowing the proportion of each residual patch type in an area will allow the design of management and conservation strategies based on natural stand dynamics and ecological variability. Both types of post-fire residual patches have so far been treated indistinctively. This could cause the loss of the unique structural features provided by patches having escaped fire for longer periods. Tree retention inside harvested areas should focus on stands having characteristics similar to post-fire residual patches, and should respect the naturally-occurring proportion of patches with short and long ecological continuity.

4.8 Acknowledgements

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CHAPITRE 5 BURNING POTENTIAL OF FIRE REFUGES IN THE MIXEDWOOD BOREAL FOREST

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Article à soumettre

5.1 Abstract

In boreal ecosystems wildfire severity, i.e., the extent of fire-related tree mortality, is affected by environmental conditions and fire intensity. A burned area usually includes tree patches that partially or entirely escaped fire. Some of these post-fire residual patches only escaped fire by chance, probably due to local meteorological conditions unsuitable for fire spread at the moment fire reached their surroundings (random patches), whereas other patches with lower fire susceptibility, also called fire refuges, escaped several consecutive fires, likely due to particular site characteristics. The objectives of this study were to model fire behavior in fire refuges in the boreal mixedwood forest, and to test which stand and landscape characteristics best explain the occurrence of fire refuges. The results highlight the important role of higher fuel moisture in fire refuges, likely attributed to their location in shallow depressions. Other factors often said to explain the occurrence of fire refuges, such as low fuel load or presence of fire breaks, did not play a key role in the present study. Indeed, the topography is flat in the study area, and fuel load in fire refuges is actually higher than in the surrounding forest matrix. Fire refuges could thus be viewed as “soaked powder kegs”. However, lower precipitation or higher frequency of drought events predicted under future climate change could affect the occurrence and persistence of post-fire residual patches.

5.2 Résumé

Au sein de la forêt boréale, les aires brûlées renferment souvent des îlots forestiers qui ont échappé aux feux. Il existe deux types d'îlots : des îlots transitoires qui ont échappé uniquement au dernier feu et des refuges, plus persistants dans le temps, qui ont la capacité d'échapper au feu de façon récurrente, du fait de leurs caractéristiques stationnelles. L'objectif de cette étude était de modéliser le comportement du feu dans les refuges en comparaison avec la matrice forestière et d'identifier les caractéristiques stationnelles qui leur permettent d'échapper aux feux qui brûlent la matrice. L'approche utilisée pour évaluer la susceptibilité au feu des refuges est fondée sur des modèles de prédiction du comportement du feu. Les résultats des simulations mettent en exergue l'importance de l'humidité stationnelle dans la rémanence des refuges, excluant les effets directs des facteurs les plus souvent invoqués dans la littérature, tels que la présence de coupe-feu dans l'environnement des îlots et l'abondance de combustible. Les conditions d'humidité particulières des refuges sont probablement attribuables à la présence de faibles dépressions topographiques masquées en surface par l'accumulation de la matière organique. Du fait de la charge en combustible des refuges, ces derniers pourraient être considérés comme des « poudrières trempées ». Les changements climatiques pourraient toutefois influencer le potentiel de création et de maintien d'îlots refuges en raison de précipitations moins abondantes ou de sécheresses plus fréquentes.

5.3 Introduction

Fire is one of the dominant ecological drivers affecting vegetation patterns and dynamics in the boreal region (Zackrisson 1977, Payette 1992). Disturbance effects vary spatially depending upon fire behavior (Swanson et al. 1988, Agee 1993) and fire return interval. A burned area usually includes residual patches that partially or entirely escaped fire (Gluck and Rempel 1996, Wallenius et al. 2004, 2005, Burton et al. 2008). Two types of post-fire residual patches have been distinguished in North American boreal mixedwood forests (Ouarmim et al. accepted): (1) "random residual patches" that only escaped the last fire, probably due to local meteorological conditions unsuitable for fire spread, and (2) "fire refuges" that escaped several consecutive fires, likely due to particular site conditions.

Fire behavior varies spatially depending on fuel features (composition, load, and spatial arrangement), landscape structure and composition, soils, topographic constraints, and weather (Swanson et al. 1988, Agee 1993). Numerous studies have documented the spatial distribution of post-fire residual patches at the landscape scale (Foster 1983, Eberhart and Woodward 1987, Cyr et al. 2007, Madoui et al. 2011, Keeton et al. 2004, Dragotescu et al. 2012). They showed that the occurrence of residual patches within burned areas could be related to topography, soil moisture, wind dynamics during fire, seasonal timing of the burn as well as timing relative to diurnal temperature and wind patterns, fuel load, or presence of fire breaks. However, the respective roles of these factors likely vary according to study region and residual patch type (refuge or not). Here we propose to evaluate the roles of different ecological factors in the occurrence and long-term persistence of fire refuges in the mixedwood boreal forest of northeastern North America. We hypothesize that environmental conditions in fire refuges are less prone to fire activity compared to random residual patches.

The objectives of the present study were threefold: (i) to simulate realistic fire behavior in mixedwood boreal forest stands, with coniferous post-fire residual patches and fire refuges embedded in a mixed mosaic, (ii) to test if refuges are less susceptible to fire than random patches, and (iii) to evaluate the respective roles of various factors in explaining the occurrence and persistence of fire refuges at the landscape scale.

A non-destructive approach for estimating susceptibility to fire of refuges is to use modeling. As post-fire residual stands (refuges or not) would be classified as conifer-dominated mixedwood stands like the surrounding matrix, we decided to characterize all forest stands based on their fuel load and tree species composition, and to combine three existing fire behavior models in order to take advantage of their respective strengths. This methodology is original because it allowed us to move from a qualitative characterization of forest stands simulating realistic values of fire behavior (Fire Behavior Prediction system (hereafter FBP, Forestry Canada Fire Danger Group 1992, Wotton et al. 2009)), to a calibrated quantitative characterization of forest stands in terms of fuels types and loads (BehavePlus system (Burgan and Rothermel 1984, Andrews 2008)) that better discriminates the different stand types while still predicting realistic fire behavior at the stand level (BehavePlus) and burned areas at the landscape level (FlmaMap3 model (Stratton 2004, Finney 2006)).

5.4 Material and methods

5.4.1 Study area

The studied landscape covers the Lake Duparquet Research and Teaching Forest (Fig. 5.1), in the eastern Canadian boreal mixedwood forest, characterized by balsam fir (*Abies balsamea* (L.) Mill.), paper birch (*Betula papyrifera* Marsh.), white spruce (*Picea glauca* (Moench), trembling aspen (*Populus tremuloides* Michx.), and eastern white cedar (*Thuja occidentalis* L.) as the main tree species

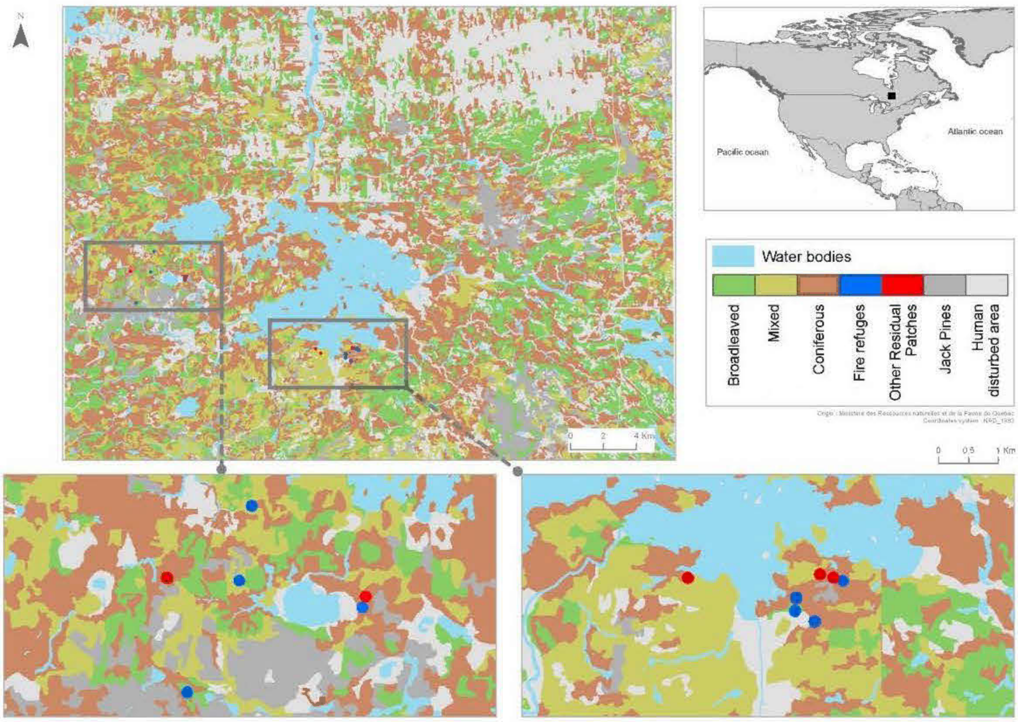

Figure 5.1: Forest fuel types in the Lake Duparquet Research and Teaching Forest. Fire refuges are indicated by red dots and other post-fire residual stands by blue circles.

(Bergeron 2000). Geomorphology is characterized by the presence of a massive clay deposit left by pro-glacial lakes Barlow and Ojibway (Vincent and Hardy 1977). The climate is cold temperate with a mean annual temperature of 0.7 °C and mean annual precipitation of 889.8 mm (Environment Canada 2011). The closest meteorological station is located at La Sarre, 42 km north of the study area.

In the eastern Canadian boreal mixedwood forest, the two main natural disturbances, wildfire and spruce budworm (*Choristoneura fumiferana* (Clem.)) outbreaks, have been widely studied (e.g., Bergeron and Dubuc 1989, Dansereau and Bergeron 1993, Morin et al. 1993). The fire cycle for the Lake Duparquet area has been estimated at 63 years prior to 1870 and more than 99 years afterwards (Bergeron 1991). The last spruce budworm outbreak (1972-1987) resulted in the death of most of the mature balsam fir trees (Bergeron et al. 1995).

5.4.2 Site selection

Typical post-fire succession in the eastern Canadian boreal mixedwood forest involves a gradual change from pioneering stands dominated by deciduous tree species (trembling aspen or paper birch) during the first *ca.* 75 years, to mixed stands with an important white spruce component in the next *ca.* 75 years, to coniferous stands dominated by balsam fir and eastern white cedar after *ca.* 150 years (Bergeron 2000). It was thus possible to distinguish post-fire residual patches from the surrounding forest matrix based on forest structure and composition retrieved from ecoforestry maps produced by the Quebec Ministry of Natural Resources (http://www.mrn.gouv.qc.ca/forets/inventaire/fiches/couches-peuplements-ecoforestiers.jsp). Thirteen post-fire residual patches were selected in areas where the last known fire occurred in 1944 or 1923, depending on site location (Dansereau and Bergeron 1993, Bergeron 2000), and the second-to-last fire occurred in 1717 or 1760. These stands were identified as coniferous old-growth forest patches (with balsam fir or eastern white cedar) embedded in a matrix of younger deciduous forests (with trembling aspen or white birch).

Based on a palaeoecological reconstruction of fire activity in the selected post-fire residual patches (Ouarmin et al. accepted), eight patches were identified as current or past fire refuges that had escaped two or more consecutive fires recently or in the more distant past. The five other post-fire residual patches only escaped the most recent fire (Table 5.1).

5.4.3 Field sampling

Stand composition, structure, and fuel load were recorded in each patch according to the sampling design set by Hély et al. (2000a), along a single 30-m sided equilateral triangle (McRae et al. 1979). Forest stand structure and canopy characteristics (tree species and diameter at breast height, total height, and canopy base height) were estimated from 24 trees (12 dominant and 12 suppressed), present near the triangle vertices and selected using the point-centered quadrant method (McRae et al. 1979).

Table 5-1: Characteristics of the 13 sampled post-fire residual stands.

Stand type	Organic matter thickness (cm)	Slope (°)
Refuge	49	0
Refuge	50.5	0
Refuge	98	0
Refuge	9	3
Refuge	59	1
Refuge	149	2
Refuge	25	0
Refuge	11	4
Residual	9	5
Residual	14	7
Residual	9	3
Residual	22	0
Residual	8	0

All fuel types defined in the BehavePlus system (Burgan and Rothermel 1984) were measured within each stand along or apart triangle sides (Hély et al.2000a) depending on fuel type. Woody debris from three American time lag classes (desiccation time) (1-h, 10-h and 100-h time lags) corresponding to pieces < 0.6 cm, 0.6 - 2.5 cm and 2.7 - 7.6 cm in diameter, respectively (Burgan and Rothermel 1984), were measured by the line intersect method (Van Wagner 1968, 1980). We used the same species coefficients and equations as in Hély et al. (2000b), as they had been adapted to the boreal mixedwood forest. Shrub, herbs and litter material were measured in six 1-m^2 quadrats (Brown et al. 1982) evenly spaced along the 90-m triangle transect. Shrub loads were estimated from basal stem diameter measurements using species dry weight – basal diameter relationships set from shrub samples previously collected in the Duparquet area (Aubin 1999, Hély unpublished data). Litter and duff layer depths were measured in six quadrats (25 cm x 25 cm) and total litter and duff material was separately collected to obtain oven-dried weights.

Stand characteristics of young (deciduous), intermediate (mixed), and old (coniferous) (The stands of *Pinus banksiana* were not be considered in the analysis) post-fire stands representative of the mixedwood boreal forest mosaic used in the studied landscape were obtained from Hély (2000) and applied to the ecoforestry map polygons (Fig. 5.1). Stand characteristics used in the fire behavior simulations are reported in Table 5.2.

Table 5-2: Fuel load characteristics.

Fuel Type	Litter load	1-h fuel load (t/ha)	10-h fuel load (t/ha)	100-h fuel load (t/ha)
Forest matrix				
Broadleaved	4	0.06	1.2	0.8
Mixed	4.6	0.1	1.2	1
Coniferous	4.5	0.3	2.1	2.9
Residual stands				
Fire refuges	6.9	0.26	0.24	3.1
Other residual patches	8.17	0.3	0.34	0.43

5.4.4 Weather data

To simulate fire ignition and early fire behavior under different weather conditions, two fire weather indices from the Canadian Fire Weather system (Van Wagner, 1987) were selected, representing moderate and high fire danger (Fire Weather Index (FWI) = 5 and 15, respectively), as used by the SOPFEU (Quebec Society for the protection of forests against fire). Two days representative of each fire danger were used in order to take into account wind or dry air effects and capture the intrinsic weather variability (Table 5.3).

Table 5-3: Fire weather indexes (Hély et al., 2000).

FWI	Scenario	Wind speed (km/h)	FFMC	ISI	BUI
Moderate (5)	1	9	87.4	4.6	11.5
	2	9	72.4	1.1	76.7
High (15)	3	22	89	11.5	15.1
	4	5	86.8	3.4	92.5

Note: FFMC = Fine Fuel Moisture Content, is a numerical rating of the moisture content of litter and other cured fine fuels. This code is an indicator of the relative ease of ignition and flammability of fine fuel. ISI = Initial Spread Index, is a rating of the expected rate of fire spread. It combines the effects of wind and FFMC on rate of spread without the influence of available fuel. BUI = Buildup index, is a numerical rating of the total amount of fuel available for combustion. FWI = Fire Weather Index, a rating of fire intensity that combines ISI and BUI. It is suitable as a general index of fire danger throughout the forested areas of Canada (Canadian Forestry Service 1987).

5.4.5 Fire behavior simulations

Stand characteristics of post-fire residual patches (refuges or random patches) were measured as mentioned above, while characteristics of matrix stand types (young, intermediate, or old) were obtained from Hély (2000).

In a first step, the FBP model was used under the four different weather conditions (Table 5.3) in order to determine fire behavior variability for each stand type in the landscape mosaic (broadleaved, mixed, and coniferous), and to use these value ranges as surrogates to real values. The FBP System is indeed regarded as producing good results when compared to natural or experimental fires (Stocks 1987a, b, Hély et al. 2001). With respect to topography, a 0° slope and a 300-m elevation were used in FBP simulations to represent the general flat landscape around Lake Duparquet. In the FBP model, stand types were mainly characterized by tree species composition and density, and fuels were qualitatively described (Forestry Canada Fire Danger Group 1992). Fire behavior (e.g., rate of spread (ROS) or head fire intensity (HFI)) was predicted from empirical relationships computed from many fire measurements recorded during wildfires and experimental fires and covering a large range of weather conditions (Stocks 1989). Different fire behavior relationships exist for spring (leafless) and summer (leaf out) in forest types that include broadleaved species. Spring fire behavior relationships were therefore selected, because spring is the most flammable season that also sustains fast propagation and high fire intensity as compared to summer (Hély et al.2000a). We also focused on spring because we assumed that if refuges are less susceptible to burn in the spring, this could not be *a priori* due to the presence of deciduous trees in their vicinity, but rather to peculiar stand characteristics. Concretely, spring broadleaved, and mixed fuel types (D1 and M1, respectively) were chosen, as they were deemed representative of the present boreal mixedwood forest. The coniferous percentage was increased in M1 stands to age stands toward late successional states dominated by coniferous trees.

In a second step, corresponding to the calibration step, the BehavePlus model was used on the same fuel types as used in the FBP model (broadleaved, mixed, coniferous). BehavePlus is a non-spatially explicit deterministic model based on the physical and combustion properties of fuel types (see below). A fuel model was attributed to each stand type based on the different loads, depths of dead (1-h, 10-h, 100-h time lag) and living (herbaceous and woody shrubs) fuel types, as well as their compactness and moisture content (Burgan and Rothermel 1984). Concretely, the generic fuel model "Moderate load broadleaf litter" available in the BehavePlus system (Andrews 2008) was used for all landscape mosaic stand types (broadleaved, mixed, coniferous), replacing fuel load values and stand canopy structures for those measured in the field (Table 5.2).

Based on the same topographical conditions and weather conditions as for the FBP model, fuel moisture content scenarios were created and all BehavePlus fuel models were calibrated with each predicted ROS by the FBP model as target. It is worth noting that for a given moisture scenario, all loads of a given fuel type had the same water content, regardless of stand type. This allowed us to test the effect of fuel composition and load in explaining fire refuge occurrence. As ROS differences between FBP and BehavePlus showed that FBP outputs were systematically higher than those from BehavePlus, as previously shown using the BEHAVE system (Hély et al. 2001), the humus load present below the litter (fermentation layer) was added to the 1-h fuel load, and the fuel bed depth was increased during the calibration process. The calibration procedure stopped when predicted ROS from BehavePlus were not significantly different from the FBP predictions (Fig. 5.2).

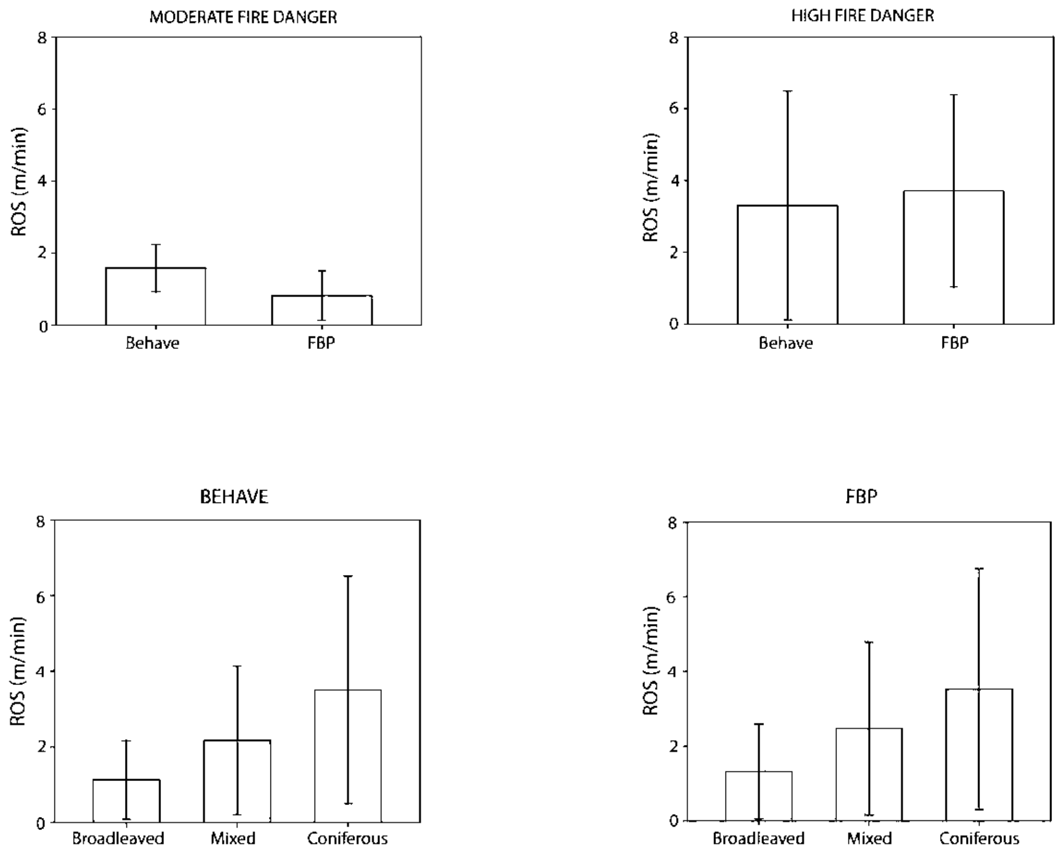

Figure 5.2: Rate of spread outputs of BehavePlus and FBP systems as a function of fire danger and fuel type.

In a third and final step, we moved from the non-spatially explicit fire behavior simulated at the stand level (BehavePlus) to spatially explicit fire simulations at the landscape level using the FlamMap3 model (Stratton 2004, Finney 2006). FlamMap3 is based on BehavePlus fuel models and fire behavior at the pixel scale (15 m × 15 m). It reports output maps of all fire behavior variables such as ROS and HFI. Moreover, as FlamMap3 propagates fire from an ignition location (randomly selected or not) through neighboring pixels over a given simulation time (see below) and a given number of ignitions (randomly selected), it also reports the burned probability map showing the number of times each pixel has burned over the total number of fires that spread over the given simulation time.

Concretely, the Lake Duparquet Research and Teaching Forest landscape characteristics in terms of slope, azimuth, water bodies, and stand composition from were rasterized from the ecoforestry map (225-m^2 spatial resolution (i.e., 15×15 m^2)) using the *ArcGIS* software to produce the following set of Ascii grids required as input data in the FlamMap3 model (Stratton 2004, Finney 2006): aspect (°N), elevation (m), slope (%), fuel model, canopy cover (%), tree height (m), crown bulk density (kg/m^3), and height-to-live crown base (m). These data allowed us to test the fire behavior in residual patches in their real location in the landscape, with their specific characteristics (topography, fuel, and distance to fire-break). In order to simulate fires whose areas corresponded to the natural variability recorded in boreal mixedwood forest, the simulation times in FlamMap were adapted (63 min, 105 min, 408 min, 4835 min) to create fire areas approximating quartiles of the distribution of burned areas.

In total, to test the fire susceptibility of refuges in their actual location in comparison to random patches and other fuel types, we assigned constant fuel moisture throughout the landscape (Fig. 5.3), and 160 000 fires were simulated (16 runs of 10 000 ignitions per simulation time and fuel moisture scenarios) for all fuel types. Then, to test for the effect of moisture content on the occurrence of fire refuges, the fuel moisture contents of all fire refuge fuel types (1h = 21%, 10h = 24 %, 100h = 26%) were increased and 10 000 randomly ignited fires were simulated per new moisture scenario based on the 408 minutes simulation time.

5.4.6 Statistical analyses

All analyses were performed using the R software (R Development Core Team, 2007). First, to test if fuel loads explain the lower susceptibility to burn of fire refuges, we looked for significant differences in burn probability among forest stand types (i.e., among fuel model types) using one-way non-parametric analyses of variance on rank scores (Kruskal-Wallis non-parametric test) followed by a multiple comparison Tukey test. Secondly, we tested the fuel moisture content effect using the same method but applied only on the series of 408-minute runs with different moisture scenarios specifically set for fire refuges. Finally, to test if, when they burn, fire refuges burn less than the other stand types in terms of maximum burning, we also compared the proportion of burning area using chi-square tests and contrast-tests. All analyses were performed not directly on the number of burns for each stand type compared to its representativeness in the forest mosaic composition. Therefore, the propensity of each forest stand to burn was computed relatively to its representation in the landscape mosaic, with a ratio higher (lower) than 1 highlighting a real propensity to burn (to escape fire).

These analyses allowed us to look at each weather-moisture scenario based on all simulation times combined to reconstruct a fire size distribution, as well as on each simulation time for each scenario. The fuel moisture content effect was tested using the same method, but only applied to the series of 408-minute runs with different moisture scenarios specifically set for fire refuges.

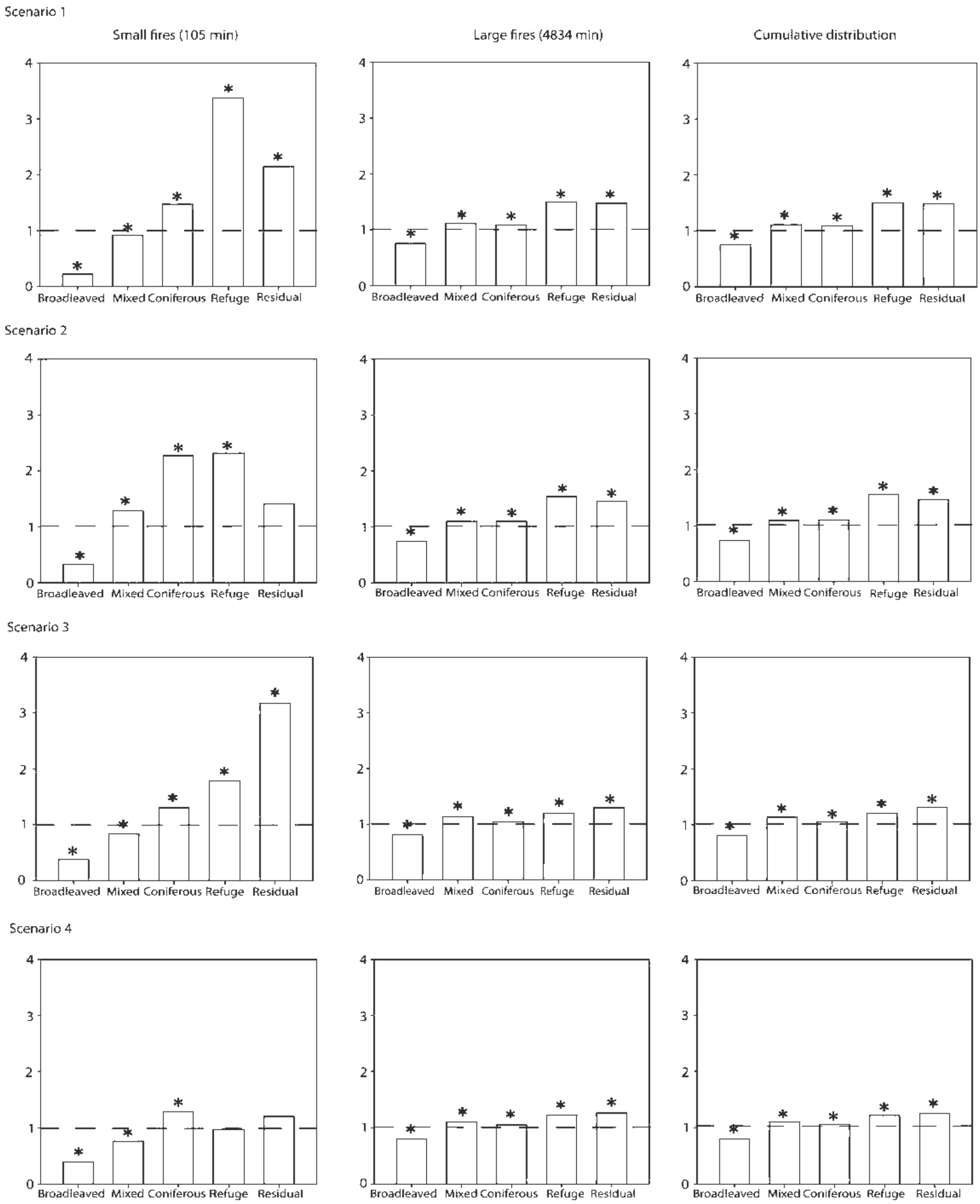

Figure 5.3: Ratio between burned area and the representative area of each fuel types, as a function of fire danger (scenarios) and size of area burned (50%, 100%, and cumulative distribution of area burned). Sterisks indicate significant differences between observed and theoretical values.

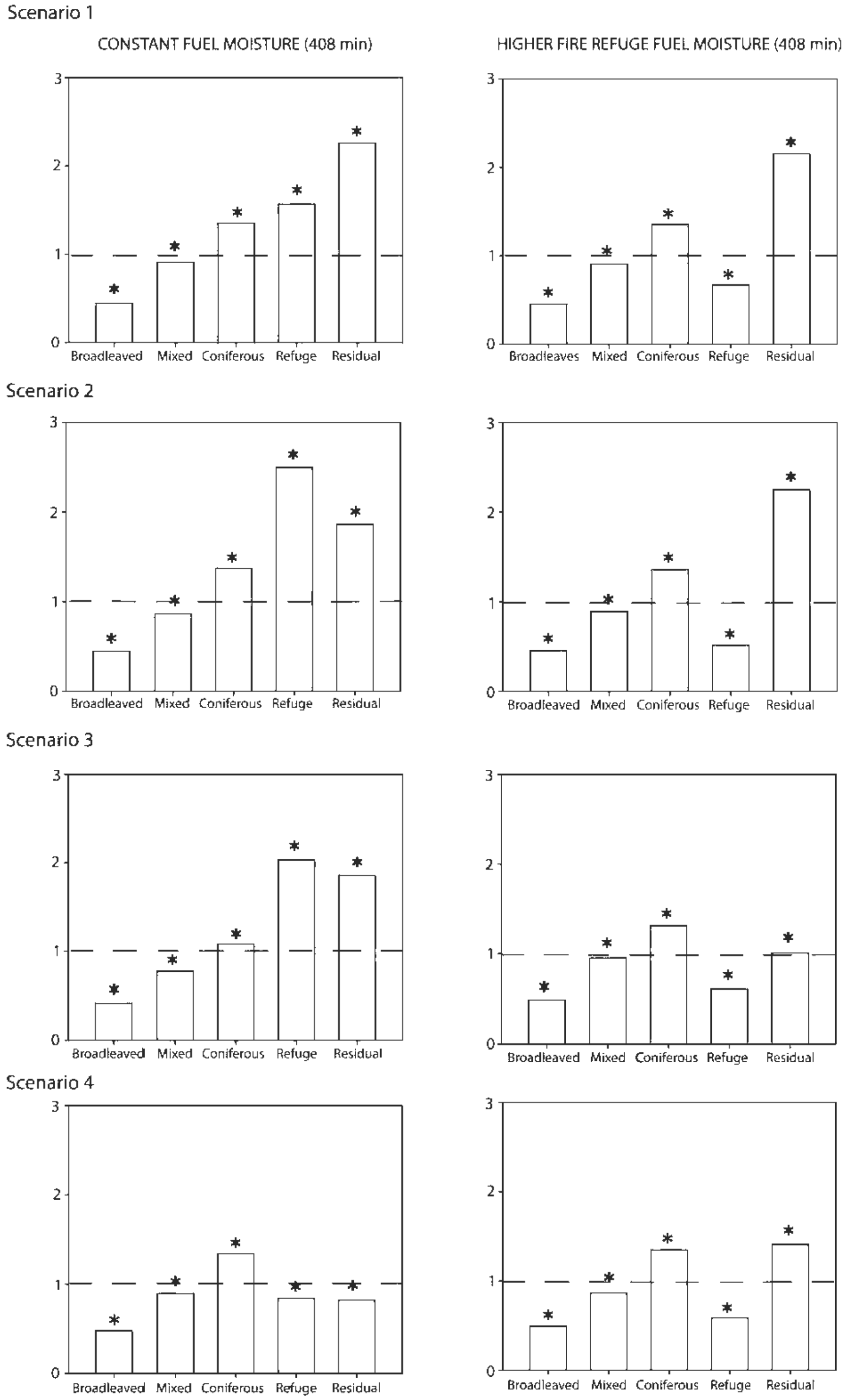

Figure 5.4: Ratio between burned area and the representative area of each fuel types, with constant fuel moisture (right) and higher moisture conditions at fire refuges (left). Asterisks indicate significant differences between observed and theoretical values.

5.5 Results

Based on the calibration procedure, the fire behavior components (ROS) predicted by the FBP and BehavePlus systems were in good agreement (Fig. 5.2), both within fire danger and stand types (Fig. 5.2). This satisfactory agreement between BehavePlus and FBP outputs confirmed that the BehavePlus model can be adapted to the boreal mixedwood forest if the fermentation layer (deep litter) is taken into account in fuel load characterization. Such adjustment of fuel load gave more realistic values for all stand types, and especially for old stands.

The FlamMap prediction system has been selected to conduct this study because it predicts burn probabilities from stand characteristics and the different fuel type loads collected within the stands for: (1) fuel moisture constant throughout the landscape (Fig. 5.3), and (2) higher fuel moisture for fire refuges than forest matrix (Fig. 5.4). The results obtained from constant fuel moisture at all stands (Fig. 5.3), show, for each fire danger, the propensity of each stand type to favor fire propagation (ratio > 1) or to escape fire (ratio < 1). The overall results show the same trend, whatever fire dangers are considered (Fig. 5.3). However, differences were reported between fuel types and the stand propensity to burn increased from broadleaved to coniferous stands, especially for small fires. The results also showed that fire refuges and random residual stands were more likely to burn than other fuel types, except in scenario 4 for small fires, likely due to ignition hazard.

When testing for the effect of higher fuel moisture in fire refuges compared to other stand types with the 4 fire dangers (Fig. 5.4), it appears that fuel moisture reduced the propensity of fire refuges to burn compared with their propensity to burn in constant fuel moisture conditions throughout the landscape (Fig. 5.4). Moreover, under moister conditions, fire refuges burned significantly less than other post-fire residual patches or matrix coniferous stands (Fig. 5.4).

5.6 Discussion

Fire behavior simulations were conducted to evaluate the susceptibility to fire of refuges in their actual location in the landscape using burn probability. The occurrence of post-fire residual patches during a fire is influenced by fire severity, location in the landscape, and fuel characteristics (Hély et al. 2000a, Keeton and Franklin 2004, Cyr et al. 2005, Romàn-Cuesta et al. 2009). Due to the influence of environmental features, fire refuges, unlike other residual patches, are not randomly distributed (Bradstock et al. 2005). The present study showed that fire refuges burned *more* than the surrounding forest matrix when fuel moisture was held constant throughout the landscape. From this first analysis, it is clear that fuel quality, topography at ground level and firebreaks do not play an important role in the spatial distribution of fire refuges. This is in contrast with previous studies indicating that the spatial development of post-fire residual stands was influenced by firebreaks, such as rock outcrops and water bodies, which disrupt horizontal fuel continuity, thus preventing fire propagation (Swanson et al. 1988, Keeton et al. 2004, Cyr et al. 2005, Madoui et al. 2011). The importance of protected topographical positions has also been reported for interior forests in eastern Washington (Camp et al. 1997) and south central Wyoming (Romme and Knight 1981), where oldest forests are found. The flat topography in our study area likely explains why no associations between the occurrence of fire refuges and landforms were found.

Hence, fire refuges in this study actually presented fuel characteristics *favorable* to fire spread. The shape, size, density, loading, chemical properties, and spatial configuration of forest fuels affects the ignition, intensity, spread, and fuel consumption of wildfires (Burgan 1987). However, fire refuges burned *less* than other stand types (except broadleaved stands) when they were assigned higher fuel moisture content in the simulations. Because fire refuges escaped multiple stand-replacing fires that have occurred in the surrounding forest matrix, the high fuel moisture levels appear to be the critical factor reducing fire intensity, as was reported in other fire refuges (Camp 1995, Camp et al. 1997). Nevertheless, under extreme fire weather conditions, even fire refuges can burn

(Ouarmim et al. accepted). Fuel moisture is related to topography and aspect (Miyanishi and Johnson 2002). The aspect determines solar-flux (cool, wet north and east facing aspects) and can impact soil moisture, which has important influences on fire behavior (Van Wagner 1977, Agee 1998, Gardner et al. 1999). However slope aspect did not appear to be an important variable in this study, as fire refuges were located on flat positions. Thick organic matter accumulation reported in most of the fire refuges indicates potential presence of shallow depressions explaining higher soil moisture and lower fire occurrence in fire refuges. These depressions have been filled by organic matter through time.

To conclude, fuel moisture content appears to be the most important factor influencing the distribution of fire refuges at the landscape scale. This result is in good agreement with paleoecological analyses performed in the same stands, which show the occurrence of aquatic taxa and moisture tolerant tree species in fire refuges (Ouarmim et al. 2014). Hence, fire refuges could be considered as "soaked powder kegs", having well enough fuel to burn, but too much humidity. As dryer climates are expected in the northeastern North American boreal forest over the next century (Flannigan et al. 2005), fire conditions leading to the burning of fire refuges could become more frequent. Simulation studies using various climate change scenarios are necessary to evaluate potential effects on the persistence of fire refuges.

5.7 Acknowledgements

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CHAPITRE 6 CONCLUSION GÉNÉRALE

L'historique à long terme des feux dans la forêt boréale nord-américaine laisse une empreinte hétérogène (Cyr et al. 2009), comme en atteste la présence d'îlots forestiers dispersés au sein de la mosaïque paysagère caractéristique de la sapinière à bouleau blanc. Ces îlots forestiers ont été épargnés par les feux et se trouvent dans de nombreux écosystèmes forestiers (Eberhart et Woodard 1987, Camp et al. 1997, Román-Cuesta et al. 2009). Les études concernant ces îlots en Amérique du nord se sont surtout intéressées à leurs caractéristiques spatiales (taille, forme, proportion et configuration spatiale) et se sont rarement penchées sur leur dynamique temporelle (Kafka et al. 2001, Madoui et al. 2011, Dragotescu et Kneeshaw 2012). Toutefois, des études réalisées notamment en Fennoscandinavie et aux États-Unis ont révélé la présence de peuplements forestiers ayant la capacité de se maintenir dans le territoire pendant plusieurs millénaires (Hemstrom et Franklin 1982, Hörnberg et al. 1998). L'objectif de cette étude était de mieux caractériser les îlots forestiers résiduels dans la forêt boréale mixte de l'est du Canada en retraçant l'historique des feux et de la végétation et en déterminant les facteurs contribuant à leur occurrence dans le paysage.

L'une des méthodes utilisées pour retracer l'historique des feux à long terme est l'analyse des charbons de bois conservés dans les sédiments lacustres et pédologiques. Contrairement à l'analyse des charbons dans les lacs où il est difficile d'identifier des feux *in situ* (Clark 1988, Higuera et al. 2011, mais voir Asselin et Payette 2005a), l'analyse des charbons de bois macroscopiques conservés dans les sols forestiers est plus appropriée à l'échelle locale (Asselin et Payette 2005b, Talon et al. 2005, de Lafontaine et Asselin 2011), pour identifier avec certitude des feux qui auraient affecté des îlots.

L'étude de l'historique des feux à partir des charbons de bois conservés dans les sols peut être compliquée par des perturbations de la stratigraphie, notamment par le déracinement d'arbres lors de trouées (Gavin et al. 2003b). Les datations ^{14}C que nous avons réalisées sur les charbons de bois des sols forestiers ne montrent pas de signes de bioturbation. En effet, aucune inversion de date n'a été enregistrée et cinq des sept dates obtenues à partir des charbons de bois correspondent aux dates de feux locaux reconstitués par des études dendrochronologiques. Néanmoins, l'emploi de dates ^{14}C obtenues de charbons de bois pour estimer l'âge des feux requiert une certaine prudence, étant donné que les dates obtenues correspondent à l'âge du bois et non à celui du feu. Ce biais dans la datation ^{14}C est désigné sous le terme « erreur induite » et implique que l'âge au radiocarbone peut être plus vieux que l'âge du feu (Gavin 2001). Bien qu'elle ne puisse pas être négligée, plusieurs indices portent à croire que l'erreur induite est faible dans les forêts de la région d'étude, étant donné que le taux de décomposition des restes ligneux au sol est relativement rapide (Naesset 1999, Boulanger et Sirois 2006). Par conséquent, l'âge des charbons de bois en forêt boréale est sensiblement le même que celui du feu auquel ils correspondent (de Lafontaine et Payette 2011).

Le feu peut également perturber la stratigraphie des sols par la combustion d'une partie de la matière organique, créant ainsi des hiatus sédimentaires (Ali et al. 2008). Des hiatus ont été observés dans trois des cinq longues séquences de cette étude (Monsabrais, Georges et Cadeau). Ces hiatus sont systématiquement associés à de fortes accumulations de charbons de bois et sont donc probablement dus à l'occurrence de feux particulièrement sévères qui ont brûlé les îlots et consumé une partie de la matière organique. En effet, l'épaisseur de la couche organique brûlée est considérée dans les écosystèmes circumboréaux comme un bon indicateur de la sévérité du feu, au même titre que l'impact sur les organismes vivants (Rowe et al. 1983, Miyanishi et Johnson 2002). Un feu sévère brûlera non seulement la strate arborée, mais consumera la couche organique en profondeur, parfois jusqu'à l'horizon minéral. Nous considérons que la faible épaisseur de matière organique dans la plupart des îlots résiduels est probablement liée à des feux récurrents qui ont consumé en profondeur la matière organique à chaque fois.

Les résultats de cette étude confirment la présence d'îlots ayant la capacité de se maintenir dans le paysage forestier au-delà de ce qui est observé habituellement dans la matrice forestière. Toutefois, pour la première fois, cette étude différencie les îlots forestiers persistants (refuges), des autres îlots résiduels, qui ne seraient que transitoires dans la matrice forestière (Chapitre 2). Les refuges font ainsi preuve d'une grande persistance dans le temps (jusqu'à 4000 ans au site Cadeau), leur conférant une certaine singularité au sein de la mosaïque paysagère. Les refuges peuvent toutefois brûler lors d'événements exceptionnels (Chapitre 2). Par conséquent, dater uniquement le dernier feu n'est parfois pas suffisant pour déterminer à quel type d'îlot appartient le site étudié. Le site Cadeau en est un exemple éloquent, ayant brûlé en 1717, mais ayant auparavant connu de longues périodes sans être affecté par les feux.

Nous avons mis en évidence que les refuges présentent un certain nombre de caractéristiques historiques, structurales et stationnelles qui permettent de les différencier des îlots résiduels. La dynamique de la végétation dans les refuges se distingue du schéma classique observé en forêt boréale mixte (Chapitre 3). En effet, les analyses macrofossiles révèlent deux principales phases dans l'historique de la végétation : une première phase humide dominée par le mélèze (*Larix laricina*) et l'épinette (*Picea* spp.) et une deuxième phase dominée par le cèdre blanc (*Thuja occidentalis*) et le sapin baumier (*Abies balsamea*). Ces espèces peuvent se maintenir dans le paysage forestier, jusqu'à près de 1700 ans. L'originalité de nos résultats tient également de la dynamique végétale post-incendie de ces milieux. En effet, la dynamique et la structuration végétale des refuges semblent peu affectées par les feux et les caractéristiques stationnelles semblent limiter en abondance le développement des espèces héliophiles de début de succession telles que le bouleau à papier (*Betula papyrifera*) et le peuplier faux-tremble (*Populus tremuloides*).

Nous avons mis en évidence deux caractéristiques permettant de distinguer sur le terrain les refuges et les autres îlots résiduels : le diamètre des arbres et l'épaisseur de la couche organique au sol (chapitre 4). Ces deux variables sont liées, dans la mesure où l'accumulation de matière organique réduit la croissance des arbres. En plus de l'épaisseur de matière organique et du diamètre des arbres, l'humidité joue un rôle primordial dans les refuges. En effet, les analyses paléocologiques révèlent durant certaines périodes la présence d'espèces associées à des milieux humides (Characeae et mélèze). Les simulations du comportement des feux à l'échelle du paysage réalisées à l'aide du modèle FlamMap3 confirment que l'humidité des combustibles et notamment de la matière organique est le paramètre déterminant l'occurrence et la persistance des îlots (Chapitre 5). Ces résultats permettent ainsi de minimiser l'effet des coupe-feu (barrières naturelles ou anthropiques) et surtout de la charge en combustible des îlots. En effet, les refuges présentent une quantité de combustible qui permettrait le déclenchement ou la propagation d'un feu sous des conditions mésiques ou xériques.

6.1 Détection des îlots refuges : implication pour la biologie de la conservation

À long terme, les pratiques sylvicoles actuelles (coupes totales ou partielles) rajeunissent sensiblement le paysage forestier régional, augmentant ainsi la proportion de jeunes forêts et diminuant l'importance des veilles forêts (Gauthier et al. 1996). Sachant qu'un des principaux enjeux de la foresterie au Québec est la préservation de la biodiversité au sein des écosystèmes, les pratiques sylvicoles des dernières décennies induisent la disparition de certains habitats, entrainant une perte potentielle d'une diversité biologique encore mal connue. La présence dans le territoire forestier d'îlots de différents âges, de différentes histoires de perturbations et de différentes caractéristiques stationnelles pourrait constituer un atout majeur pour la biodiversité en forêt boréale mixte. C'est le cas notamment des refuges, qui ont fait l'objet de très peu d'études et qui n'ont donc pas été considérés jusqu'à présent dans les plans d'aménagement forestier.

Quelques attributs forestiers sont liés au temps depuis le dernier feu, incluant la composition spécifique, la structure, l'abondance des débris ligneux et l'épaisseur de la matière organique (Cyr et al. 2009). La plupart des refuges présentent ou ont présenté par le passé une longue continuité écologique avant de brûler lors d'un feu particulièrement sévère. Les études sur la continuité écologique sont le plus souvent associées à des hypothèses de richesse spécifique (Nordén et Appelqvist 2001). Avec le temps, les forêts acquièrent des caractéristiques écologiques qui peuvent être essentielles à l'établissement de certaines espèces (Esseen et al. 1997, Hunter 1999). Ainsi les vieux peuplements caractérisés par une structure verticale irrégulière, la présence de vieux arbres, de débris ligneux de tailles et de stade de décomposition variés, et de petites ouvertures causées par la mortalité d'individus, sont autant de conditions favorisant une diversité de micro-habitats favorables à différentes espèces (Boddy 2001, Boudreault et al. 2002, Rubinio et McCarty 2003), que la sylviculture habituelle restreint ou élimine. Ces caractéristiques qui sont rencontrées dans les îlots à longue continuité écologique permettraient d'abriter une biodiversité particulière. Par exemple, les refuges se distinguent des îlots résiduels par le diamètre moyen des arbres et l'épaisseur de la matière organique. Ces deux caractéristiques spécifiques aux refuges pourraient s'avérer importantes pour la biodiversité, fournissant des environnements uniques, notamment pour la faune et la flore cryptiques (invertébrés, bryophytes, lichens).

L'association de l'historique des perturbations, des caractéristiques des peuplements et du milieu, sont autant de spécificités des refuges que l'on ne trouve ni dans la matrice forestière, ni dans les îlots résiduels. Ces spécificités sont autant d'indices qui permettent de supposer que les refuges pourraient constituer des écosystèmes à haute valeur pour la conservation. En revanche, d'autres caractéristiques peuvent constituer des freins au développement de la biodiversité dans ces milieux. En effet, la taille et la forme des îlots sont des paramètres importants. Selon la théorie de la biogéographie insulaire (MacArthur et Wilson 1967), la taille des îlots et leur distance de la population d'origine pourraient expliquer la variabilité de richesse spécifique d'un îlot à l'autre. Les analyses réalisées sur la diversité génétique du thuya occidental des îlots résiduels démontrent un échange allélique important avec la mosaïque forestière (Xu et al. soumis). La forme des îlots est aussi importante à considérer par son influence sur la proportion de forêts intérieures, moins soumises aux influences de la matrice forestière environnante. Des études ont montré que les forêts résiduelles de forme linéaire subissaient un effet de bordure qui modifie les caractéristiques des peuplements et altère la qualité de l'habitat pour les espèces de vieilles forêts

(Schmiegelow et al. 1997). Plus la taille des îlots résiduels est grande, plus l'effet de bordure sera limité.

Finalement, cette étude a permis d'identifier, parmi les îlots forestiers résiduels en forêt boréale mixte, les peuplements qui seraient plus à même de contenir une biodiversité particulière. Les refuges présentent une susceptibilité moindre aux feux et ont la capacité de persister dans le paysage forestier pendant des siècles, voire des millénaires. Ils ont donc une valeur de conservation intrinsèque en tant que biotopes de la forêt boréale. Étant donné que les îlots sont généralement petits (quelques hectares) et qu'ils sont dispersés dans la matrice forestière, les modèles conventionnels de protection des forêts (parcs, réserves naturelles, etc.) ne sont pas appropriées. Les îlots pourraient néanmoins être utilisés avantageusement dans la sélection des « forêts à haute valeur pour la conservation » (FHVC) et ainsi bénéficier d'une protection dans les parterres de coupes. Ce concept a été mis en place par le *Forest Stewardship Council* (FSC), un organisme international créé pour favoriser l'aménagement durable des forêts. Les refuges pourraient ainsi correspondre à la catégorie « Aires boisées qui, à l'échelle mondiale ou nationale, présentent des concentrations de valeurs qui contribuent à la biodiversité». Pour obtenir la certification FSC, les exploitants forestiers pourraient mettre en place une politique de gestion tenant compte des îlots refuges (persistants) pour une protection à long terme, mais aussi des îlots forestiers résiduels (temporaires) pour une gestion écosystémique plus dynamique intégrant un rythme de perturbation plus lent que dans le reste du paysage forestier.

6.2 Perspectives

Cette étude constitue une première étape dans la caractérisation des refuges en forêt boréale mixte canadienne. De nombreuses questions restent encore sans réponses précises, notamment celles s'articulant autour de l'évaluation de la biodiversité de ces îlots. Cette évaluation de la biodiversité (animale et végétale) permettrait de compléter notre compréhension du fonctionnement de ces écosystèmes particuliers et de déterminer leur rôle dans le fonctionnement global de la forêt boréale.

Étant donné que la fréquence des feux est basse dans les refuges, nous supposons que la principale perturbation qui régit la dynamique forestière dans ces derniers est les épidémies de tordeuse des bourgeons de l'épinette (TBE) (*Choristoneura fumiferana* (Clem.)). Cet insecte défoliateur est le principal ravageur forestier de l'est de l'Amérique du Nord. Son aire de répartition coïncide avec celle du sapin baumier (principal hôte de l'insecte), présent dans la plupart des îlots étudiés. L'historique des épidémies de tordeuse des bourgeons de l'épinette ne couvre que quelques siècles pour la région étudiée (Morin et al. 1993) et le rôle de l'insecte dans la dynamique forestière à long terme des refuges reste encore à déterminer.

La susceptibilité au feu des refuges pourrait changer en réponse aux changements climatiques. Ces changements pourraient se traduire par une augmentation de la fréquence des feux dans la matrice forestière. Ces modifications pourraient compromettre la capacité des refuges à persister dans le paysage forestier. Dans ce contexte, il serait intéressant de simuler le comportement des feux dans les îlots en adaptant les scénarios d'humidité à ceux prédits pour les prochaines décennies. Ces simulations serviraient à évaluer les effets sur la propagation du feu des changements climatiques, notamment de variations du taux d'humidité. Les résultats pourraient servir à évaluer le potentiel de persistance des îlots au cours des prochaines décennies.

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