UNIVERSITÉ DU QUÉBEC À MONTRÉAL

CYCLE DES FEUX, VIEILLES FORÊTS ET AMÉNAGEMENT EN FORÊT BORÉALE DE L'EST DU CANADA

THÈSE

PRÉSENTÉE

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DOMINIC CYR

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AVANT-PROPOS

Cette thèse est composée de quatre chapitres principaux et d'un chapitre annexe rédigés sous forme d'articles scientifiques. Le style d'écriture varie légèrement d'un chapitre à l'autre puisqu'ils ont été publiés ou sont en préparation pour des revues différentes.

De plus, par soucis de clarté et de logique, j'ai cru bon présenter dans cette thèse les articles dans un ordre qui n'est pas chronologique. Le premier chapitre, intitulé *Assessment of accuracy and precision of three types of survival analyses for estimating the length of fire cycle from dendroecological reconstruction in the boreal forest of North America,* est en fait le dernier chapitre a avoir été élaboré. J'ai été le principal responsable de tous les aspects du développement de ce chapitre. Mes co-auteurs sont les co-superviseurs de cette thèse Sylvie Gauthier et Yves Bergeron, qui ont apporté leur aide principalement au cours de la rédaction.

Le second chapitre, intitulé *Scale-dependent determinants of heterogeneity in fire frequency in a coniferous boreal forest of eastern Canada*, a été publié en 2007 dans *Landscape Ecology* (22:1325–1339). J'ai été le principal responsable de tous les aspects du développement de ce chapitre. Mes co-auteurs sont les co-superviseurs de cette thèse Sylvie Gauthier et Yves Bergeron. Ils ont apporté leur aide au cours de chacune des étapes de ce travail.

Le troisième chapitre, intitulé *Canopy composition patterns created by heterogeneity in fire frequency in the boreal forest of eastern Canada*, a été soumis à *Journal of Vegetation Science* et était sous évaluation par les pairs au moment du dépôt initial de la thèse. Encore une fois, les co-auteurs de cet article sont les co-superviseurs de cette thèse Sylvie Gauthier et Yves Bergeron, qui ont apporté leur aide à chacune des étapes de l'étude.

Le quatrième chapitre, intitulé *Forest management is driving the eastern north american boreal forest outside its natural range of variability* a été publié en 2009 dans *Frontiers in Ecology and The Environement* (7:519-524). Il s'agit dans ce cas d'une nouvelle analyse de données préalablement publiées par Christopher Carcaillet et collaborateurs dans *Journal of Ecology* (89 : 930-946) qui est basée sur une idée proposée par Yves Bergeron. J'ai été le principal responsable de l'élaboration de la méthodologie adoptée pour cette nouvelle analyse ainsi que de la rédaction de l'article. Les co-auteurs sont Sylvie Gauthier, Yves Bergeron et Christopher Carcaillet, qui ont apporté leur aide au cours de chacune des étapes.

Le chapitre annexe intitulé *A simple Bayesian Belief Network for estimating the proportion of old-forest stands in the Clay Belt of Ontario using the provincial forest inventory* a été publié en 2010 dans *Canadian Journal of Forest Research (40: 573-584)*. Cet article a été rédigé au cours d'un contrat avec le Ministère des Ressources Naturelles de l'Ontario en collaboration avec mes co-superviseurs Sylvie Gauthier et Yves Bergeron ainsi que Dave Etheridge et Gordon Kayahara. Bien

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À cette époque où les réseaux sociaux s'élargissent de façon étourdissante, on ne peut que réaliser l'importance de ceux que l'on peut encore et toujours compter sur les doigts d'une seule main.

Cher Alekse,

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RÉSUMÉ

Les feux de forêts constituent l'un des processus les plus importants de la forêt boréale en établissant les fondements d'une mosaïque dynamique de peuplements forestiers à l'intérieur de laquelle une multitude d'autres processus interagissent. En initiant une succession secondaire, ils déterminent en partie la composition, la structure et la répartition spatiale des différents types d'habitats rencontrés en forêt boréale. Voilà pourquoi il est souvent suggéré que les impacts des perturbations anthropiques (e.g. coupes) sur les paysages aménagés seront atténués si celles-ci émulent le mieux possible les patrons et processus normalement générés par les perturbations naturelles (e.g. feux de forêt).

Le cycle des feux, défini comme le temps nécessaire à ce qu'une superficie cumulée égale au territoire à l'étude ait brûlé de nouveau, est un paramètre important du régime des feux puisqu'il détermine la proportion des classes d'âge à l'échelle du paysage. Or, les cycles des feux relativement longs documentés dans l'est du Canada suggéraient que les paysages forestiers produits au terme de la première rotation forestière industrielle seraient amputés d'une portion importante de la variété d'habitats qui caractérisent les paysages produits par les perturbations naturelles. L'objectif principal de cette thèse était donc de documenter le cycle des feux sur la Côte-Nord, une région caractérisée par une présence particulièrement importante de vieilles forêts, ainsi que ses répercussions sur la dynamique successionelle des principales espèces d'arbres et les implications sur l'aménagement forestier en forêt boréale de l'est du Canada

Dans un premier chapitre, nous avons évalué le cycle des feux sur la Côte-Nord ainsi que l'incertitude qui lui est associée à l'aide d'une approche par modélisation. Nous y comparons aussi trois méthodes d'analyses de survie pouvant être utilisées pour estimer le cycle des feux. Il s'est avéré que l'approche non-paramétrique, la régression de Cox, permet l'obtention d'une estimation plus robuste aux variations temporelles de l'activité des feux, la source de biais potentiel la plus importante. À l'aide de cette méthode, nous avons pu estimer à environ 227 ans le

cycle des feux récent dans le territoire à l'étude, une valeur à laquelle est toutefois associée un intervalle de confiance à 95% de ±60 à 70 ans.

Dans un second chapitre, nous avons isolé les facteurs responsables d'une hétérogénéité spatiale de la fréquence des feux sur la Côte-Nord, qui se sont avérés dépendre fortement de l'échelle spatiale à laquelle ils sont décrits en raison du caractère contagieux des feux de forêt. Il s'est avéré qu'au sein d'un même paysage, certaines grandes zones dominées par des versants exposés au sud étaient 2 à 6 fois plus susceptibles que d'autres, affectant ainsi la répartition de peuplements forestiers distincts au niveau de la composition et/ou de la structure.

Nous avons ensuite testé l'influence de cette hétérogénéité sur la dynamique des peuplements au moyen d'analyses multivariées des communautés végétales. Nous avons ainsi tenté d'isoler l'influence du temps depuis le dernier feu en tant que tel de l'appartenance à un contexte où les feux sont plus ou moins fréquents. De façon générale, c'est seulement dans les zones à faible fréquence des feux que le principal spécialiste de fin de succession, le sapin baumier, arrive à supplanter l'espèce globalement la plus abondante en forêt boréale de l'est du Canada, l'épinette noire, en raison du temps depuis le dernier feu généralement plus long. Nos résultats suggèrent aussi que la succession de *P. mariana* vers *A. balsamea* peut se produire longtemps après ce qui est généralement couvert par les reconstitutions dendroécologiques de l'historique des feux dans ce type de paysages boréaux (>200-300 ans).

En dernier lieu, nous nous sommes intéressés à un autre paysage forestier boréal, situés à l'extrême ouest du Québec en partie sur la portion nord de l'Abitibi et au sud de la Jamésie. Nous avons examiné la variabilité à plus long terme (6800 ans) de l'activité des feux au moyen d'une reconstitution paléoécologique basée sur les fragments de charbon enfouis dans les sédiments de lac stratifiés. Cette analyse nous a permis de décrire ce que nous soutenons être une plage de variabilité naturelle pertinente pour l'établissement de cibles d'aménagement, qui fut comparée à l'état actuel du paysage étudié. Nos résultats confirment les appréhensions selon lesquels l'aménagement néglige une importante proportion des paysages boréaux naturels, i.e. les vieilles forêts, puisque celles-ci semblent avoir occupé une portion importante de ce paysage au cours de l'ensemble de son histoire post-glaciaire, une réalité qui a rapidement été altérée au cours des trois dernières décennies de récolte extensive.

MOTS CLÉS : Feux de forêt / Côte-Nord / Abitibi / Québec / Aménagement forestier écosystémique / Épinette noire / Cycle des feux / Fréquence des feux / Paléoécologie / Analyses de survie /

INTRODUCTION GÉNÉRALE

Les feux de forêt sont depuis longtemps perçus comme l'un des processus les plus importants de la dynamique naturelle de la forêt boréale (Johnson, 1992 ; Payette, 1992 ; Wein and MacLean, 1983). Leurs manifestations sont spectaculaires, touchent de très grandes superficies, et leurs effets sont à la fois immédiats et persistants. Par la combustion d'une importante quantité de matière organique, ils constituent en effet le point de départ d'une succession secondaire, l'un des processus écologiques les plus étudiés en écologie. La succession se produit la plupart du temps sur plusieurs centaines d'années pour n'être interrompu que par une perturbation majeure, souvent le feu en forêt boréale.

L'intérêt pour l'étude des feux de forêt continue à croître à mesure que progressent nos connaissances sur la dynamique naturelle de la forêt boréale ainsi que la pression que l'être humain exerce sur celle-ci à travers son exploitation, et ce, pour plusieurs raisons. D'abord, les feux de forêts ont une influence directe sur l'exploitation des ressources en constituant une contrainte majeure à la planification forestière. Ils affectent de façon très imprévisible des surfaces forestières considérables, provoquant ainsi d'importantes pertes de volumes de bois, bien qu'il soit parfois possible d'en récupérer une partie lorsque les superficies brûlées sont accessibles à l'intérieur de délais raisonnables. Deuxièmement, les feux de forêt jouent un rôle prépondérant dans le cycle du carbone (Carcaillet *et al.*, 2002 ; Kurz and Apps, 1994). Une quantification des régimes de feux ainsi que des émissions de carbone produites lors de ceux-ci devient donc essentielle au calcul du budget de carbone des pays et secteurs industriels reliés à la forêt boréale, un enjeu considérable pour l'atteinte de cible de réduction des émissions de GES et dans la perspective d'une économie du carbone (Kurz *et al.*, 2008). Enfin, et c'est sur cet aspect que je m'attarderai tout au long de cette thèse, les feux de forêt sont de plus en plus perçus comme un processus-clé de la dynamique naturelle de la forêt boréale dans son ensemble, un processus duquel on peut s'inspirer à travers nos aménagements pour maintenir son intégrité écologique (sensu Kohm and Franklin, 1997), non seulement pour des raisons éthiques, mais aussi par utilitarisme. Les services rendus par les écosystèmes forestiers boréaux sont en effet nombreux. Ils incluent ceux dont il a été mention précédemment mais un très grand nombre d'autres dont la plupart sont méconnus ou insoupçonnés. C'est donc dans une perspective de développement durable que les feux de forêts sont graduellement devenus un sujet d'étude incontournable en plus de continuer à susciter un intérêt important sur le plan de l'écologie fondamentale.

Rédigée dans le cadre d'un programme de doctorat en sciences de l'environnement, cette thèse aborde principalement la question des régimes de feux de forêt dans une perspective appliquée. C'est aussi dans une telle perspective, que nous pourrions qualifier de pragmatique, mais aussi fondamentalement enracinée dans le principe de précaution et le développement durable (Brundtland, 1987), que se sont développés les concepts de *filtre brut*, ou *d'aménagement écosystémique* qui sont abordés dans la section suivante. Autour de tels concepts s'est récemment modelé un nouveau paradigme d'aménagement forestier dont les paramètres sont de plus en plus définis par la dynamique des perturbations naturelles (Bergeron *et al.*, 2001 ; Gauthier *et al.*, 2008 ; Perera and Buse, 2004), importants vecteurs de changement auxquels peuvent être assimilées les coupes forestière et autres perturbations anthropiques. Ce nouveau paradigme est d'ailleurs au cœur du nouveau régime forestier de la province de Québec adopté en 2010 (Ministère des Resources Naturelles et de la Faune du Québec, 2010), une refonte faisant suite à l'une des principales recommandation de la commission d'étude sur la gestion de la forêt publique québécoise présidée par Guy Coulombe (2004). Dans la présente introduction, je décrirai d'abord brièvement quelques éléments théoriques de d'écologie du paysage et d'étude des systèmes complexes pour ensuite les mettre en relation avec ce nouveau paradigme d'aménagement forestier. Ce faisant, je soulignerai l'importance des feux de forêt dans la mise en application de ce paradigme en soulignant l'importance des feux de forêt y jouent en forêt boréale.

Feux de forêts et écologie du paysage

On associe parfois aux feux de forêt des régions boréales le vocable de « perturbation catastrophique » en raison des grandes superficies affectées sévèrement. À cet épithète – catastrophique – est facilement attribuée une connotation négative bien qu'il n'en soit pas ici question. C'est d'ailleurs en partie pourquoi le terme *large infrequent disturbance* (*LID*) lui a été préféré par certains auteurs (e.g. Romme *et al.*, 1998 ; Turner and Dale, 1998), terme qui convient bien aux feux de forêt en région boréale, mais aussi aux ouragans ou aux tsunamis en régions côtières. Même si ce terme permet d'éviter toute forme de connotation indésirable dans le contexte d'études scientifiques portant sur un processus naturel, il ne permet pas un formalisme pur en conservant une certaine part d'arbitrarité reliée à ce qui peut ou doit être considéré comme « grand » et « peu fréquent ». Ce type de difficulté est souvent rencontré dans le domaine de l'écologie du paysage, un sujet d'étude pour lequel il est même difficile de produire une définition universelle ou, du moins, ancrée dans le concret, de son principal objet d'étude : le paysage. Une des définitions les plus simples suggérée pour la notion de paysage est qu'il s'agit d'une surface ou une zone contenant deux écosystèmes contigus ou davantage (Sanderson and Harris, 2000). Ce type de définition peut sembler insatisfaisante dans la mesure où elle renvoie à la définition d'écosystème, elle-même ambiguë puisque tout système écologique est ultimement ouvert et niché à l'intérieur d'une hiérarchie d'autres écosystèmes. Cette difficulté s'explique par le fait que la notion d'échelle spatio-temporelle demeure centrale et varie en fonction des organismes ou processus à l'étude. Afin de tester des hypothèses provenant de n'importe laquelle des théories mentionnées plus haut, il est souvent nécessaire de définir de façon *ad hoc* le paysage à l'étude. Le paysage d'une harde de caribou de la toundra ou d'une population d'oiseaux migrateurs sera forcément de taille différente de celui d'une population d'insectes xylophages ou encore de bactéries, par exemple.

La théorie de la biogéographie insulaire (MacArthur and Wilson, 1967) est parmi les plus influentes du corpus théorique à la base de l'écologie du paysage et de la biologie de la conservation. Les éléments centraux de cette théorie sont que la taille et l'éloignement des habitats potentiels influencent les taux d'extinction et de recolonisation des populations et, par conséquent, la richesse en espèce. Bien qu'elle encore aujourd'hui influente, notamment en prodiguant certaines balises pour la mise en place de réseaux d'aires protégées, cette théorie reste très générale puisque principalement élaborée pour prédire la richesse en espèces, mais souffre surtout d'un manque de considération du caractère très dynamique de certains systèmes affectés régulièrement par des perturbations naturelles. La théorie des métapopulations est à plusieurs égards une mise à jour de la biogéographie insulaire et qui a notamment permis l'intégration du caractère parfois très dynamique de l'abondance et de la répartition spatiale des parcelles d'habitats potentiels (Hanski, 2001 ; Hanski and Ovaskainen, 2003 ; Levins, 1969) tout en devenant beaucoup plus spécifique au niveau des besoins de chaque espèces à travers l'importance accordée à la niche écologique de celles-ci. La prise en considération de ce dynamisme est particulièrement appropriée dans le contexte de la forêt boréale affectée par les feux de forêt qui déclenchent des processus successionels modifiant les attributs d'habitats et impliquant d'inévitables extinctions locales. Plus récemment, la théorie neutre de la biodiversité (Hubbell, 2001) empruntait à la théorie des métapopulations en ce qui a trait à l'importance du dynamisme créé par les perturbations mais revenait au caractère « neutre » de la théorie de la biogéographie insulaire puisqu'elle délaissait la notion de niche. Cette théorie propose en effet que toutes les espèces d'une communauté appartenant à un même niveau trophique soient équivalentes et que la stochasticité de la dispersion après perturbation détermine l'abondance relative des espèces. Un point commun à toutes ces théories est que la variabilité spatiale et/ou temporelle des parcelles d'habitats disponibles joue un rôle prépondérant dans la distribution et l'abondance des espèces. Les feux de forêt sont sans contredit l'un des principaux générateurs de variabilité spatiotemporelle en forêt boréale, variabilité qui constitue le sujet central de cette thèse.

Un autre champ d'étude relativement récent situé à la jonction de la physique et de l'écologie tente d'attaquer le problème de la complexité des systèmes écologiques et, notamment, d'intégrer les différentes échelles spatio-temporelle qui interagissent et contribuent à limiter notre capacité à les modéliser adéquatement. Il s'agit des théories de la hiérarchie (Allen and Starr, 1982 ; O'Neill, 2001 ; O'Neill *et al.*, 1986). Tout comme la biogéographie ou la théorie des métapopulations, les théories de la hiérarchie situent tout phénomène dans son échelle spatiotemporelle propre. Toutefois, elles partent du principe qu'il existe une corrélation entre échelle d'espace et échelle de temps, et que les vitesses de fonctionnement des phénomènes définissent des niveaux. Conséquemment, les différents niveaux sont identifiables puisque sous l'influence prédominante d'un ou de quelques processus clés. À cela s'ajoute la notion importante selon laquelle les interactions entre les niveaux sont multiples, i.e. que certains processus font le pont entre différentes échelles spatiotemporelles. C'est là où le cadre théorique rejoint le cadre plus appliqué en ce qui concerne les feux de forêts. En effet, les feux de forêt agissent principalement à des échelles spatiotemporelles très similaires à celles de l'aménagement forestier extensif dominé par les coupes totales. Bien qu'il y ait d'importantes nuances à apporter lorsque qu'on établit un parallèle entre les feux et les coupes totales (Franklin *et al.*, 2000 ; Haeussler and Kneeshaw, 2003 ; McRae *et al.*, 2001 ; Nguyen *et al.*, 2000), on peut tout de même établir que ces deux types de perturbation initient une succession secondaire, phénomène dont la lenteur définit l'échelle temporelle, tout comme ils structurent de grandes superficies de territoire.

Feux de forêts et aménagement forestier

Devant l'impossibilité de planifier nos aménagements en considérant les innombrables éléments et processus composant les écosystèmes forestiers boréaux, des auteurs comme Noss (1987, 1990) et Hunter (1990, 1999) ont suggéré d'appliquer l'approche du *filtre brut*, une approche en biologie de la conservation qui consiste à maintenir la variété d'habitats forestiers représentatifs des forêts naturelles ainsi que certaines de leurs caractéristiques clés comme la structure d'âge à l'échelle du paysage et la quantité de vieilles forêts, la composition en espèces, l'agencement spatial des peuplements, les îlots et les arbres résiduels (vivants et morts) dans les zones perturbées, et la matière organique résiduelle (Gauthier *et al.*, 2008). Cela permettrait de considérer la majorité des habitats et processus nécessaires à son fonctionnement. Le filtre brut est donc principalement une approche pragmatique de conservation reconnaissant notre compréhension limitée du fonctionnement des écosystèmes boréaux. C'est aussi une approche permettant une certaine souplesse puisqu'elle n'implique pas la protection intégrale du territoire pour en maintenir une certaine intégrité écologique, mais plutôt le maintien des principaux attributs d'habitats, habituellement à des échelles spatiales relativement grandes, tout en permettant si nécessaire l'ajout de mesures de protections spécifiques à certaines espèces focales jugées particulièrement sensibles et importante.

En forêt boréale, les feux de forêts ont rapidement été ciblés comme un important vecteur de variabilité environnementale dont il conviendrait de s'inspirer afin d'appliquer un filtre brut pour la conservation (Attiwill, 1994 ; Hunter, 1993). En effet, les feux de forêts mettent en place les fondements d'une mosaïque forestière à l'intérieur de laquelle d'autres perturbations et processus écologiques de toute sorte interagissent. Les paramètres du régime des feux comme la fréquence et la distribution de taille déterminent ainsi la distribution d'âge (Bergeron *et al.*, 1999a) et la configuration spatiale des éléments de cette mosaïque (Hunter, 1993) et, conséquemment, d'un grand nombre d'habitats. C'est d'ailleurs autour de ces caractéristiques des paysages boréaux que résident d'importantes préoccupations liées à l'effet de l'aménagement extensif tel que pratiqué jusqu'à présent en forêt boréale nord-américaine. L'utilisation presque exclusive de méthodes de coupes à faible rétention de couvert végétal contribue à altérer considérablement la distribution des classes d'âge à l'échelle des paysages puisque les cycles des feux observés jusqu'à présent sont généralement plus longs que les rotations forestières planifiées avec la seule contrainte du rendement soutenu qui sont situent généralement entre 60 et 100 ans. Ainsi, en négligeant de considérer le rythme des feux et la configuration spatiale qu'ils génèrent, l'exploitation forestière transforme considérablement les paysages forestiers, et ce, même lorsque la remise en production est assurée. Bergeron et collaborateurs (2006) ont fait la synthèse des estimations de cycle des feux au Québec, qui sont davantage de l'ordre de 140 à 295 ans (0.34% à 0.71% d'aires brûlées par année), ce qui contraste avec les taux de coupe observés à l'échelle du territoire boréal québécois, par exemple, qui sont généralement de plus de 1% sur le territoire commercialement exploitable.

D'autres caractéristiques des paysages forestiers boréaux naturellement influencés par les feux de forêts sont considérablement altérées par l'aménagement forestier extensif, notamment la configuration spatiale des massifs de forêts matures ou surannées et des zones en régénération. Au Québec par exemple, l'historique de l'aménagement extensif en forêt boréale peut être résumé par la progression d'un front de coupes du sud vers le nord. Alors que sous un régime de perturbations naturelles on pouvait retrouver une matrice paysagère principalement composée de grands massifs de forêts matures et surannées interrompus par des zones en régénérations distribuées plus ou moins aléatoirement, le progrès du front de coupe du sud vers le nord fait graduellement rétrécir la taille et la connectivité de ces massifs en les confinant aux portions encore inexploitées au nord. Parallèlement à cela, les zones en régénération récemment perturbées au sud se juxtaposent en ne laissant que très peu de forêts matures ou surannées résiduelles. Le caribou des bois (*Rangifer tarandus caribou*) est l'exemple le plus connu et médiatisé d'organisme affecté par cette transformation du paysage puisqu'il dépend en bonne partie de ces grands massifs de vieilles forêts (Courtois *et al.*, 2008). La sévérité des feux et la variabilité qui lui est associée peuvent aussi être prises en considération à travers nos aménagements puisqu'elles déterminent de façon plus locale les habitats résiduels après le passage des feux (Kafka, Gauthier and Bergeron, 2001), les patrons de régénération (Jayen, Leduc and Bergeron, 2006) ainsi que les processus biogéochimiques ayant cours dans les sols (Thiffault *et al.*, 2007 ; Wardle, Nilsson and Zackrisson, 2008).

Dans le cadre de cette thèse, je m'attarde davantage aux considérations reliée à la fréquence des feux, donc principalement à la question des proportions de vieilles forêts, à leur dynamique, ainsi qu'aux enjeux d'aménagement qui en découlent pour la forêt boréale de l'est du Canada. Les vieilles forêts se distinguent de différentes façons, selon leur composition et/ou leur structure, l'abondance de bois mort ou la présence de dépressions et de monticules (*pits and mounds*), d'arbres à forts diamètres etc... Toutefois, une définition basée davantage sur les processus successionnels a été suggérée par Kneeshaw et Gauthier (2003) pour la forêt boréale et stipule que le statut de vieilles forêt est atteint lorsque la majorité des arbres de la cohorte initiée suite à la dernière perturbation de grande envergure (e.g. feu, coupe) ont disparu et sont graduellement remplacés par des arbres s'étant établis sous couvert. Ce processus donne lieu à une modification fondamentale de la variabilité des conditions environnementales, qui deviennent alors plus hétérogènes à une échelle spatiale fine.

Objectif principal de la thèse et présentation des chapitres

Il y a certes un parallèle à faire entre les feux de forêts et les coupes à faible rétention de couvert végétal puisqu'ils initient tous deux une succession secondaire. Toutefois, l'utilisation presque exclusive de ces coupes totales a longtemps été justifiée par le mythe selon lequel les cycles des feux sont tels dans l'ensemble de la forêt boréale qu'ils limitent fortement la présence de forêts dépassant l'âge l'exploitabilité (Gauthier *et al.*, 2008). Nous savons maintenant que cette croyance est fausse, notamment dans l'est du Canada (Bergeron *et al.*, 2006), mais aussi dans d'autres portions de la forêt boréale nord-américaine (cf chapitre annexe ; Cyr *et al.*, 2010 ; Kneeshaw and Gauthier, 2003 ; Senici *et al.*, 2010) tout comme en Fennoscandie (Kuuluvainen, 2002) où les cycles relativement longs permettent à de très fortes proportions des paysages d'être occupées par des vieilles forêts. Le décalage entre la fréquence à laquelle les peuplements sont affectés par une perturbation réinitiant une succession secondaire dans un régime de perturbations naturelles et dans un système aménagé de façon extensive en suivant une rotation de 60 à 100 ans fait en sorte que le niveau hiérarchique de la forêt boréale normalement organisé par les feux, qui correspond à ce qui est appelé fréquemment l'échelle du paysage, est en voie d'être considérablement transformé, avec d'importantes répercussions sur l'abondance relative des jeunes et vieilles forêts. Cela est particulièrement vrai sur la Côte-Nord, où les données d'archives couvrant les dernières décennies indiquaient un cycle des feux plus long que dans la majeure partie de la forêt boréale (Gauthier *et al.*, 2001).

L'objectif principal de cette thèse est donc de documenter les cycles des feux de paysages-échantillons de l'est du Canada, leurs variations spatiotemporelles, ainsi que leurs répercussions sur la dynamique successionelle des principales espèces d'arbres et l'aménagement forestier. Ces vastes questions sont circonscrites et subdivisées de la façon suivante:

- Quantification du cycle des feux pour les 300 dernières années à partir d'une reconstitution dendroécologique : comparaison de trois types d'analyses de survie à l'aide d'une approche par modélisation.
- Évaluation de la variabilité spatiale de la fréquence des feux et des échelles spatiales où cette variabilité est observable.
- Répercussions de la variabilité spatiale de la fréquence des feux sur la dynamique successionelle des principales espèces d'arbres.
- Analyse de la variabilité temporelle à long-terme et définition de la plage de variabilité naturelle à long-terme dans une optique d'aménagement.

Les trois premiers chapitres sont spécifiques au territoire de la Côte-Nord tandis que le dernier tire profit d'une reconstitution paléoécologique de la fréquence des feux dans l'ouest du Québec afin de proposer une méthode permettant de reconnaître la variabilité naturelle associée à la fréquence des feux pour établir des cibles d'aménagement.

Dans le premier chapitre, intitulé *Assessment of accuracy and precision of three types of survival analyses for estimating the length of fire cycle from dendroecological reconstruction in the boreal forest of North America*, je m'attarde d'abord à la simple quantification du cycle des feux, défini comme le temps requis pour brûler une superficie cumulée équivalente à l'aire d'intérêt. Cela implique que certains certaines zones puissent brûler plusieurs fois au cours de la durée d'un cycle alors que d'autres ne brûle pas du tout. Dans la forêt boréale de l'est du Canada, et particulièrement sur la Côte-Nord, l'estimation du cycle des feux est complexifiée par des intervalles entre deux feux successifs (au même endroit) relativement longs lorsque comparés à la longévité des principales espèces d'arbres présentes sur le territoire. C'est en bonne partie pour cette raison que le recours aux analyses de survie est fréquent et essentiel. Le temps depuis le dernier feu devient de plus en plus difficile à déterminer à mesure que les peuplements vieillissent et les analyses de survie permettent de considérer adéquatement cette perte graduelle d'information. Toutefois, les différents types d'analyses de survie produisent des estimations du cycle qui peuvent différer considérablement à partir d'un même jeu de données. L'objectif principal de ce chapitre était donc d'évaluer et de comparer la justesse ainsi que la précision de trois types d'analyses de survie dans une gamme de conditions proches de celles rencontrées dans les reconstitutions dendroécologiques de l'historique des feux en forêt boréale principalement affectée par des feux sévères réinitiant une succession secondaire. Plus précisément, les sources d'erreur pouvant affecter l'estimation du cycle des feux qui ont été considérées sont: 1- l'effort d'échantillonnage, 2- la proportion d'observation avec une connaissance incomplète du temps écoulé depuis le dernier feu et 3- les variations temporelles de l'activité des feux. Pour évaluer l'effet de ces trois sources d'erreur, je procède à une expérience de modélisation qui permet de comparer les estimations du cycle des feux avec les valeurs réelles de l'activité des feux, et ce, en simulant le plus fidèlement possible les contraintes normalement rencontrées dans les études empiriques. Le second objectif principal est de choisir la méthode la plus appropriée pour estimer le cycle des feux sur le territoire de la Côte-Nord à la lumière des résultats obtenus suites aux simulations.

Dans le deuxième chapitre, intitulé *Scale-dependent determinants of heterogeneity in fire frequency in a coniferous boreal forest of eastern Canada*, j'explore diverses sources d'hétérogénéité spatiale pouvant potentiellement influencer la fréquence des feux sur la Côte-Nord. J'y évalue d'abord l'influence des facteurs édaphiques, physiographiques et biologiques pour ensuite faire une analyse multi-échelles de la topographie, plus particulièrement l'exposition dominante des versants. Outre l'énumération des facteurs environnementaux influençant la fréquence des feux et la description des échelles spatiales où ces facteurs sont influents, l'objectif de ce deuxième chapitre est de déterminer si une éventuelle variabilité spatiale est causée de façon prédominante par des facteurs environnementaux de type ascendant (*bottom-up*) ou descendant (*top-down*).

Dans un troisième chapitre, intitulé *Canopy composition patterns created by heterogeneity in fire frequency in the boreal forest of eastern Canada*, il est question de l'impact de l'hétérogénéité spatiale de la fréquence des feux sur la dynamique des espèces d'arbres dominantes. J'y évalue l'hypothèse selon laquelle l'hétérogénéité spatiale de la fréquence des feux mise en évidence dans le deuxième chapitre influence l'importance relative des spécialistes de début de succession (pin gris, peuplier faux-tremble, bouleau blanc), de fin de succession (sapin baumier) et les espèces généralistes du point de vue successionel (épinette noire et épinette blanche). Deux principaux éléments sont à la base de cette hypothèse et découlent d'une hétérogénéité spatiale vraisemblablement permanente de la fréquence des feux. D'abord, dans une perspective spatiale, l'hétérogénéité de la fréquence des feux favorise une agrégation des jeunes et des vieilles forêts au sein du territoire, influençant donc potentiellement les probabilités et vitesses de recolonisation de chacune des espèces par l'entremise des sources de propagules disponibles dans le voisinage (Greene *et al.*, 1999). De façon similaire, mais dans une perspective plus locale, une fréquence des feux plus ou moins grande sur un site donné est susceptible d'influencer la probabilité que ce site soit occupé par une jeune ou une vieille forêt. Il a été démontré dans plusieurs régions que la composition en espèces avant le feu influence la composition en espèce et la trajectoire successionnelle empruntée après le feu par l'entremise d'un leg biologique (Foster, Knight and Franklin, 1998 ; Franklin *et al.*, 2002 ; McCune and Allen, 1985 ; Motzkin *et al.*, 1999). Cet historique *in situ* n'est souvent pas connu et est souvent évoqué comme explication possible de la variance inexpliquée de la composition en espèce. Dans le cadre de ce chapitre, nous utilisons des contextes contrastant de fréquence des feux comme *proxy* de l'historique *in situ*.

Dans le quatrième et dernier chapitre principal, intitulé *Forest management is driving the eastern north american boreal forest outside its natural range of variability*, je propose une méthode pour définir une plage de variabilité naturelle en forêt boréale pouvant être utilisée comme référence pour l'aménagement forestier. Comme je l'ai mentionné précédemment, le cycle des feux est souvent suggéré comme base pour la mise en œuvre d'un filtre brut pour la conservation des principaux attributs de la forêt boréale puisqu'il détermine les proportions du paysages occupées par les différentes classes d'âge et types de peuplements (Bergeron *et al.*, 1999b ; Harvey *et al.*, 2002). Certains ont critiqué cette approche sous prétexte que le cycle des feux a lui-même varié, principalement en raison des changements climatiques passés, et que l'utilisation d'une seule valeur-référence est par conséquent trop restrictive puisqu'elle ne tient pas compte du caractère « changeant » de la forêt boréale.

Dans ce chapitre, je propose un modèle simple permettant de traduire la plage de variabilité naturelle de la fréquence des feux, estimée à partir d'une reconstitution paléoécologique couvrant les 6800 dernières années, en une plage de variabilité de la représentation des classes d'âge à l'échelle du paysage. De cette façon, j'ai cherché à élaborer des cibles d'aménagement offrant davantage de flexibilité pour l'aménagement forestier puisque basées sur la variabilité naturelle observée pour l'ensemble de l'Holocène. Toutefois, comme cette approche requiert l'utilisation de données paléoécologique n'étant pas encore disponibles pour la Côte-Nord, cette étude porte sur un territoire de 15 000 km^2 localisé à l'extrême ouest du Québec, à la frontière de l'Abitibi et de la Jamésie.

Dans une conclusion générale, je tenterai de faire ressortir les principales contributions originales de chaque chapitre, ainsi que d'en faire une synthèse sous un angle pratique et théorique. Finalement, je présente un chapitre annexe intitulé *A simple Bayesian Belief Network for estimating the proportion of old-forest stands in the Clay Belt of Ontario using the provincial forest inventory*, qui constitue selon moi un exemple d'application en recherche sur les feux de forêt de techniques développées récemment en intelligence artificielle. De telles techniques permettront de tirer profit du nombre croissant de reconstitutions dendroécologiques de l'historique des feux en forêt boréale en les combinant avec d'autres sources d'information complémentaires. Une telle approche contribuera à une meilleure connaissance de l'intégralité du territoire forestier ainsi qu'à ouvrir ou d'aborder efficacement de nouvelles questions de recherche.

CHAPITRE I

ASSESSMENT OF ACCURACY AND PRECISION OF THREE TYPES OF SURVIVAL ANALYSES FOR ESTIMATING THE LENGTH OF FIRE CYCLE FROM DENDROECOLOGICAL RECONSTRUCTION IN THE BOREAL FOREST OF NORTH AMERICA

1.1 Résumé

La quantification du cycle des feux en forêt boréale est nécessaire à la compréhension de la dynamique passée et présente des écosystèmes boréaux ainsi que pour prédire leur dynamique future. De plus, la longueur du cycle des feux influence directement les budgets de carbone des pays et secteurs industriels reliés à la forêt boréale ainsi que les allocations de bois dans un contexte de rendement soutenu. Les intervalles entre deux feux relativement longs caractéristiques de la forêt boréale de l'est du Canada ainsi que l'importante variabilité temporelle de l'activité des feux en général compliquent l'estimation du cycle des feux. Le recours à de longues périodes de référence est donc nécessaire à l'obtention d'estimations régionalement spécifiques valables. Par conséquent, nous effectuons des analyses de survie à partir d'échantillons du paysage actuel où le temps depuis le dernier feu (TDF) est obtenu à l'aide de méthodes dendroécologiques. Cela permet de quantifier le cycle des feux pour les 300 dernières années. Certains auteurs ont critiqué cette approche sous prétexte que d'importants postulats inhérents à ces méthodes étaient irréalistes et pourraient ainsi mener à d'importants biais. Puisqu'il n'existe pour le moment aucune alternative valable au recours à cette approche et compte tenu de la grande importance du cycle des feux à titre de paramètre de l'aménagement forestier moderne, l'objectif de cette étude était d'évaluer la justesse et la précision de trois types d'analyses de survie. Deux de ces méthodes sont paramétriques et sont basées sur les distributions exponentielles négative et Weibull, tandis que la troisième, la régression de Cox, est non-paramétrique. Nous avons adopté une approche par modélisation afin d'incorporer plusieurs sources d'erreur, ce qui nous a permis de

quantifier les biais potentiels, l'ampleur des intervalles de confiance et les facteurs affectant le plus la justesse et la précision des estimations du cycle des feux. Nous avons évalué l'influence de la proportion d'intervalles censurés (TDF minimum), de l'effort d'échantillonnage et des variations à court terme de l'activité des feux. Nous avons ensuite comparé les estimations du cycle des feux entre les trois méthodes dans une étude de cas sur la Côte-Nord, dans l'est du Québec. Nos résultats supportent les études analytiques antérieures qui suggéraient que les variations à court terme de l'activité des feux est un important facteur confondant pouvant mener à d'important biais au niveau de l'estimation du cycle des feux. Parallèlement à cela, l'effort d'échantillonnage et la proportion d'observations censurés influencent surtout la précision des estimations et non leur justesse. La régression de Cox semble être la méthode la plus robuste vis-à-vis les variations temporelles de l'activité des feux. En ce qui concerne l'étude de cas sur la Côte-Nord, les tendances centrales des estimations du cycle des feux obtenus se situent entre 206 (régression de Cox) et 295 ans (exponentielle négative), mais les résultats de nos simulations suggère que la valeur obtenue à l'aide de la régression de Cox, ajustée pour un léger biais (226 ans) est la plus digne de confiance.

1.2 Abstract

Quantifying fire cycle (FC) in the boreal forest is crucial for understanding the past and present dynamics of the boreal ecosystems as well as for predicting its future dynamics. The FC is also important because it affects carbon budget accounting and AAC forecasting. The typically long fire return intervals that are encountered in Eastern Canada and the important temporal variability associated with them make it difficult to properly assess FCs. Long reference periods are therefore required to obtain valid regionally specific estimates. This is why survival analyses conducted from cross-sectional samples of the landscape (snapshot image) where the time since last fire (TSF) is dendroecologically measured are necessary. Several authors have criticized this approach because the assumptions underlying the commonly used methods were deemed unrealistic and could lead to bias in estimating FC. Because of a lack of alternatives and given the tremendous importance of the length of the FC as a parameter of modern forest management, the objective of this study was to assess the accuracy and precision of three types of survival analyses, two parametric ones that are based on the negative exponential and Weibull distributions, and one non-parametric, the Cox regression. We used a simple modelling approach to incorporate multiple sources of error, which allowed us to quantify potential biases, the width of the associated confidence intervals and the key factors that affect accuracy and precision. We tested the effect of the proportion of censored observations (minimum TSF), sampling effort, and short-term temporal variations in fire activity. Then we compared the FC estimated using these three methods in a real case study in the

North Shore region of eastern Quebec. Our results support previous analytical studies that suggested that a short-term variation in fire activity is the most important confounding factor that can lead to substantial biases in estimating FC. On the other hand, sampling effort and the proportion of censored observation mainly influence the precision of the estimates. Cox regressions appear to provide the most robust estimator with regards to temporal variation in fire activity. The central estimators of the FC for the last 300 years in the case study area range from 206 (Cox regression) to 295 years (negative exponential), but our simulation results suggest that the lowest one adjusted for a slight global bias (226 years) is the most trustworthy considering the suspected recent variations in fire activity.

1. 3 Introduction

Fire is a fundamental process in the natural dynamics of the boreal forest of North America. Quantifying fire regime characteristics is therefore crucial for the understanding of past and present dynamics of the boreal ecosystems as well as for predicting its future dynamics. It has also become a necessary step for many important forest management planning issues. Over the last few decades, there has been a shift from a commodity production-oriented approach to an ecosystem-based approach in forest management that aims to maintain ecological integrity of the boreal forest (Gauthier *et al.*, 2009 ; Perera and Buse, 2004). Fire regimes are central in this paradigm shift as new management strategies are developed in order to better align with the characteristics and relative importance of stand-initiating disturbances (fire) and other types of natural disturbances that usually occur at finer spatial scales or that are more selective in nature (e.g. wind, insects). Also, a total exclusion of fire and replacement by harvesting is economically unrealistic and ecologically questionable (Hirsh *et al.*, 2001). Consequently, there is a growing interest in incorporating fire *a priori* in strategic forest management planning to prevent eventual shortfalls in timber supplies caused by fire (Armstrong, 2004 ; Boychuk and Martell, 1996 ; Leduc *et al.*, in prep). Furthermore, fire is a key element of the carbon cycle in the boreal forest, which makes the quantification of the fire regime necessary to the assessment of the carbon budget of countries and industrial sectors related to the boreal forest (Amiro *et al.*, 2009). Such an assessment will directly affect the effort and levels of mitigation needed to reach atmospheric CO_2 stabilization targets in a carbon economy.

An important characteristic of the fire regime is the fire cycle (FC), defined as the number of years required to burn an area equal to the total area surveyed. The FC is equivalent to the mean fire return interval over the area surveyed, and both concepts are also reciprocal to the mean burn rate or fire frequency, depending on whether it is used from an area-based or point-based perspective (Johnson and Gutsell, 1994). In this study, we will mainly use the term fire cycle (FC).

It is generally difficult to accurately and precisely quantify FC in Eastern Canada because the typical fire return intervals are relatively long (≥150 years, cf Bergeron *et al.*, 2006) compared to the maximum longevity of most boreal tree species (generally between 100 and 300 years) and also because the area burned annually is associated with a large inter-annual and inter-decadal variability. This difficulty is exacerbated by the fact that burned areas started being identified, delineated and organized within provincial or national databases only during the last few decades (Stocks *et al.*, 2003). Moreover, aging and "over-burning" of the forest gradually erase traces of past fire events as these fires are indeed typically stand-replacing and because multiple fire scars are only rarely encountered. The most reliable estimations of FCs currently available in the eastern boreal forests of Canada are those obtained from dendroecological reconstructions, through which the age of the first post-fire tree cohort (most commonly) or fire scars (seldom) are sought to infer the time elapsed since last fire (TSF) and then processed through survival analyses (SA). Valid representative surveys of large landscapes are also sometimes made difficult because of limited road access, hence reducing the number of points that can be visited through random or systematic sampling. Aside from allowing us to quantify the FC and to relate it to environmental covariates that create spatiotemporal heterogeneity, SA allows us to consider the fire intervals that are known only to a limited extent. That happens when no traces of past fire events can be found, in which case only a minimum amount of time since last fire can be attributed to the site. The probability of observing such a minimum interval increases with the time elapsed since the last fire event, and consequently, the proportion of such stands across the landscape increases with the length of the FC. They usually become dominant in the landscape when the FC reaches or exceeds 200-300 years. It was shown that these minimum intervals, which are referred to as censored observations in the SA literature (Allison, 1995 ; Hosmer and Lemeshow, 1999 ; Lawless, 2003), represent incomplete but meaningful information that cannot be omitted as missing observations without risking major biases (Moritz *et al.*, 2009). An important proportion of censored observations, however, decreases the precision of the FC estimates in a similar way to that of a decreasing sampling effort (Allison, 1995).

Several analytical approaches involving SA have been described and used to quantify FC or other closely related metrics (Johnson and Gutsell, 1994 ; Reed, 1994, 1997) and those do not necessarily yield the same results. The first two methods assessed consist in fitting the negative exponential (Van Wagner, 1978) and the Weibull (Johnson, 1979) distributions to the time-since-fire distribution obtained from a representative sample (or complete time-since-fire map) of an area of interest. The third one consists in using the baseline non-parametric hazard function of a Cox regression model (Cox, 1972) to quantify the length of the FC. Although we provide a brief description of these three methods further in this paper, the interested reader is invited to refer to specialized literature for a more complete description of the mathematical grounds as well as a wider spectrum of applications of these methods (Allison, 1995 ; Hosmer and Lemeshow, 1999 ; Lawless, 2003). The general objective of this paper is to assess and compare the accuracy and precision of three different SA-based methods for estimating the fire cycle from dendroecological reconstructions of fire history by means of a modelling experiment designed to simulate a range of conditions that are representative of what is typically encountered in such studies (Bergeron *et al.*, 2004 ; Bergeron *et al.*, 2001 ; Drever *et al.*, 2006 ; Grenier *et al.*, 2005 ; Lauzon, Kneeshaw and Bergeron, 2007 ; Lesieur, Gauthier and

Bergeron, 2002 ; Senici *et al.*, 2010). More specifically, we first compare the accuracy and precision of three methods against three sources of uncertainty that constrain the estimation of historical FCs: 1- The proportion of censored observations, which is related to the length of the FC relative to the longevity of the main tree species, 2- the sampling effort, which is a ubiquitous constraint in empirical field studies, and 3- past variations in fire activity, which has been recognized as a potential bias and source of assumption violation for some analytical approaches (Boychuk *et al.*, 1997 ; Clark, 1989 ; Polakow and Dunne, 1999, 2001). Most of these criticisms were indeed related to the assumption that the disturbance process is stationary, which has been suggested to be unrealistic. We therefore tried to assess the extent to which that assumption violation affects the validity of FC estimation in eastern Canada, namely in looking at the effect of variation in fire activity on these estimations. Here our main focus is on the practical implications of the use of these methods for estimating FC from dendroecological studies. The second objective is to apply the resulting outcomes of this modelling experiment to a case study of a 1.5 M ha boreal landscape of Eastern North America.

Before presenting the modelling approach used in this study, we first present some general aspects of survival analyses applied to fire ecology, and the three SA-based methods for estimating the FC. Then we present the modelling approach and a case study in the North Shore region of Quebec, in Eastern Canada.

1.4 Theoretical background

1.4.1 Time intervals, censoring and truncation in the context of FC estimation from time-since-fire dataset

Generally, SA involves the modelling of time to event data. Ideally, both the "birth" and "death" dates of a subject are known, in which case the lifetime is unambiguous. However, it is relatively common in survival data to know the length of the lifetime only to a limited extent, i.e. that it is at least a certain duration (when the birth is known but the death is unknown or the reverse situation). This is called a censored observation. The most common type of censoring is *right-censoring* and typically occurs when an experience is terminated before the event of interest could be observed (the time axis is represented from left to right). *Left-censoring* is also possible and occurs when the lifetime of an individual began prior to the beginning of the experiment with no way of retrospectively determining the moment at which it in fact began. In the present situation, the event of interest is a stand-replacing fire and, in an ideal dataset, two successive fire events would have to be known to observe a closed interval, i.e. uncensored (e.g. Baker, 1989 ; Moritz, 2003 ; Polakow and Dunne, 2001). Most of the time, however, it is not possible to obtain such complete information with landscape-scale dendroecologically reconstructed fire history data, especially in regions where fire-free intervals are long. In fact, in a stand-replacing fire context only one past fire event can usually be dated on each site using archives or dendroecological methods. Fire history is in fact reconstructed by conducting a cross-sectional field survey, sometimes combined with archival data, to obtain a "snapshot" or static image at the time of sampling based on a representative sample or complete fire map. This approach is most applicable to fire regimes that are dominated by stand-replacing fires. A TSF distribution is then obtained and used as survival data.

It has been shown in Eastern Canada that, in the absence of fire for more then 100-150 years, the post-fire cohort is gradually replaced by new trees in the canopy (Bergeron, 2000 ; Gauthier *et al.*, 2010), hence erasing the traces of the initial post-fire cohort whose age is used to infer the time since last fire. This causes left censoring because the beginning of the lifetime is unknown except for the fact that it occurred prior to the age of the oldest trees assuming they did not survive the last fire. In the case of cross-sectional field surveys, the entire TSF distribution can also be considered to be censored at the time of sampling because no other fire event had yet occurred. That is *right censoring* and affects all the observations. With the type of datasets that are available for the boreal forest of North America where there is already a relatively high percentage of left-censored observation because of typically long fire-free intervals, and rare complete interval, we usually consider the time of sampling as time t=0 to avoid the issue of right censoring, mainly because of a lack of alternatives. In fact, at least one complete time-to-event observation is needed for survival function fitting. Then we work in reverse time (cf Reed *et al.*, 1998) to transform cases of left censoring into right censored observations, which is relatively straightforward to consider using standard SA.

To assess and compare the three above-mentioned SA-based methods for estimating the FC, we simulated the aging and burning of a virtual landscape. That allowed us to record a "true" fire history and associated FC. At each time step, we sampled the virtual landscape, simulated the censoring process that naturally occurs around the stand break-up of a post-fire cohort and conducted SA to estimate the FC in similar conditions that prevail in a real field sampling. Then we analyzed the differences between SA-based estimates of FC and true FC statistics as a function of the length of the FC, sampling effort, and past variations in FC.

1.4.2 Survival analyses

Survival datasets can be described using several interrelated functions. In statistical terms, the three most important are the cumulative density function, the probability density function and hazard function, but following the terminology used by Johnson and Gutsell (Johnson and Gutsell), who put these functions in the context of stand-replacing fire regimes, the cumulative density function corresponds to the survivorship distribution function $A(t)$, which is the probability of having gone without fire (survived) longer than time t, that is,

$$A(t) = P(T>t) \text{ where } t \geq 0 \qquad \text{eq. 1}$$

The probability density function corresponds to the fire interval distribution $f(t)$, which is the probability of having a fire in the interval t to $t+\Delta t$

$$f(t) = \frac{dA(t)}{dt} \qquad \text{eq. 2}$$

Finally, the hazard function, or hazard of burning function, is the chance of each element that survived to time t to burn in the interval t to $t+\Delta t$

$$\lambda(t) = \frac{f(t)}{A(t)} \qquad \text{eq. 3}$$

1.4.3 Estimating FC using parametric survival regressions

Survival data can be fit using parametric models based on many distributions, upon which the most commonly used for FC estimations are the negative exponential and the two-parameter Weibull distribution, the former being a special case of the latter. When fit to the more general Weibull distribution, the survivorship distribution is

$$A(t) = e^{-(tb)^c} \qquad \text{eq. 4}$$

where e is the Napierian base, t is time, b is dimensioned in time and is the scale parameter, and c is dimensionless and is known as the shape parameter. The negative exponential is a special case of the Weibull distribution where $c = 1$, which stands for the following equations presenting the fire interval and hazard of burning distributions fit on a Weibull distribution (or negative exponential). The fire interval (probability density) distribution is

$$f(t) = \frac{ct^{c-1}}{b^c} e^{-(t/b)^c} \qquad \text{eq. 5}$$

and the hazard of burning function

$$\lambda(t) = \frac{ct^{c-1}}{b^c} \qquad \text{eq. 6}$$

Here we can easily see the special case of the negative exponential where c=1 makes the hazard constant through time (1/b).

From these distributions it is possible to estimate the FC (area-based), or average fire interval (element-based), which is

$$FC = b\Gamma(1/c + 1) \qquad \text{eq. 7}$$

where Γ is the gamma function. Then again, the equation is considerably simplified when c=1 as the FC equals b. When not fixed to 1 as in the special case of the negative exponential, the shape parameter c is adjusted in order to allow the hazard burning to change over time. As we just mentioned, the hazard function is constant at 1/b when c=1. The hazard increases with time when c>1 and decreases with time when c<1.

In this study, we use the *survreg* function in R package 'survival' (Therneau, 2009) which provides maximum likelihood estimates of Weibull and negative exponential parameters.

1.4.4 Estimating FC using non-parametric regressions

The Cox regression (Cox, 1972) is the most widely used type of survival regression in general but has rarely been used in forest fire studies with some exceptions (e.g. Bouchard, Pothier and Gauthier, 2008 ; Clark, 1989 ; Cyr, Gauthier and Bergeron, 2007 ; Senici *et al.*, 2010). The Cox regression is a semi-parametric survival model. One interesting feature of the Cox regression that explains its enormous popularity in other fields is that it does not require that we choose some particular probability distribution to represent survival times. In other words, the underlying hazard function is left unspecified at first, except that it cannot be negative, and can take any form depending on the empirical observations (Allison, 1995). The hazard function is the non-parametric portion of the model. Although the baseline hazard is unspecified, the Cox model can still be estimated by the method of partial likelihood, developed by Cox (1972) in the same paper in which he introduced the Cox regression model. Even though the resulting estimates are not as efficient as maximum-likelihood estimates for a correctly specified parametric hazard regression model, not having to make arbitrary, and possibly incorrect, assumptions about the form of the baseline hazard is a compensating virtue of Cox's specification. It is also relatively straightforward to fit a Cox model using the *coxph* function in R package 'survival' and extract the baseline hazard function using the *bazehaz* function, also in the R package 'survival'(Therneau, 2009). By default, *basehaz* yield Nelson-Aalen cumulative hazard estimates (Tsiatis, 1981). To estimate the FC, we simply identify the time t at which the cumulative hazard reaches or exceeds 1 in the survival sample, indicating one full cycle, and adjust according to the exact value of the corresponding cumulative hazard.

$$FC = \Lambda(t)/t \qquad \text{eq. 8}$$

where t is the time at which the cumulative hazard reaches or exceeds 1 and $\Lambda(t)$ is the corresponding cumulative hazard. In the eventuality that the cumulative hazard does not reach 1, the highest obtained value is used in the same way.

1.5 Method

1.5.1 Modelling approach

1.5.1.1 Aging and burning

In this study we simulated an aspatial virtual 1.5961 M ha landscape that consisted of a vector of 1 596 100 elements representing 1 ha each. The simulation started with TSF=0 for all elements, and was carried on for 4000 years with a yearly time step. Aging and burning were simulated through an iterative process where the TSF of each element increased by 1 at every time step, except for a random portion of the landscape whose TSF was reset to 0 to simulate burning.

The size of individual fire events was modeled as a serially independent draw from a log-normal probability distribution. The log-normal distribution, which is sometimes used to approximate burned area size distribution (Armstrong, 1999), has probability density function

$$f(x;\mu,\sigma) = \frac{1}{x\sigma\sqrt{2\pi}} e^{\frac{(\ln(x)-\mu)^2}{2\sigma^2}} \qquad \text{eq. 9}$$

where x is the fire size, μ the mean of the natural logarithm of the fire sizes, and σ is the standard deviation of the natural logarithms of the fire sizes. The parameters were estimated from the empirical size distribution of all fires ignited by lightning within a 100-km distance of the outermost boundaries of the case study area (N=123) during 1959-1999, obtained from the Large Fire Data Base (Stocks *et al.*, 2003).

We modeled different FCs to assess their influence on subsequent survival-based estimators. Because the FC can be calculated as:

$$FC = \frac{T \times A}{\bar{S} \times N} \qquad \text{eq. 10}$$

where A is the study area, T is the length of the simulation (years), S is the mean fire size and N is the number of fires. Isolating N allowed us to determine the number of fire events to draw from the log-normal fit of the fire size distribution and simulate in each FC scenario. The fire series was then randomly distributed in time, allowing for multiple fires in the same years, in which cases the individual fire sizes were summed up to obtain the annual area burned. The annual area burned determined the number of 1-ha elements whose TSF had to be reset to 0 at every time step.

1.5.1.2 Censoring

At every time step from $t = 1001$ to the end of each simulation ($t = 4000$), we randomly sampled the virtual landscape to simulate a typical field cross-sectional survey of TSF distribution. We started field sampling simulation after 1000 years to allow for initialization and stabilization of the virtual landscape. Several sampling efforts were simulated in order to assess its impact on survival-based estimates of FC.

To model the loss of information that is caused by the aging of the forest, when traces of the initial post-fire cohort gradually disappear making it impossible to date the last fire event from within-stand age structure, we applied a linear censoring function (Fig. 1.1). This function determines the probability that a sample of particular TSF will be censored. It was decided from the authors' personal experience in reconstructing fire history in eastern North America that a linearly increasing probability of censorship between TSF = 100 and TSF = 300 was a valid approximation of what is generally observed in the boreal forest of eastern North America. Stand break-up indeed usually occurs between 100 and 150 years, depending on the species (Gauthier *et al.*, 2010), but a successful determination of TSF is often possible for several decades after the initial post-fire cohort breaks up as veteran stems are targeted in dendroecological analyses. Fires that occurred more than 250 to 300 years earlier are almost never dated as this period of time roughly corresponds to the longevity of the longest-living and most common species in this area, *Picea mariana*. When it was determined that TSF should be censored, the true TSF was replaced by a new minimum TSF value that was randomly drawn from a uniform distribution bordered by 100 and the highest value between the original true TSF (if less than 300) or 300. This approach simulates the gradual replacement of veterans in the canopy by younger stems that established after the initial cohort.

We simulated four distinct fire regimes on the basis of the length of the global FC. As mentioned above, all fire regimes are characterized by the same size distribution of individual fire events and only distinguish themselves by the overall number of fire events, although a higher number of draws from the log-normal distribution increased the probability of occurrence of large fire events. We simulated the FCs of 75, 140, 253, and 539 years. To simulate varying sampling effort, all four simulated landscapes were sampled at every time step with the following sampling efforts, 10, 20, 30, 50, 75, 94, 250, corresponding to the number of randomly selected elements of the virtual landscape. Moreover in each simulation we also kept the true TSF and estimated fire cycle from these uncensored samples.

1.5.2 Analysis

1.5.2.1 True FC statistics

The main purpose of a simulation approach is to have access to long-term " true " statistics on fire activity as a basis for comparing the SA-based estimation methods. While the period of time covered by dendroecologically reconstructed fire history is limited by the gradual loss of traces of post-fire initial cohort, which is simulated by the censoring function here, the quantification of true FC requires the period of reference to be determined beforehand. We mainly used a 300-year reference because it roughly corresponds to the time span covered by real dendroecologically reconstructed fire history. It also corresponds to the time at which the model's censoring function was parameterized to reach a probability of 100%, meaning that the simulated samples on which this function is applied contain no stands of known TSF greater than 300 years. The true FC_{300} at time t=4000, for example, was thus obtained by dividing the total study area by the average annual area burned during the interval beginning at time t= 3701 and ending at time t= 4000. The true FC_{300} was computed at every time step for all simulations and was used as the main reference for further analyses, but the true FC_{150}, FC_{50}, based on the last 150 years and last 50 years, respectively, and mean TSF (based on uncensored values) were also computed and reported for comparative purposes.

1.5.2.2 SA-based estimates of FC

The negative exponential- and Weibull-based parametric survival models as well as Cox regression models were fit to each censored and uncensored TSF sample (3000 samples for each simulation; t[1001:4000]) in order to obtain estimates of the FC. Then we compared the accuracy and precision of the three SA-based methods by analyzing the difference between estimated FC and the true FC (estimated FC – true FC; hereafter called residuals_{300}). First, we analyzed the central tendency and distribution of residuals as a function of 1) the length of simulated FCs, 2) percentage of censored observations, and 3) the sampling effort. The central tendency of residuals was analyzed to assess whether a global bias could be observed, hence providing a quantification of each method's global accuracy, while the distribution of residuals and associated 2.5% and 97.5% percentiles were calculated to quantify the global precision of each method.

Although we applied a constant hazard function at the scale of each entire simulation, we used the random variations within each fire series to assess how temporal variations in fire activity affect the estimates of FC at several time scales. In order to do so, we calculated the difference in mean percent annual area burned between the most recent reference period of a given length and the previous one of equal length. For example, the past variation in fire activity at time t=4000, for a reference period of 5 years, equals the difference between mean percent annual area burned between the intervals of time t[3996-4000] and t[3991-3995]. The same calculation was repeated at every time step for all reference periods ranging from 5 to 300 years indicated in Table 1.1. Then we plotted residuals$_{300}$ (y-axis) as a function of these past variations in fire activity (x-axis) and linear regressions that were fit (Appendix 1.1). The slopes of these linear trends indicate the bias introduced by variations in fire activity. Flat curves suggest that past variations in fire activity do not cause any bias in the SA-based estimates, while positive or negative slopes indicate an over- or underestimation of FC, respectively, associated with an increase in fire activity in the recent period as compared with the previous one. We computed these slopes for all combinations of residuals$_{300}$ and temporal scopes. For the sake of simplicity, we focused on one level of sampling effort that corresponds to the actual sampling effort of the case study (N=94) as the relationships followed the same patterns with all sampling efforts (results not shown).

1.5.3 The case study area and fire history data

We also aimed at quantifying the FC in a coniferous boreal landscape of Eastern Canada in light of the information that was sought about the accuracy and precision of the three above-mentioned SA-based methods. The case study area covers 15 961 km^2 (1.5961 M ha) of boreal forest in Eastern Quebec, specifically in the North Shore region, between longitudes 67.00° W and 69.00° W and between latitudes 49.00° N and 50.25° N (Fig. 1.2). This region has a cold, maritime climate with an average annual temperature of 1.4°C and average precipitation of 1 018 mm, measured in Baie Comeau in the southwest corner of the study area. Precipitation is evenly distributed during the year, and is about 70% rain (Environment Canada, 1996). The topography is moderately uneven with high hills with rounded summits and many rocky escarpments. The highest hills, located in the northeastern part of the area, are just over 700-m high while other sparsely distributed hills reach above 500 m. The average elevation ranges within landscape subunits vary between 150 m and 200 m. Three of these landscape subunits, as described by Robitaille and Saucier (1998), make up for almost all of the case study area. The average slope is 15%. The hydrography is complex with numerous small lakes and rivers of varying sizes, some of them very large. The configuration of the topography produces a drainage system with a mainly north-south orientation (Robitaille and Saucier, 1998). There are rocky outcrops on slightly more than a third of the total land area, while the rest of the land area consists mainly of shallow tills on sloping areas and deep tills at the bottoms of slopes. To a lesser extent, there are glaciofluvial deposits on valley floors (Robitaille and Saucier, 1998).

Black spruce (*Picea mariana* (Mill.) BSP) and balsam fir (*Abies balsamea* (L.) Mill.) are the dominant species, making up a very connected coniferous matrix, along with white spruce (*Picea glauca* (Moench) Voss) and white birch (*Betula papyrifera* Marsh.). Also to be found in the region, but more sporadically, are trembling aspen (*Populus tremuloides* Michx.) and jack pine (*Pinus banksiana* Lamb.), mainly in recently burned areas. Tamarack (*Larix laricina* (Du Roi) K. Koch) can also be found along with black spruce in a few rare hydric stations in the region.

Information from various sources was used to compile the fire history of this area. All fires affecting a surface area of one or more hectares and occurring in the period since 1941 are listed in Quebec's *Ministère des Ressources Naturelles et de La Faune* archives (MRNFQ - *Direction de l'environnement et de la protection des forêts*), and aerial photographs dating back to 1931–32 were interpreted in order to map two older fires (1923 and 1896). In some areas, dendroecological surveys conducted for decadal forest inventories of the MRNFQ were used to assess the amount of time elapsed since the most recent fires. In order to take full advantage of this available data and focus our efforts on ground sampling in the areas where the fire history was less well known, a preliminary time-since-fire map of the area was carried out. This rough demarcation included recently mapped fires and sections of the study area covered mainly by even-aged forests of black spruce, which were determined with the help of dendroecological surveys carried out during MRNFQ forest inventory campaigns.

A total of 94 points made up the final sample. The MRNFQ map archives were used to directly assign a fire date to some recent fires, i.e. 12.8% of cases. Dendroecological analyses were used to estimate the time interval elapsed since the most recent fires for the rest of the sample, based on data gathered in the MRNFQ decadal inventories (37.2%) and during the sample-gathering campaign carried out for this study (50%). The time intervals since the most recent fires, estimated with the help of the dendroecological surveys, were inferred based on the conventional methods of Arno and Sneck (1977). Between 10 and 15 dominant trees were cut at the root collar and dated at each site. Fire dates were deemed sufficiently reliable if they concerned even-aged stands of a pioneer species commonly establishing itself after a fire. A minimum age (censored data) was assigned to uneven-aged stands, i.e. where a 20-year interval included less than 60% of the sampled dominant trees.

However, a visual examination of each stand's age structure suggested that this 20-year interval was too restrictive in the case of some of the older stands that seemed in fact even-aged, probably because of an increasing imprecision of dating with stand age, we thus chose to extend it to 30 years for stands older than 200 years. A minimum age was also assigned to stands consisting primarily of one species that usually does not establish itself after a fire, such as balsam fir, independently of their age structure. The median fire-free interval was estimated to be 191 years in a previous study (Cyr, Gauthier and Bergeron, 2007) and a preliminary estimate of the fire based on a negative exponential fitting of the survival data was 295 years, with 53.2% of the observed TSF censored.

Fire behavior is known to be characterized by large, intense, stand-replacing fires. The largest fire that occurred in the area in recorded history was a little more than 200 000 ha in size and partly affected the south western portion of the case study area (Stocks *et al.*, 2003). Some exceptional sites show multiple-scarred *P. banksiana* that suggest an alternative, more frequent and less severe fire regime. However, this possible alternative fire regime will be ignored in the present study because the scarcity of evidence suggests that it does not play a major role in structuring the landscape in general, although it might be important in explaining the distribution of fire dependent *P. banksiana* in this area characterized by generally long fire-free intervals.

1.5.4 Estimation of FC in the case study area

The empirical survival data obtained from the field survey in the case study area was submitted to the three above-mentioned methods to estimate the FC (negative exponential fitting, Weibull fitting, and Cox regression). Associated 95% confidence intervals (95CI) were computed by means of bootstrapping consisting of

10 000 resamplings of the original empirical sample using the 2.5 and 97.5 percentiles. Three levels of resampling were successively applied, i.e. 50%, 100% and 200% of the original sample, in order to evaluate the level of resampling effort that would yield a 95CI that is comparable in width to the one obtained in the simulation of similar FC.

1.6 Results

1.6.1 Empirical fire size distribution

The mean size of recorded fires ignited by lightning within a 100-km radius of the case study area is 6 365 ha. The maximum likelihood estimates of the log-normal distribution that was fit to the empirical size distribution of individual fire sizes are μ= 7.4058 (SE= 0.136) and σ=1.51 (SE=0.096) (units: ln(ha); Fig. 1.3).. Individual fire sizes were drawn from this log-normal distribution for all scenarios.

1.6.2 Description of simulated landscapes and associated temporal series of annual area burned

Fig. 1.4a-d, which shows the first 2000 years of the simulations, illustrates how the true FC (FC_{50}, FC_{150} and FC_{300}) and the mean TSF vary as a function of annual area burned. The initialization phase of 1000 years allows all simulated landscapes to reach a mean TSF that is approximately equal to the length of the global FC, even in the case of the longest one (539 years). In general, 2 to 2.5 times the length of the global FC seems to allow the landscape with all elements' TSF starting at zero to reach a point where mean TSF seems to be stabilized, although exceptionally large fire events may of course disrupt this process at any time.

While the mean TSF increases at a slow rate approaching a 1:1 slope in periods of very low fire activity, transient drops in mean TSF can be observed simultaneously with large fire events. The magnitude of the variations in true FC is inversely proportional to the length of the reference period (Fig. 1.4a-d, see also Table 1.2). The range of variations in true FC_{50} is indeed much wider than the ones for FC_{150} or FC_{300} for all simulated global FCs. The true FC_{300} is very similar to the mean TSF.

1.6.3 Effect of sampling effort on FC estimates

1.6.3.1 Central tendency of distribution of residuals (global accuracy)

Estimates of FC_{300} for all three methods applied to samples on which the censoring function was applied (Fig. 5a-d, red lines) appears relatively unbiased for simulation with global FC = 75 and 140 years (Fig. 5a-b) as there is no notable departure from 0 of the central tendencies of residuals even with the smallest sampling effort (N = 10). Biases are observed when simulated FC = 253 (Fig. 1.5c), especially when sampling effort is small ($N \leq 30$). The bias associated with the negative exponential fit is relatively small while the one associated with the Weibull fit is more substantial. The Cox regression, however, appears to slightly underestimate the FC even when based on larger samples, although the underestimation is relatively small compared with the width of the 95CI (-23 years, when N=94; cf Table 1.2). A similar but accentuated pattern is observed for the longest simulated FC (539 years, Fig. 1.5d) where only the negative exponential-based estimates seem to remain globally unbiased, as the Weibull-based estimates become even more biased than the Cox regression-based ones in absolute value when sampling effort N=94 (Table 2). Estimates based on uncensored samples (Fig 5a-d, orange lines) are relatively unbiased for all simulated FCs.

1.6.3.2. Distribution of residuals (precision)

The width of 95CI quickly stabilizes when sampling effort reaches 30 in the shortest FC simulated (75 years; Fig. 1.5a), with almost no discernable differences between estimates obtained from uncensored samples and from the one on which the censoring function was applied. The stabilization of the width of the 95CI occurs gradually later as the length of the simulated FC increases but does not decrease notably after sampling effort N=50, except for the longest simulated FC in the case of the Weibull fit regressions, which appears to be the most unstable estimator of FC. The width of 95CI obtained from censored observations becomes considerable as the length of simulated FC increases. For the longest FC (539 years), the width of the 95CI for sample size = 94 reaches approximately 100% of the length of simulated FC in the case of the negative exponential fit and the Cox regression, and even more in the case of the Weibull fit, while it is approximately 70% of the length when simulated FC = 253 for the negative exponential fit and Cox regression, and approximately 100% for the Weibull fit (Table 2). The 95CI are largely asymmetric for negative exponential and Weibull fit, which seems to produce overestimates of FC more often than the opposite, while they are almost exactly symmetric for Cox regressions.

The proportion of censored observation seems to be a major source of imprecision as the differences between 95CI obtained from uncensored and censored samples increases as the length of the simulated FC increases, which is directly related to the percentage of censored observations. However, Cox regression seems to be less affected by the proportion of censored observations as the difference between the 95CI obtained from uncensored and censored samples is not as important as with other methods (Fig. 1.5 a-d).

1.6.4 Effect of the percentage of censored observations on FC estimates

Figure 1.6 illustrates how $residuals_{300}$ behaves as a function of the percentage of censored observations with constant sampling effort of N = 94. These results suggest that the impact of censored observations on SA-based estimates of FC is minimal in absolute terms until their percentage of the sample reaches approximately 40% for all methods. When the amount of censored data increases, the negative exponential and Cox regressions seem to behave similarly to further increases in the proportion of censored observations. However, Cox regressions seem to underestimate FC slightly more often with high percentages of censored observations. Weibull-based estimates of the FC become very unstable as the percentage of censored observations reaches about 50%. Furthermore, the density of the scatter plot in the case of the Weibull fit is the most asymmetric as there are many more occurrences of underestimates that are compensated by less frequent but more extreme overestimates (some outsiders are in fact located outside the region covered by the *y*-axis for the highest percentages of censored observations).

1.6.5 Effect of temporal variations in fire activity on FC estimates

The differences between estimated FC and true FC_{300} years ($residuals_{300}$) were plotted over shorter term variations in fire activity and a linear regression was fit using the least squares method (cf. Appendix 1.1 for individual regressions). The slopes of these regressions indicate the bias associated with variations in fire activity. When positive, it indicates that the FC tends to become overestimated when there is an increase in fire activity in the recent reference period as compared with the previous one. Inversely, a negative slope indicates that the FC tends to be underestimated when recent fire activity is higher than that of the previous reference period. The slopes resulting from of all the linear regressions presented in the Appendix 1.1 were then compiled and plotted over the temporal scope considered in

Figure 1.7 in order to analyze how our three SA-based estimation methods were affected by variations in fire activity for each simulated global FC. As these slopes indicate the direction and amplitude of the bias in the estimation of FC associated with every 1% increase in mean percent annual area burned in the recent reference period as compared with the previous one, they must be put in the perspective of the typical magnitude of these variations, which are inversely related to the length of the reference periods that were used in our modeled environment (Table 1.4).

The effect of variation in fire activity was considerably different depending on the global FC that was simulated. The longer the simulated FC is, the larger the differences among the estimation methods are (Fig. 1.7). There are few or no differences among the three methods in terms of how they respond to variations in fire activity for the two shortest simulated FCs. While all methods slightly underestimate the length of the FC_{300} when an increase in fire activity is observed, and vice-versa, the three methods react differently when the length of the simulated FC and, consequently, the proportion of censored observations, increases. For the two longest simulated FCs the negative exponential fit and the Cox regression never tend to overestimate the FC when there is an increase in fire activity. On the contrary, they tend to underestimate FC when fire activity increases using reference periods of 50 to 300 years, or 100 to 300 years, for the negative exponential fit and Cox regression, respectively. The Weibull fit, however, may overestimate the length of the FC when fire activity is increasing using short reference periods (5-125 years), while it underestimates the length of the FC similarly to the other methods when an increase is observed when using 125- to 300-year reference periods. Therefore, in decreasing order of sensitivity to variations in fire activity, the three methods are the Weibull fit, the negative exponential fit, and finally the Cox regression.

1.6.6 FC estimation in the case study area

The Weibull fit and the Cox regression estimates of the FC for the case study area are very similar to each other and shorter than the one obtained from the negative exponential fit (Fig. 1.8). The Weibull fit and Cox regression-based estimates of the FC for the period covered by the dendroecological reconstruction (approx. last 300 years) are indeed 212 and 206 years, respectively, when resampling effort N=94 (100% of the original sample), and the negative exponential-based estimate is 294 years. The mean estimated FC does not vary substantially with the resampling effort within each method, only the width of the 95CI based on 2.5% and 97.5% percentiles does (Fig. 1.8; legend). When compared with the one obtained from the simulation of 140 and 253 years global FC (Table 3), the width of the 95CI obtained from bootstrapping from the case study area appears to be too narrow for all resampling efforts (50%, 100% and 200%) in the case of the Weibull fit for a FC that is most likely within the 200-300-year range (Fig. 1.5c) with just a little more than 50% of censored observation (Fig. 1.6). As a comparison, the width of 95CI appears to be more realistic for all levels of resampling, but especially for the 100% level (N=94) as the width of bootstrap 95CI (160 and 130 years for the negative exponential fit and Cox regression, respectively) are the most similar to the one obtained in the simulations of a global FC of 253 years (≈180 years for both methods; Table 2).

The age-class distribution at the landscape level from which these estimates were obtained (Fig. 1.9) shows an irregular shape. A relatively constant fire activity would have produced the "J" shape of the negative exponential distribution. Here, younger stands clearly appear to be underrepresented when compared with the negative exponential, suggesting a decrease in recent fire activity.

1.7 Discussion

In agreement with a previous modelling study (Li, 2002), our results show that the estimates of FC are not static but change over time. In the context of cross-sectional field survey-based fire history reconstruction such as those simulated in the present study or our case study, sources of uncertainty in the estimation of FC are multiple and include: 1- the variation inherent to sampling, 2- the (pseudo)spatial stochasticity of the phenomenon, which involves random burning of a landscape through which stands of various TSF are affected, and 3- temporal variations in fire activity, which interfere with the assumption of a stationary process that is needed for substituting observed TSF to complete fire intervals (Polakow and Dunne, 2001). Despite this, our results suggest that SA conducted from cross-sectional field surveys provide useful estimates of FC as most of the simulations yielded estimates of FC that were, globally, relatively unbiased. Moreover, our simulations allowed us to identify the extent to which sources of error affected the estimates and which methods were the most robust. One common result for all methods, however, is that the associated 95CI are relatively wide, which may represent a limit to some of the applications of this important parameter of the fire regime. This aspect will be further developed below.

We will start by discussing the global accuracy and precision of the three investigated methods. We will then discuss the effect of temporal variations in more detail. The four simulated global FCs are treated in each section as they allow us to integrate the simultaneous effect of generally longer/shorter fire-free intervals alongside the proportion of censored observations. Then, we will discuss the results obtained in the case study area in light of the simulation results and end with a discussion of management implications.

1.7.1 Global accuracy and precision

In terms of global accuracy, all methods appear to provide equally valid estimates with simulated global FCs of 75 and 140 years as they are all relatively unbiased. Typically longer fire-free intervals seem to induce some global biases associated with the Cox regression and Weibull-based estimates with the longest simulated FC (253 and 539 years), an issue, however, that can addressed by adjusting the estimate of FC accordingly (discussed below). On the other hand, it was easily predictable that the negative exponential-based estimates would be globally unbiased since fire was modelled as a completely random process in space and time, hence meeting the constant hazard assumption of the negative exponential. Although such global assessment of the biases associated with each method may represent useful information when no prior indication of past fire activity is available, it is of very limited used in most real case studies considering that each method reacts differently to the confounding factors that affect the estimates of FC, especially temporal variations in fire activity. By using the random variations in fire activity that were produced through our modelling approach and by relating these variations to the error in the estimation of FC, we were able to provide a better assessment of the direction and magnitude of potential bias. That exercise revealed that the globally unbiased method in the modelled environment, the negative exponential, is not necessarily the best method in specific cases as it is quite sensitive to temporal variations in fire activity, especially when considering the 100- to 300-year time frame. In terms of precision, it appears that sample size is only important when it is smaller than about 50 and the gradual loss of information caused by over-burning and censoring prevent the estimate from being more precise as sample size is further increased. All methods appear to be limited in the same way as their associated 95CI all reach similar widths, although the sample size needed for this stabilization to be reached varies.

1.7.2 Effects of temporal variation in the context of gradual loss of information due to censoring and over-burning

Although we applied a constant hazard function at the scale of each entire simulation, we used the random variations within each fire series to assess how temporal variations in fire activity affect the estimates of FC. Our simulations allowed us to single out temporal variations in fire activity as an important factor that interferes with estimates of FC from cross-sectional sampling, confirming previous criticism in that regard (Clark, 1989 ; Polakow and Dunne, 2001). This is because the survival analyses are based on time-since-fire data and not on complete fire-return intervals, which can be treated interchangeably only if the failure process (fire) is assumed to be stationary (Polakow and Dunne, 2001), which it is at the temporal scale of each entire simulation (4000 years), but not necessarily at shorter temporal scales because of random variations or in a real case study. For all methods, increases in fire activity are associated with underestimates of the length of the FC, and vice-versa, when considering reference periods that roughly correspond to the time during which censoring occurs (100-300 years) in the case of the three longest simulated FCs (140, 253, and 539 years), or earlier in the case of the shortest simulated FC (75 years). In this latter case, a similar bias is observed when considering a wider range of reference periods, 75 to 300 years. This bias appears to be related to the gradual loss of information that is caused by over-burning and/or censoring, which both create conditions where the most recent fire activity has a greater importance in estimating FC. Substantial increases in fire activity mean that records of lower amounts of area burned in previous periods (older stands) get "erased" from the landscape. In the opposite situation, when fire activity decreases, it is censoring that gradually erases records of the higher proportions of stands that were initiated in earlier decades when fire activity was higher. These two processes occurred in all simulations, but the number of censored observations that are more important when simulated FC is longer (253 and 539 years) contribute to accentuating this source of error.

Although the negative exponential is globally unbiased, it was revealed to be quite sensitive to variations in fire activity when simulated global FC was long (253 and 539 years). The negative exponential was indeed the most prone to underestimating the FC with increasing fire activity using reference periods of 50 to 300 years, and the inverse. The relationship appears to be symmetrical enough to explain why this method is globally unbiased, i.e. that the over- and underestimations occur similarly with opposite trends in fire activity. In comparison, the Cox regression is also affected by the same bias, but to a lesser extent, most likely because the hazard function is only "locally" determined by the extent of each individual fire event. Only the Weibull-based estimates show a distinct inversed pattern when considering shorter-term variations. Recent variations in fire activity indeed seem to affect the Weibull-based estimates of FC in the opposite direction than the aforementioned loss of information caused by censoring and/or over-burning, i.e. that variations in fire activity are positively related to a bias in the estimates of FC. Large recent fire events strongly affect the estimation of the shape parameter c of the Weibull distribution, which determines how the hazard of burning increases or decreases along the time axis. Weibull fit on survival samples affected by a recent increase in fire activity will typically yield a survival model associated with a decreasing hazard of burning along the time axis (in reverse time), a trend that is perpetuated towards infinity. This is of course unrealistic as it implies that older forests see their vulnerability to fire decrease in a monotonic manner down to zero at infinity. Since the length of the FC is numerically equivalent to the mean fire return interval (Johnson and Gutsell, 1994) and as averages are strongly influenced by extreme values, overestimates of FC are therefore produced. Only the two longest simulated global FCs seem to be substantially affected by this artifact. This is most likely because greater short-term variations in fire activity induce much more instability in the estimation of the shape parameter. In general, the two parametric methods (negative exponential and Weibull) are thus the most sensitive to temporal variations in fire activity. Moreover, the Weibull-based estimates of FC appear to be the less reliable ones in the modelled conditions. The additional degree of freedom that is allowed by the shape parameter in fact just generates more instability in the estimation compared with the special case of the negative exponential.

The interest of working with Weibull-based survival models in fire ecology is related to their ability to formally test age-dependency of hazard of burning within a parametric framework (Johnson, 1979 ; Johnson and Van Wagner, 1985). This has been a commonly used approach to test the effect of fuel loading as an endogenous source of variation in hazard of burning, especially in fire prone Mediterranean types of ecosystems (Moritz, 2003 ; Moritz *et al.*, 2004 ; Polakow and Dunne, 1999). In the context of the boreal forest of Eastern Canada, however, typical fire return intervals are long enough that exogenous factors affecting the hazard of burning such as climate may change concurrently with potential endogenous factors, which considerably complicates the interpretation of the shape parameter that defines how hazard of burning changes along the time axis. Moreover, it appears unrealistic that any relationship between age and fuel loading would be monotonous on the entire typical lifespan of a boreal stand (e.g. Schoenberg *et al.*, 2003). In fact, one would rather expect to find thresholds related to the delay in the establishment of a fuel load sufficient to carry fire, as well as succession from broadleaf species to coniferous or the reverse. In this context, the potential advantages related to the use of Weibull-based survival models to estimate FC compared with the negative exponential are much more likely outweighed by the aforementioned artifacts that were observed in our simulations. We also suggest that it might be more appropriate to incorporate such empirically and independently developed relationships between age and fuel loading (Schoenberg *et al.*, 2003) within a Cox regression model as a time-dependent covariate (e.g. Anderson, 1992 ; Fleming and Harrington, 1984) which would allow the exogenous factors such as climate and land use to be treated separately by the unspecified hazard function. In summary, for this reason and because the Cox regression does not require that we choose some particular probability distribution to represent survival time, we therefore recommend the use of Cox regression to estimate FC from cross-sectional field surveys such as those modelled in our study. In our opinion, the global underestimation of FC by Cox regression, which appears to be independent of temporal variations in fire activity, is a minor drawback if some indication of its extent is known. Depending on the extent of this bias, one can choose to simply neglect it if it is relatively small compared with the length of the FC and with the width of the 95CI, or adjust the estimates of the FC accordingly.

1.7.3 Estimation of the FC in the study area

The three estimates of FC for the last 300 years in the case study area of eastern Canada are between 206 and 295 years, with 95Cl that considerably extend the domain of possible values. Given the results of our simulations, however, we believe that the Cox regression-based estimates of FC for the last 300 years is the most credible, implying that the true FC is more likely closer to 206 years than 295 years. Moreover, an increasing trend in the length of the FC (decreasing trends in fire activity) have been observed in all areas where fire history has been reconstructed for the last 300 years or so in the boreal forest of Eastern Canada (Bergeron *et al.*, 2006). According to the results obtained from the simulation of a global FC of 253 years, which is the simulation that is the most similar to our case study, this trend over such time frame is associated with a considerable overestimation of the length of the FC by the negative exponential, whereas it is more difficult to assess in the case of the Weibull. The same simulation (global FC = 253 years) also suggests that the Cox regression globally underestimate the FC by approximately 10%. It is therefore more likely that the true FC for the last 300 years in the case study area was a approximately 10% higher than the unadjusted estimate made by the Cox model, i.e. ≈ 226 years.

Regardless of the method used, it is important to highlight the fact that a wide confidence interval must be associated with estimates of FC for the last 300 years. Considering the percentage of censored observations in our cross-sectional field sample and the estimates that we obtained using the Cox regression, the 95CI should be somewhere between those obtained from the simulations of 140 and 253 years global FC, i.e. between 100 and 180 of overall width, which is similar to the one obtained from bootstrapping the field sample with a resampling effort of 100% (N=94). Although this correspondence is not the consequence of a direct relationship between the two methods as the resulting 95CIs were obtained independently from different sources of information, it suggests that bootstrapping the empirical dataset yields a realistic 95CI for the case study area. Further studies involving comparisons with more empirical datasets are necessary to assess the extent to which this assertion is generalizable.

1.7.4 Implications for management

The TSF distributions obtained from natural fire regimes that make up boreal landscapes are often suggested as **guidelines** for forest management because they constitute a very integrative characteristic of boreal landscapes that also determine to the relative influence of finer scale types of disturbances (Gauthier *et al.*, 2009).

Reproducing these natural patterns through harvesting is therefore believed to act as a coarse filter for conservation of biodiversity (Hunter, 1993) and other known and unknown ecosystem services (Attiwill, 1994 ; Christensen *et al.*, 1996). With this approach, the FC is the key parameter defining the respective proportions of young and old forest, as well as the relative importance of silvicultural practices that better emulate their dynamics. The age structure at the landscape level from which the survival sample is obtained, however, is only one realization of a stochastic process (Armstrong, 1999) and for this reason some criticisms arose which argued that using the FC as one strict reference may be too restrictive and does not adequately recognize the changing nature of fire-regulated boreal forests (Armstrong *et al.*, 2003 ; Boychuk and Perera, 1997). Our results show that the estimation of the FC itself is subject to considerable imprecision. In the boreal forest of Eastern North America, however, the idea that stands exceeding in TSF the length of typical harvesting rotations under low-retention harvesting regime (≈60-100 years) made up the vast majority of large productive landscape remains unchallenged. Even with a FC at the lower limit of the bootstrap 95CI (≈148 years), the proportion of stands older than 100 years would be around 50%. Considering the central measure of the estimated FC for the last 300 years (unadjusted: 206 years; adjusted: 226 years), the proportion of old forests varied around 61-64% of the landscape. Of course these proportions varied more at finer spatiotemporal scales, but there are no indications whatsoever from any kind of proxy (e.g. dendroecological, or paleoecological) that boreal landscapes made up by a majority of young stands (TSF < 100 years) were the norm rather than the exception in Eastern North America.

Our results also illustrate that FC estimated from long reference periods, i.e. minimum 150 years and ideally 300 years, is more closely related to the true mean

TSF of the forest, especially in Eastern Canada where fire free intervals are typically long. The use of mean TSF to set target for age structure and composition was indeed previously suggested (Bergeron *et al.*, 2006 ; Gauthier *et al.*, 2002), as it better summarizes the overall age-class distribution at the landscape level than FC estimated from short reference periods, and because it takes the inertia of large landscapes into better consideration.

The uncertainty associated with FC estimates, however, may impose more restrictive limits to other applications of the knowledge of the length of the FC that require a more precise quantification. For instance, it may considerably complicate the detection of changes in fire regime in the past and near future because of the great variability inherent to the process, which is an important issue on many levels in the context of climate change. Average annual area burned has shown long-term trends in the past in relation to climate change, and is expected to increase in most of the boreal forest, but these changes will very likely need to be quite dramatic to be statistically discernable. Consequently, not only is the baseline contribution of fire disturbance to the global carbon cycle difficult to assess, recent and future changes in fire regime that might be needed to document are considerably uncertain (Kurz *et al.*, 2008). This also applies to the effect of fire on annual allowable cut predictions in strategic forest management planning (e.g. Leduc *et al.*, in prep). This is why we stress the importance of integrating uncertainty into the management decision-making process by using a wide array of scenarios.

1.7.5 Conclusions

The simulation approach used in this study is a transparent way to incorporate multiple types of uncertainty and to provide an integrative assessment of accuracy and precision of survival model-based estimates of FC. We showed that even with an increased sampling effort, wide 95CIs are obtained, which is explained by the stochastic nature of forest fire (in our modelled environment but in real landscapes as well). The length of the FC itself also proved to be a major parameter influencing the precision and accuracy of the estimated FCs as long FC increase the proportion of censored observations and induce more short-term variations in annual area burned.

Our study confirms some of the statistical issues that were put forward with the use of survival analyses for estimating the FC for the last 300 years from a cross-sectional sample of the landscape, mainly the influence of temporal variations in fire activity (Clark, 1989 ; Polakow and Dunne, 2001). The length of the FC remains important information to seek for many practical management issues, however, and sources of information are limited especially where typical fire return intervals are long. Using a modelling approach allowed us to better quantify the impact of current methodological limitations and showed that SA conducted on cross-sectional sampling of large boreal landscapes can provide valid estimates of FC even though they are associated with wide 95CIs, but also revealed that additional statistical development is needed to allow more rigorous estimates of FC from such source data.

All methods are not equal, however. Most previous studies used parametric SA based on either the negative exponential or the Weibull distribution, which are the most sensitive methods to low sampling effort and, more importantly, temporal variations in fire activity. The unrealistic assumptions underlying the use of these methods that are related to how hazard of burning varies (or not) along the time axis can be minimized by using the baseline non-parametric hazard function that was fit through the process of a Cox regression. Cox regressions are not perfect either, as ecological processes related to the aging of stands still generate the censoring of a large proportion of the landscape when FC is relatively long, causing a gradual loss of information about past fire activity that is suspected to have changed substantially during the last decades and centuries. Despite this, our simulation results suggest that basic Cox regression-based estimation of FC is the least sensitive to this potential source of error.

1.8 References

Allison, P.D. (1995). Survival analysis using the SAS system: A practical guide. Cary, North Carolina, SAS Institute Inc.

Amiro, B. D., A. Cantin, M. D. Flannigan and W. J. De Groot. 2009. «Future emissions from Canadian boreal forest fires». *Canadian Journal of Forest Research*, vol. 39, no 2, p. 383-395.

Anderson, P.K. 1992. «Repeated assessment of risk factors in survival analysis». *Statistical Methods in Medical Research*, vol. 1, p. 297-315.

Armstrong, G. W. 1999. «A stochastic characterisation of the natural disturbance regime of the boreal mixedwood forest with implications for sustainable forest management». *Canadian Journal of Forest Research*, vol. 29, no 4, p. 424-433.

--------. 2004. «Sustainability of timber supply considering the risk of wildfire». *Forest Science*, vol. 50, no 5, p. 626-639.

Armstrong, G. W., W. L. Adamowicz, J. A. Beck Jr, S. G. Cumming and F. K. A. Schmiegelow. 2003. «Coarse filter ecosystem management in a nonequilibrating forest». *Forest Science*, vol. 49, no 2, p. 209-223.

Arno, S.F., and K.M. Sneck (1977). A method for determining fire history in coniferous of the mountain west, USDA Forest Service

Attiwill, Peter M. 1994. «The disturbance of forest ecosystems: The ecological basis for conservative management.». *Forest Ecology and Management*, vol. 63, no 2-3, p. 247-300.

Baker, W. L. 1989. «Effect of scale and spatial heterogeneity on fire-interval distributions». *Canadian Journal of Forest Research*, vol. 19, no 6, p. 700-706.

Bergeron, Y., D. Cyr, C.R. Drever, M. Flannigan, S. Gauthier, D. Kneeshaw, E. Lauzon, A. Leduc, H. Le Goff, D. Lesieur and K. Logan. 2006. «Past, current, and future fire frequencies in Quebec's commercial forests: Implications for the cumulative effects of harvesting and fire on age-class structure and natural disturbance-based management». *Canadian Journal of Forest Research*, vol. 36, no 11, p. 2737-2744.

Bergeron, Y., S. Gauthier, M. Flannigan and V. Kafka. 2004. «Fire regimes at the transition between mixedwood and coniferous boreal forest in northwestern Quebec». *Ecology*, vol. 85, no 7, p. 1916-1932.

Bergeron, Yves. 2000. «Species and stand dynamics in the mixed woods of Quebec's southern boreal forest.». *Ecology*, vol. 81, no 6, p. 1500-1516.

Bergeron, Yves, Sylvie Gauthier, Victor Kafka, Patrick Lefort and Daniel Lesieur. 2001. «Natural fire frequency for the eastern Canadian boreal forest: Consequences for sustainable forestry.». *Canadian Journal of Forest Research*, vol. 31, no 3, p. 384-391.

Bouchard, M., D. Pothier and S. Gauthier. 2008. «Fire return intervals and tree species succession in the North Shore region of eastern Quebec». *Canadian Journal of Forest Research*, vol. 38, no 6, p. 1621-1633.

Boychuk, D., and D. L. Martell. 1996. «A multistage stochastic programming model for sustainable forest-level timber supply under risk of fire». *Forest Science*, vol. 42, no 1, p. 10-26.

Boychuk, D., and A.H. Perera. 1997. «Modeling temporal variability of boreal landscape age-classes under different fire disturbance regimes and spatial scales». *Canadian Journal of Forest Research*, vol. 27, no 7, p. 1083-1094.

Boychuk, Dennis, Ajith H Perera, Michael T Ter-Mikaelian, David L Martell and Chao Li. 1997. «Modelling the effect of spatial scale and correlated fire disturbances on forest age distribution.». *Ecological Modelling*, vol. 95, no 2-3, p. 145-164.

Christensen, N.L., A.M. Bartuska, J.H. Brown, S. Carpenter, C. D'Antonio, R. Francis, J.F. Franklin, J.A. MacMahon, R.F. Noss, D.J. Parsons, C.H. Peterson, M.G. Turner and R.G. Woodmansee. 1996. «The report of the Ecological Society of America committee on the scientific basis for ecosystem management». *Ecological Applications*, vol. 6, no 3, p. 665-691.

Clark, J. S. 1989. «Ecological disturbance as a renewal process: theory and application to fire history». *Oikos*, vol. 56, no 1, p. 17-30.

Cox, D.R. 1972. «Regression models and life-tables (with discussion)». *Journal of The Royal Statistical Society B*, vol. 34, p. 187-220.

Cyr, D., S. Gauthier and Y. Bergeron. 2007. «Scale-dependent determinants of heterogeneity in fire frequency in a coniferous boreal forest of eastern Canada». *Landscape Ecology*, vol. 22, no 9, p. 1325-1339.

Drever, C. R., C. Messier, Y. Bergeron and F. Doyon. 2006. «Fire an Canopy Species Composition in the Great Lakes-St. Lawrence Forest of Temiscamingue, Quebec». *Forest Ecology and Management*, vol. 231, no 1-3, p. 27-37.

Environment Canada. 1996. *Canadian climate normals 1947-1996*: Canadian Climate Program. Environment Canada. Atmospheric Environment Service.

Fleming, Thomas R., and David P. Harrington. 1984. «Nonparametric estimation of the survival distribution in censored data». *Communications in Statistics - Theory and Methods*, vol. 13, no 20, p. 2469 - 2486.

Gauthier, S., D. Boucher, J. Morissette and L. De Grandpré. 2010. «Fifty-seven years of composition change in the eastern boreal forest of Canada». *Journal of Vegetation Science*, vol. 21, no 4, p. 772-785.

Gauthier, S., P. Lefort, Y. Bergeron and P. Drapeau (2002). Time since fire map, age-class distribution and forest dynamics in the Lake Abitibi Model Forest. Saint-Foy, Qc., Natural Resources Canada, Canadian Forest Service, Laurentian Forestry Centre, Information Report LAU-X-125E

Gauthier, S., M.-A. Vaillancourt, A. Leduc, L. De Grandpré, D. Kneeshaw, H. Morin, P. Drapeau and Y. Bergeron. 2009. *Ecosystem management in the boreal forest*. Québec: Les Presses de l'Université du Québec.

Grenier, D. J., Y. Bergeron, D. Kneeshaw and S. Gauthier. 2005. «Fire Frequency for the Transitional Mixedwood Forest of Timiskaming, Quebec, Canada». *Canadian Journal of Forest Research*, vol. 35, no 3, p. 656-666.

Hirsh, K., V. Kafka, C. Tymstra, R. McAlpine, B. Hawkes, H. Stegehuis, S. Quintilio, S. Gauthier and K. Peck. 2001. «Fire-smart forest management: A pragmatic approach to sustainable forest management in fire-dominated ecosystems.». *The Forestry Chronicle*, vol. 77, no 2, p. 357-363.

Hosmer, D.W. Jr., and S. Lemeshow. 1999. *Applied Survival Analysis: Regression modeling of time to event data*. New York: John Wiley & Sons, Inc.

Hunter, M.L. Jr. 1993. «Natural fire regimes as spatial models for managing boreal forests». *Biological Conservation.*, vol. 65, no 2, p. 115-120.

Johnson, E A. 1979. «Fire recurrence in the subarctic and its implications for vegetation composition». *Canadian Journal of Botany*, vol. 57, no 12, p. 1374-1379.

Johnson, E A, and C.E. Van Wagner. 1985. «The theory and use of two fire history models». *Canadian Journal of Forest Research*, vol. 15, p. 214-220.

Johnson, E.A., and S.L. Gutsell. 1994. «Fire frequency models, methods and interpretations.». *Advances in Ecological Research*, vol. 25, p. 239-287.

Kurz, W. A., G. Stinson, G. J. Rampley, C. C. Dymond and E. T. Neilson. 2008. «Risk of natural disturbances makes future contribution of Canada's forests to the global carbon cycle highly uncertain». *Proceedings of the National Academy of Sciences of the United States of America*, vol. 105, no 5, p. 1551-1555.

Lauzon, E., D. Kneeshaw and Y. Bergeron. 2007. «Reconstruction of fire history (1680-2003) in Gaspesian mixedwood boreal forests of eastern Canada». *Forest Ecology and Management*, vol. 244, no 1-3, p. 41-49.

Lawless, J.F. 2003. *Statistical models and methods for lifetime data*, 2nd Edition. Hoboken, NJ.: Wiley.

Leduc, A., F. Raulier, S. Gauthier, P. Y. Bernier and Y. Bergeron. in prep. «Wildfire as a hidden harvester in the assessment of annual allowable cut for North American boreal forests».

Lesieur, D., S. Gauthier and Y. Bergeron. 2002. «Fire frequency and vegetation dynamics for the south-central boreal forest of Quebec, Canada». *Canadian Journal of Forest Research*, vol. 32, p. 1996-2008.

Li, C. 2002. «Estimation of fire frequency and fire cycle: A computational perspective». *Ecological Modelling*, vol. 154, no 1-2, p. 103-120.

Moritz, M. A. 2003. «Spatiotemporal analysis of controls on shrubland fire regimes: Age dependency and fire hazard». *Ecology*, vol. 84, no 2, p. 351-361.

Moritz, M. A., T. J. Moody, L. J. Miles, M. M. Smith and P. de Valpine. 2009. «The fire frequency analysis branch of the pyrostatistics tree: Sampling decisions and censoring in fire interval data». *Environmental and Ecological Statistics*, vol. 16, no 2, p. 271-289.

Moritz, M.A., J.E. Keeley, E.A. Johnson and A.A. Schaffner. 2004. «Testing a basic assumption of shrubland fire management: how important is fuel age?». *Frontiers in Ecology and the Environment*, vol. 2, no 2, p. 67-72.

Perera, A.H., and L.J. Buse. 2004. «Emulating natural disturbance in forest management: An overview». In *Emulating natural forest landscape disturbances: Concepts and applications,* A.H. Perera, L.J. Buse et M.G. Weber, p. 3-7. New York: Columbia University Press.

Polakow, D. A., and T. T. Dunne. 1999. «Modelling fire-return interval T: Stochasticity and censoring in the two-parameter Weibull model». *Ecological Modelling*, vol. 121, no 1, p. 79-102.

--------. 2001. «Numerical recipes for disaster: Changing hazard and the stand-origin-map». *Forest Ecology and Management*, vol. 147, no 2-3, p. 183-196.

Reed, W J, C P S Larsen, E A Johnson and G M MacDonald. 1998. «Estimation of temporal variations in historical fire frequency from time-since-fire map data.». *Forest Science*, vol. 44, no 3, p. 465-475.

Reed, W. J. 1994. «Estimating the historic probability of stand-replacement fire using the age-class distribution of undisturbed forest.». *Forest Science*, vol. 40, no 1, p. 104-119.

--------. 1997. «Estimating historical forest-fire frequencies from time-since-last-fire-sample data». *IMA Journal of Mathematics Applied in Medicine and Biology*, vol. 14, no 1, p. 71-83.

Robitaille, A, and J.P. Saucier (1998). Paysages régionaux du Québec méridional. Québec, Les Publications du Québec

Schoenberg, F. P., R. Peng, Z. Huang and P. Rundel. 2003. «Detection of non-linearities in the dependence of burn area on fuel age and climatic variables». *International Journal of Wildland Fire*, vol. 12, no 1, p. 1-6.

Senici, D., H.Y.H Chen, Y Bergeron and D. Cyr. 2010. «Spatiotemporal variations of fire frequency in central boreal forest». *Ecosystems*, vol. 13, p. 1227-1238.

Stocks, B.J., J.A. Mason, J.B. Todd, E.M. Bosch, B.M. Wotton, B.D. Amiro, M.D. Flannigan, K.G. Hirsch, K.A. Logan, D.L. Martell and W.R. Skinner. 2003. «Large forest fires in Canada, 1959-1997». *Journal of Geophysical Research*, vol. 108, p. doi:10.1029/2001JD000484.

Therneau, T. (2009). R package 'survival', version 2.35-8 En ligne. <http://cran.r-project.org/web/packages/survival/survival.pdf>.

Tsiatis, Anastasios A. 1981. «A large sample study of Cox's regression model». *The Annals of Statistics*, vol. 9, no 1, p. 93-108.

Van Wagner, C.E. 1978. «Age-class distribution and the forest fire cycle.». *Canadian Journal of Forest Research*, vol. 8, p. 220-227.

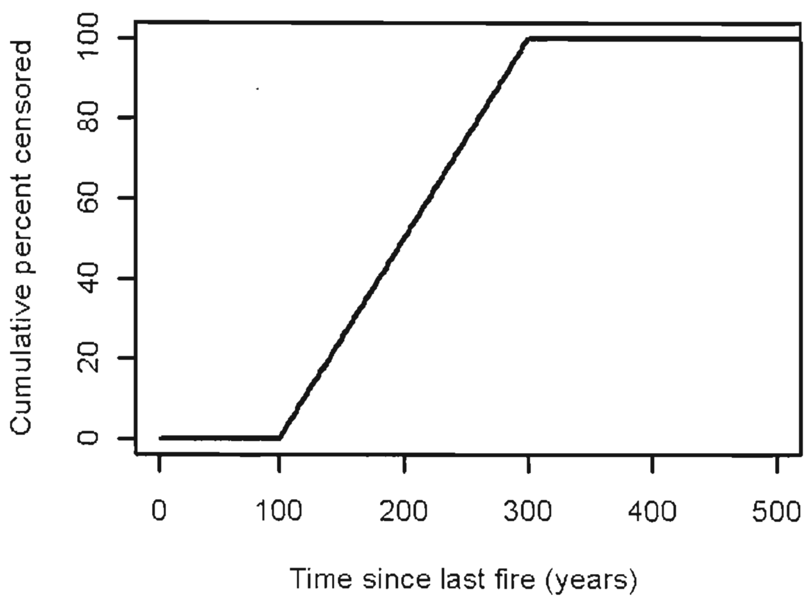


Figure 1.1 Censoring function applied to simulate gradual loss of information about the last fire event as time since last fire (TSF) increases.

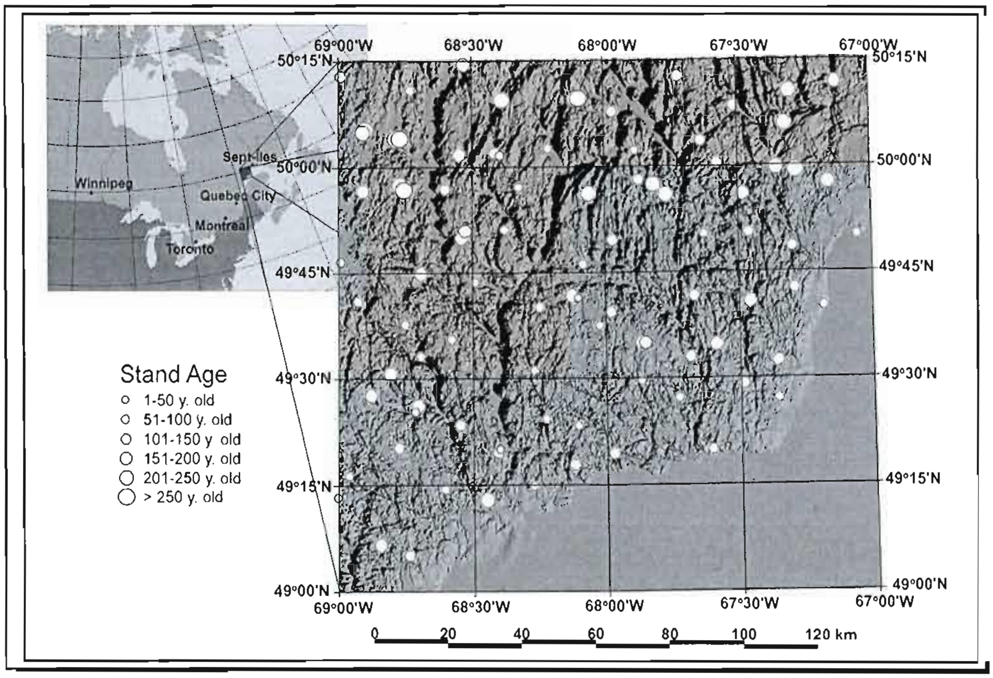


Figure 1.2 Case study area and spatial distribution of sample stands.

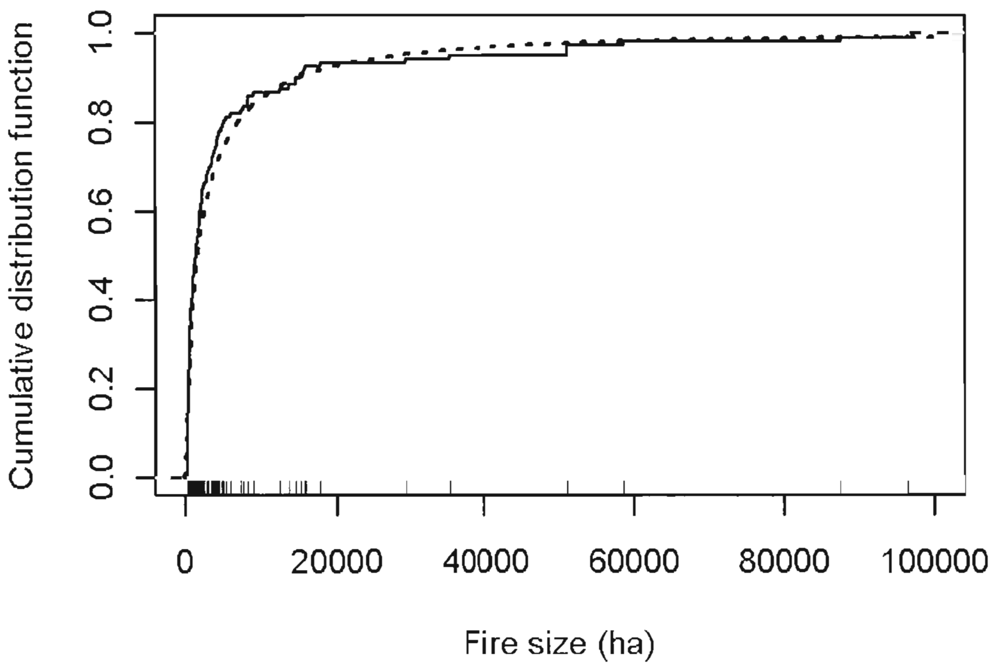


Figure 1.3. Empirical (full line) and fit (dotted line) fire size cumulative distribution functions. Upper tick marks on the lower axis indicate fire occurrences.

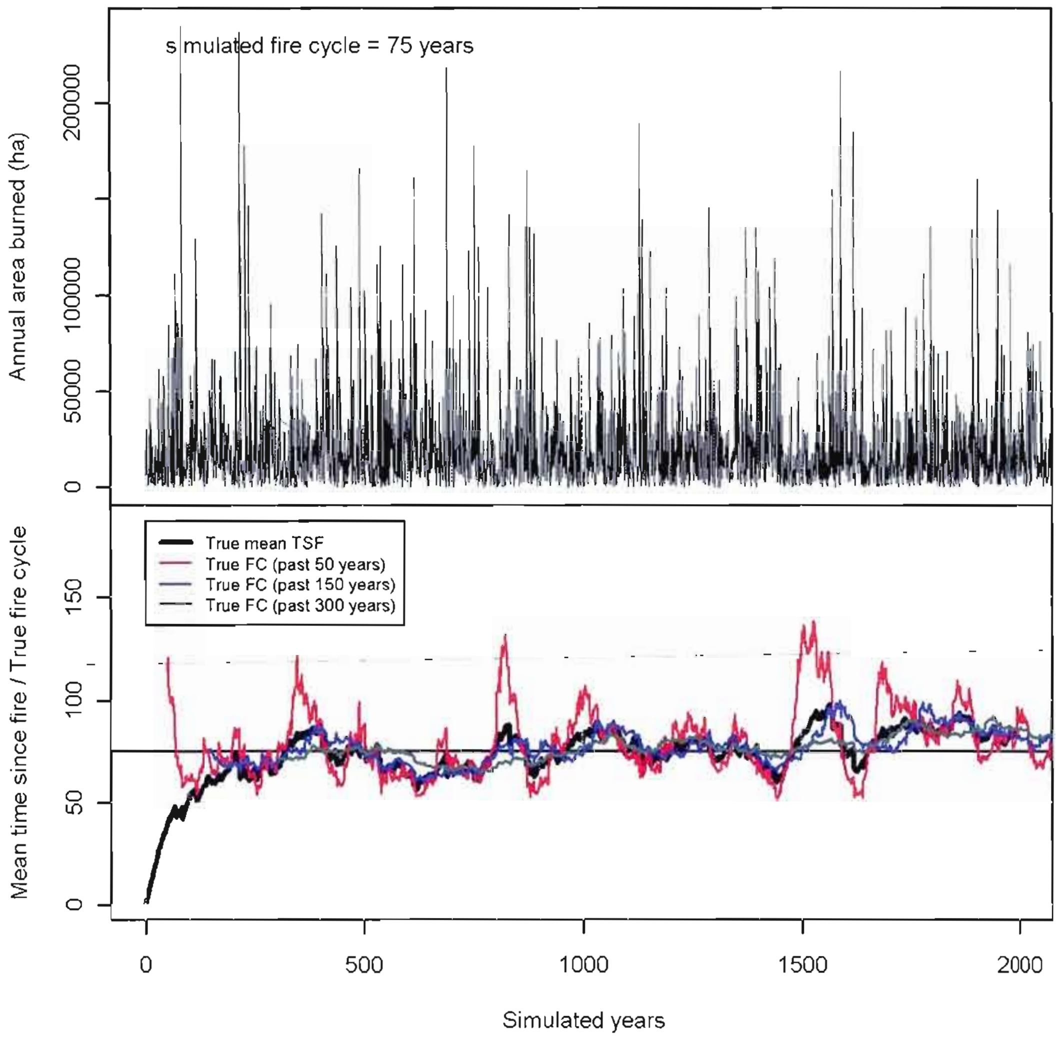


Figure 1.4a Simulated annual area burned and mean time since fire (TSF), and true fire cycle (FC) for a global fire cycle of 75 years.

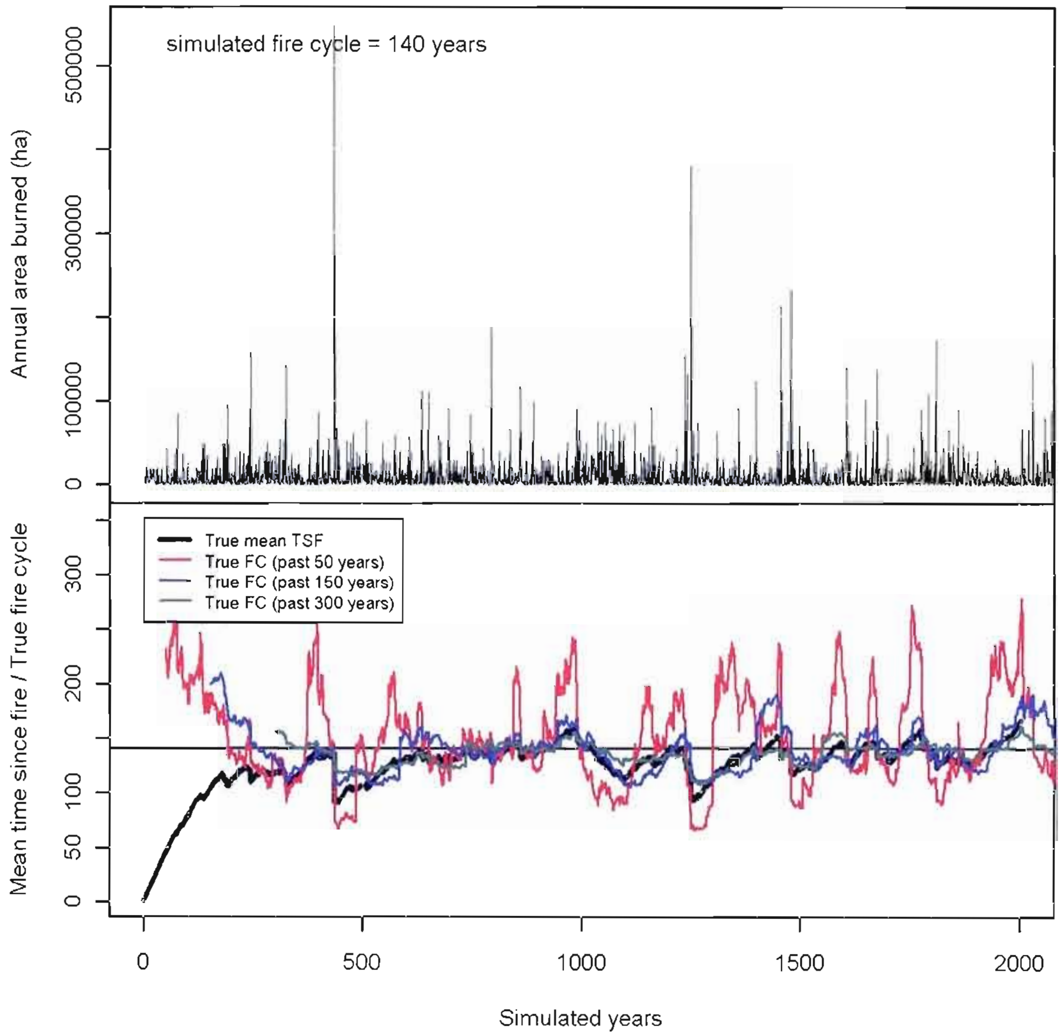


Figure 1.4b Simulated annual area burned and mean time since fire (TSF), and true fire cycle (FC) for a global fire cycle of 140 years.

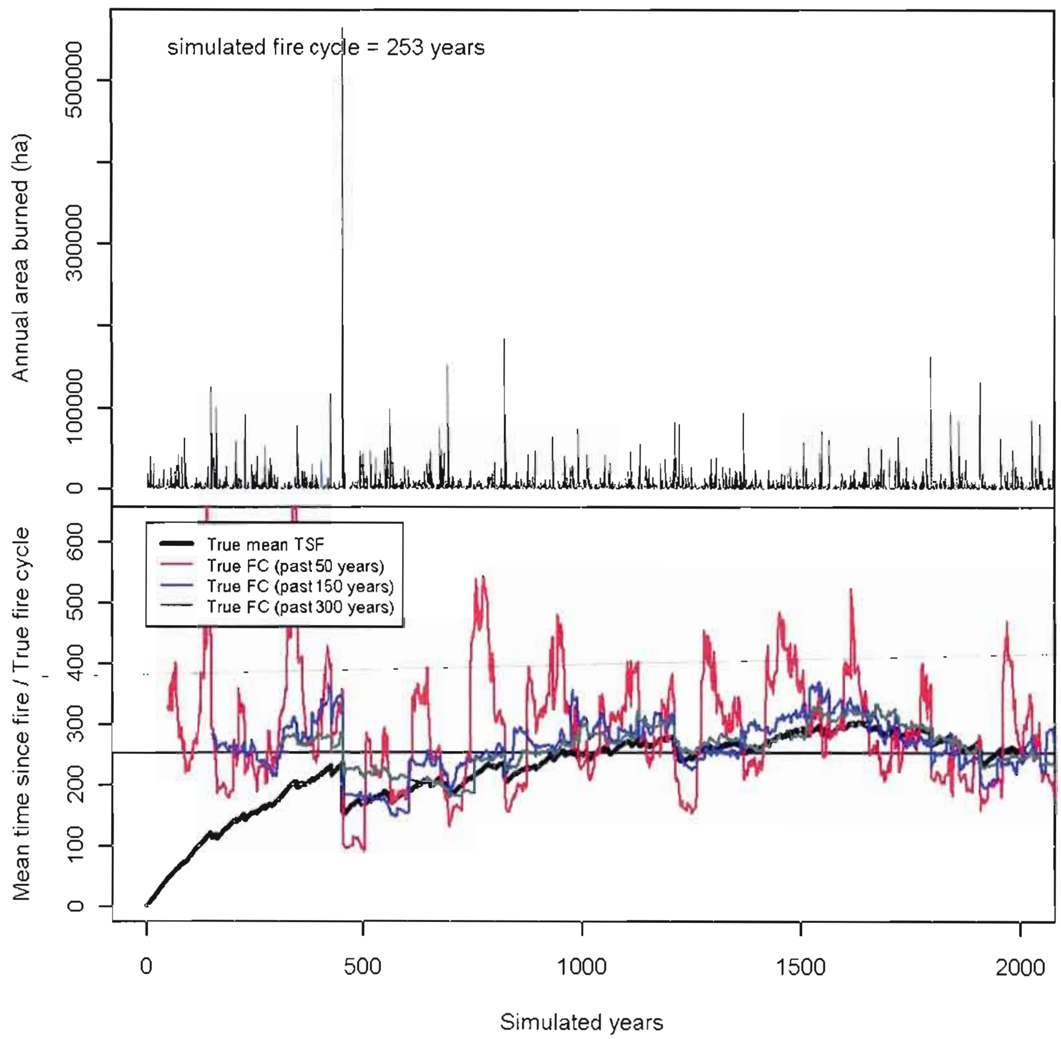


Figure 1.4c Simulated annual area burned and mean time since fire (TSF), and true fire cycle (FC) for a global fire cycle of 253 years.

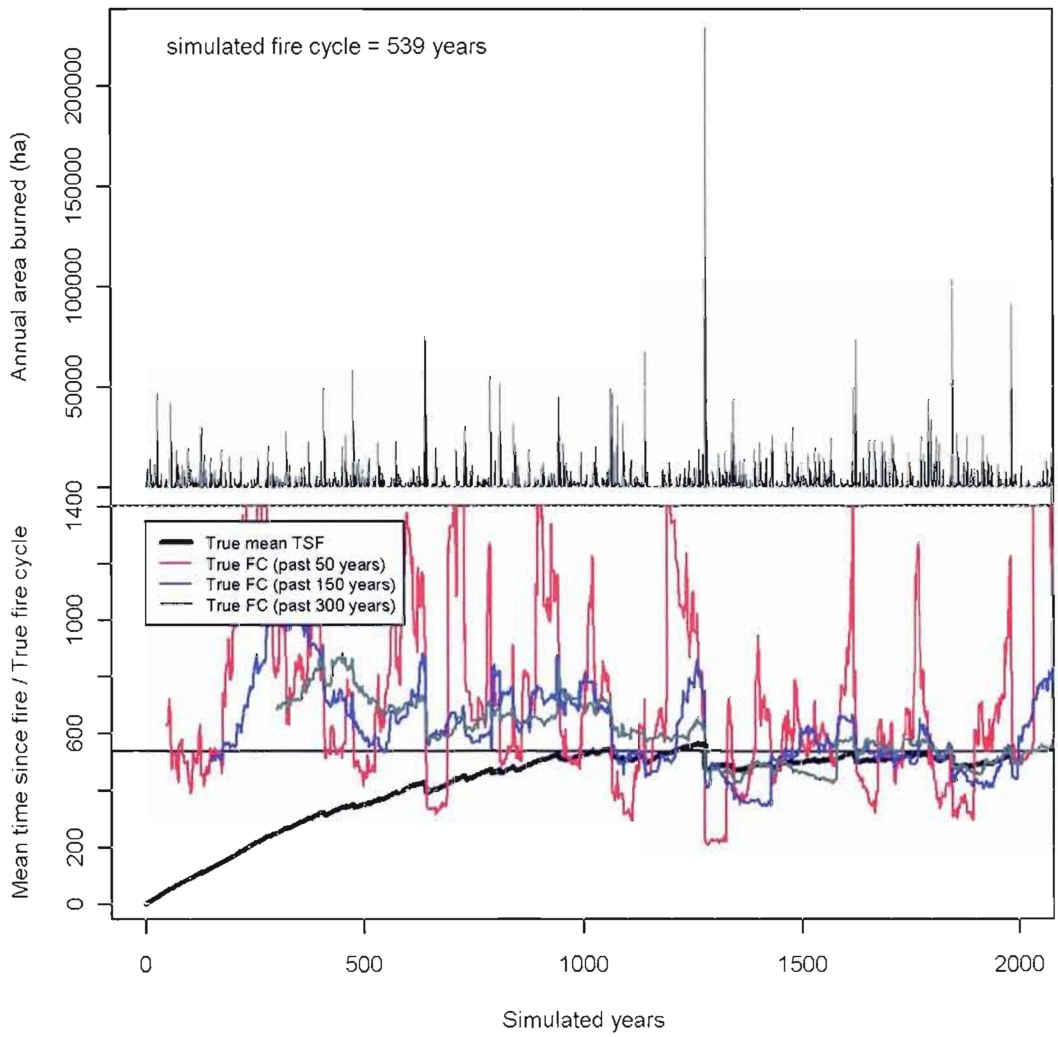


Figure 1.4d Simulated annual area burned and mean time since fire (TSF), and true fire cycle (FC) for a global fire cycle of 539 years.

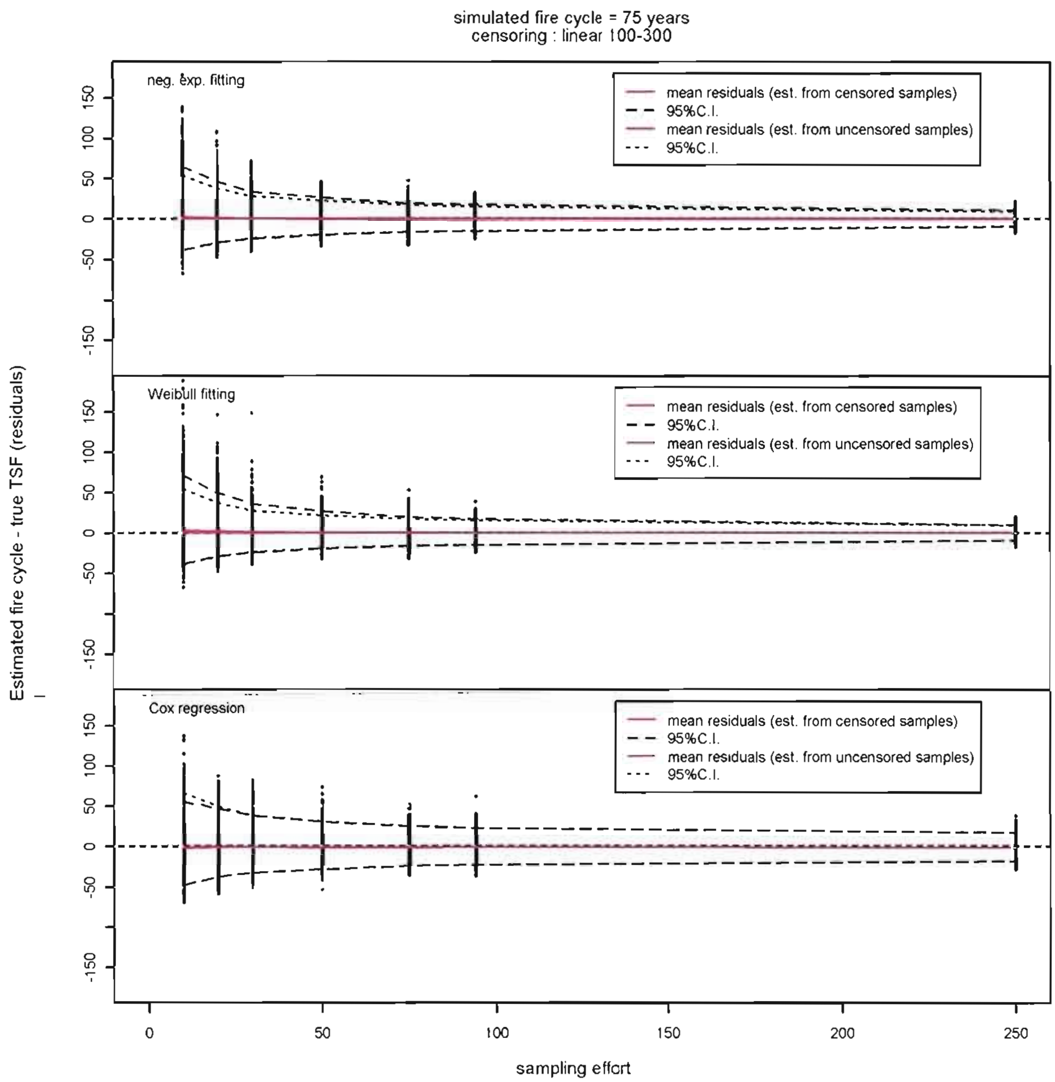


Figure 1.5a Central tendency and distribution of residuals (Estimated FC – True FC, past 300 years) for the three SA-based methods, as a function of sampling effort, with and without the censoring effect, with associated 95% C.I. for simulated global FC of 75 years.

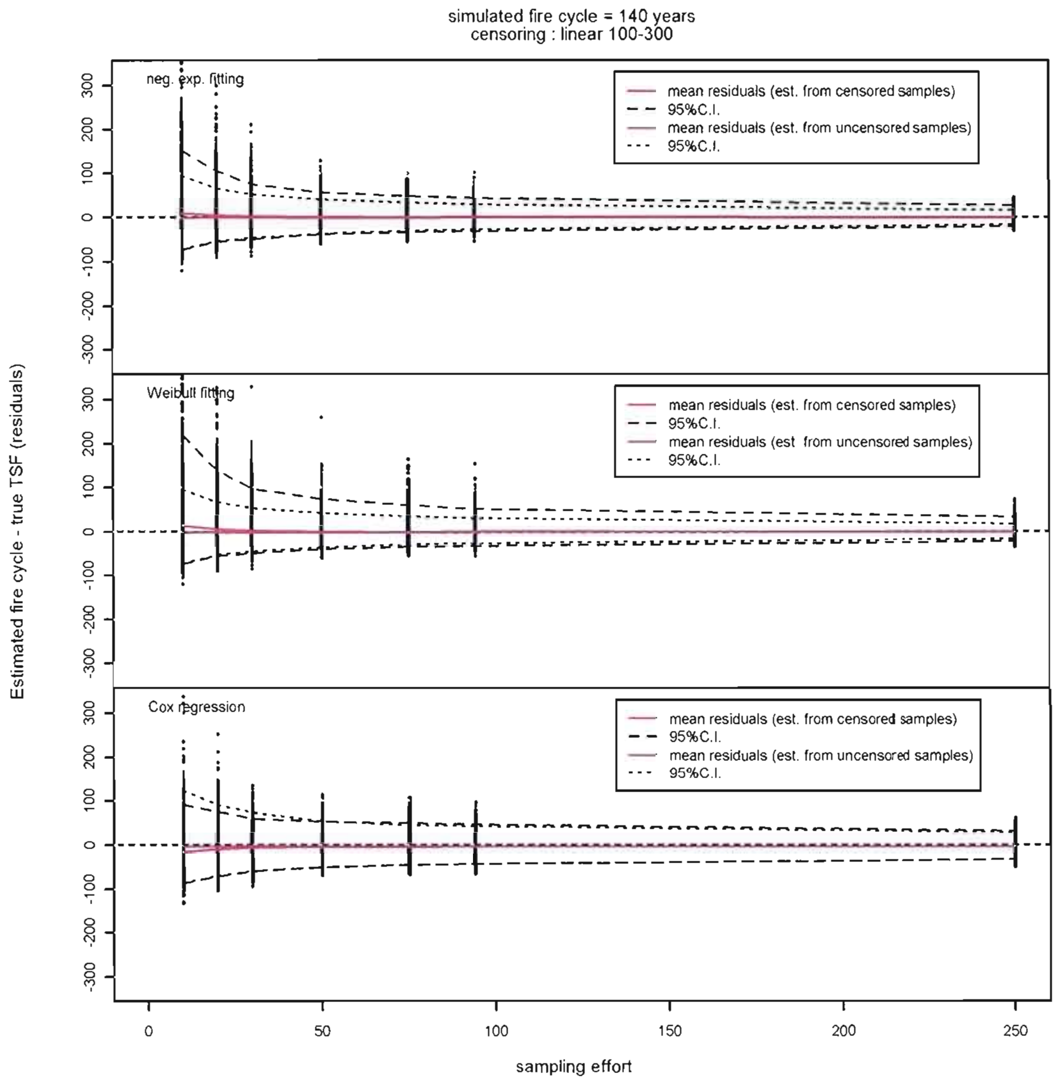


Figure 1.5b Central tendency and distribution of residuals (Estimated FC – True FC, past 300 years) for the three SA-based methods, as a function of sampling effort, with and without the censoring effect, with associated 95% C.I. for simulated global FC of 140 years.

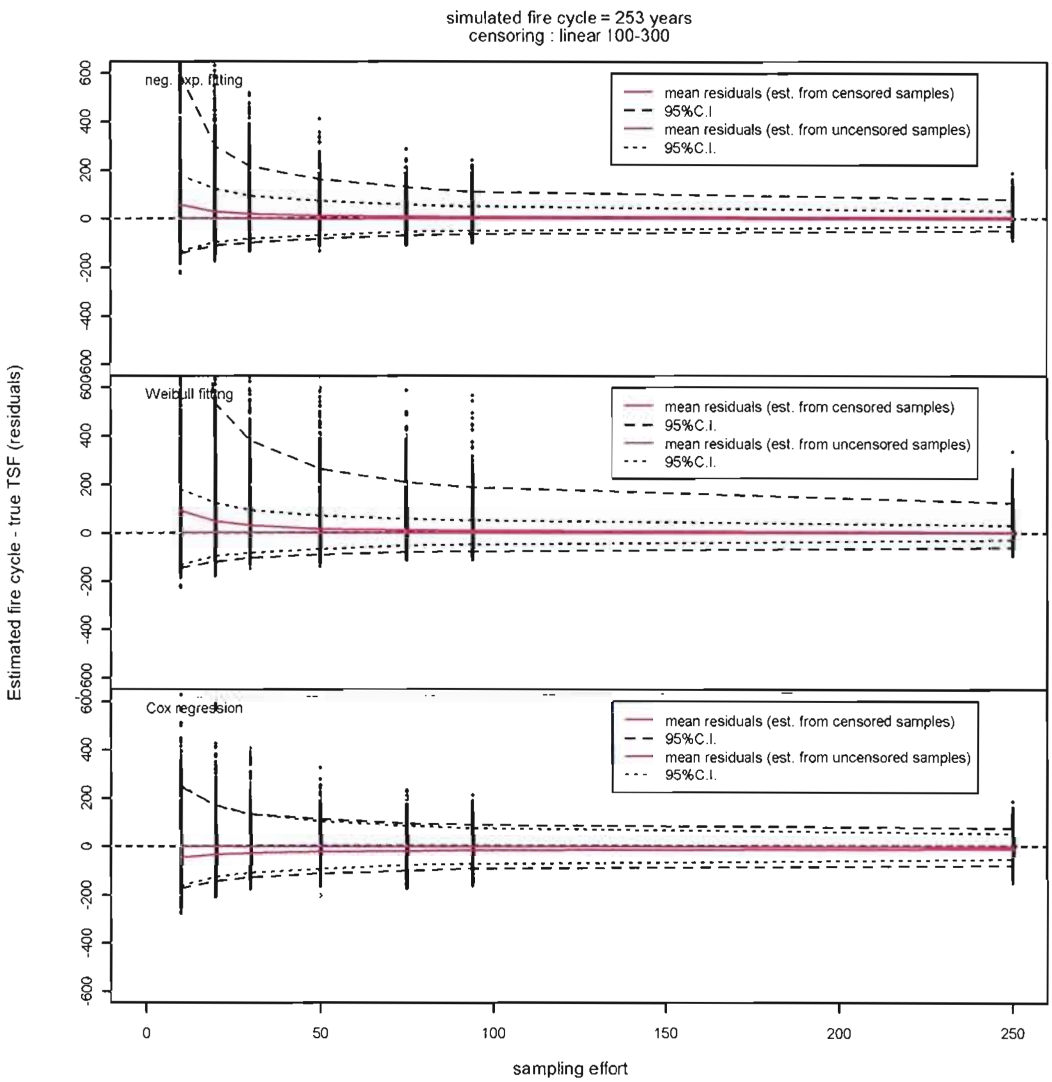


Figure 1.5c Central tendency and distribution of residuals (Estimated FC – True FC, past 300 years) for the three SA-based methods, as a function of sampling effort, with and without the censoring effect, with associated 95% C.I. for simulated global FC of 253 years.

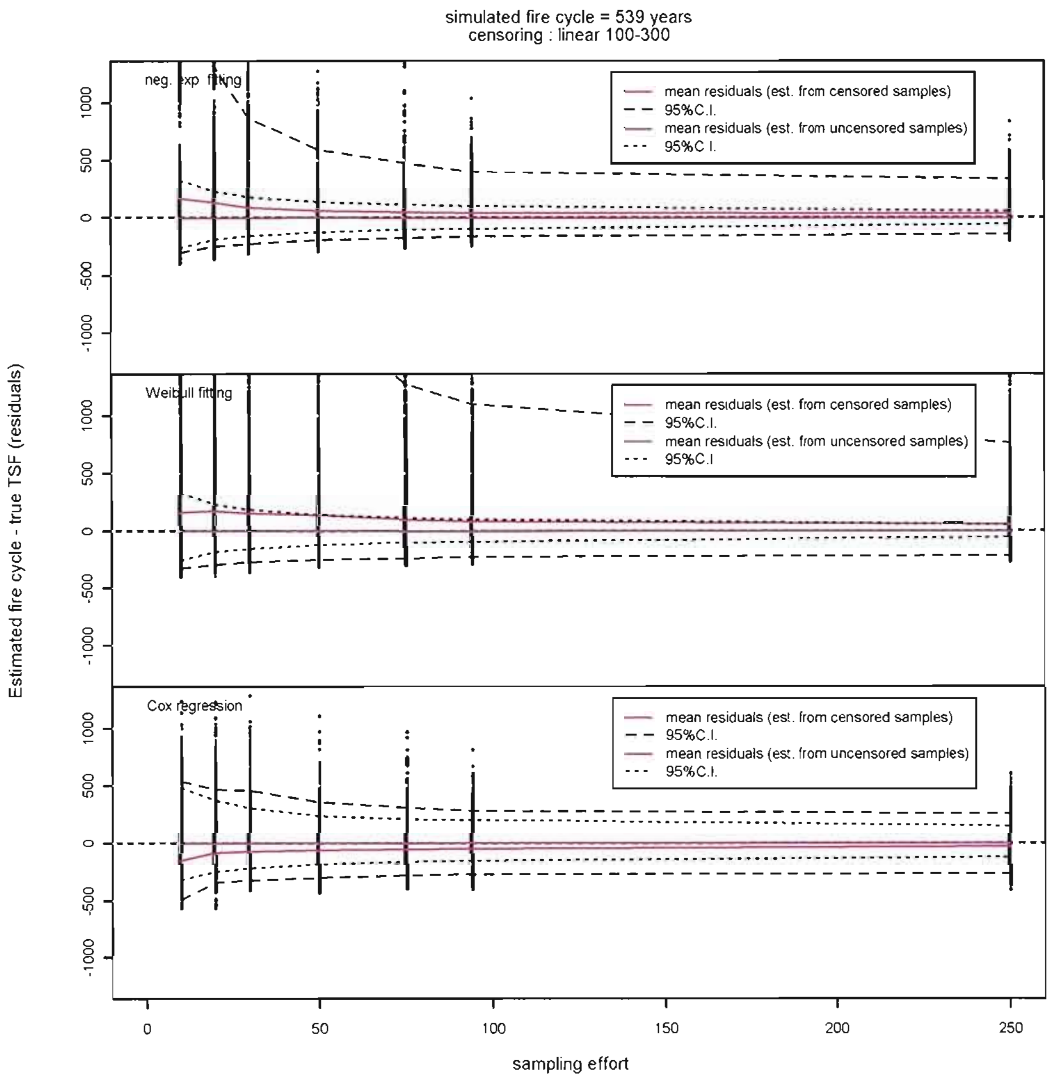


Figure 1.5d Central tendency and distribution of residuals (Estimated FC – True FC, past 300 years) for the three SA-based methods, as a function of sampling effort, with and without the censoring effect, with associated 95% C.I. for simulated global FC of 539 years.

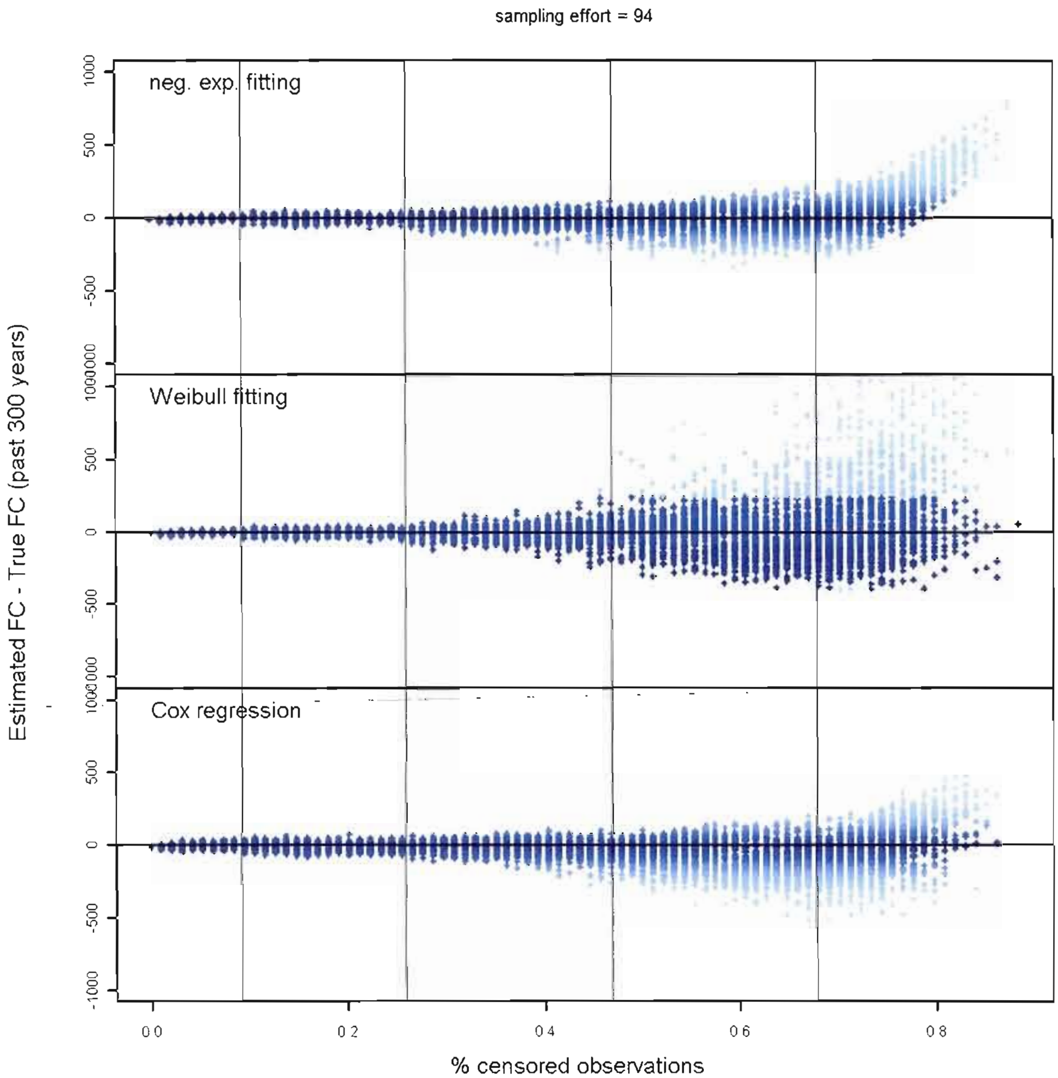


Figure 1.6 Distribution of residuals when sampling effort N=94 as a function of the percentage of censored observations (all simulations pooled). Vertical lines indicate the average percentage of censored observations in each simulation (from the shortest FC (75 yrs) on the left to the longest FC (539 yrs) on the right. Color density is proportional to the density of observations.

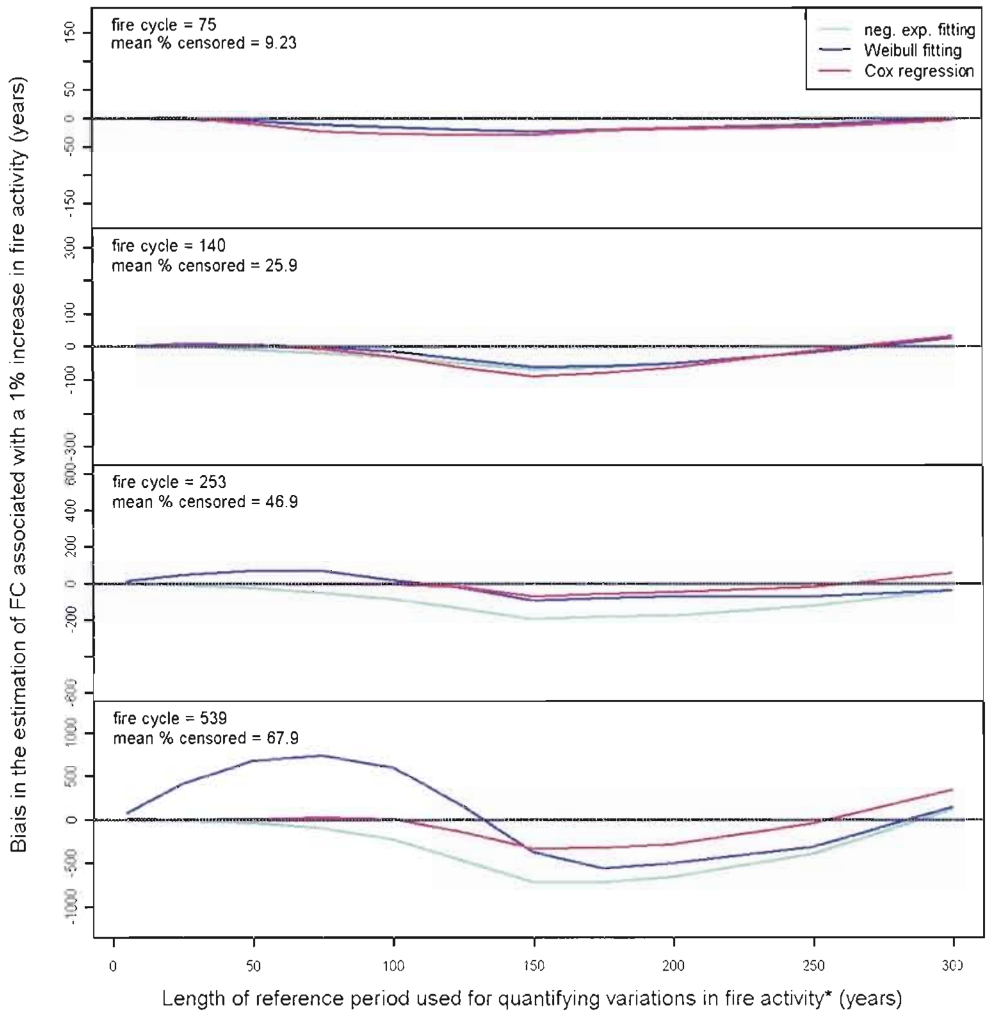


Figure 1.7 Effect of temporal variation in fire activity (difference in mean percent annual area burned between the current reference period and the preceding one) at varying temporal scopes on the estimation of FC for the past 300 years. The x axis represents the length of the reference periods for calculating variations in fire activity, while the y axis represents the associated bias (estimated FC – true FC_{300}).

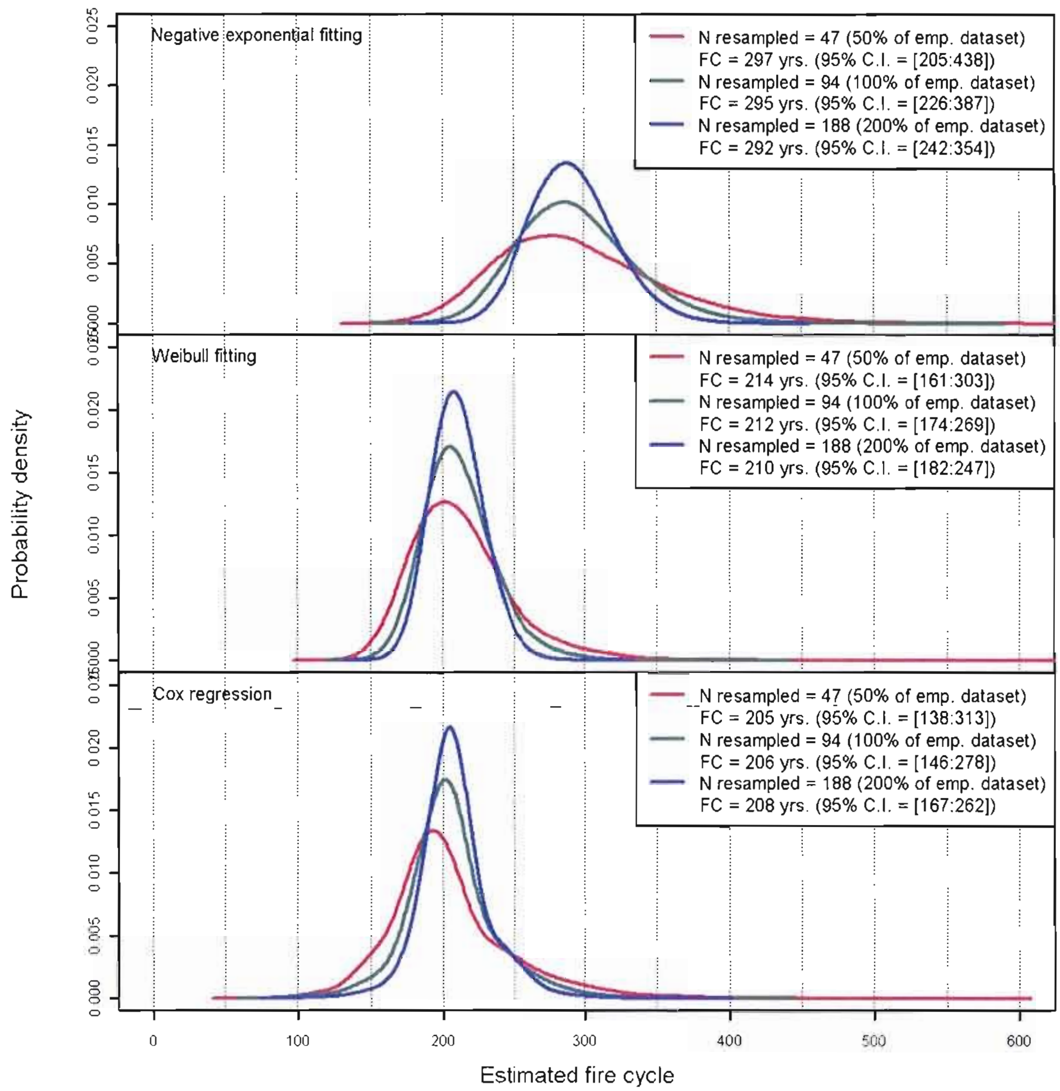


Figure 1.8 Bootstrap distribution (10 000 resamplings) of FC estimates using three levels of resampling effectives (50%, 100% and 200% of the original sample), for the three SA-based methods. Mean estimates and 95% confidence intervals are indicated in the legends.

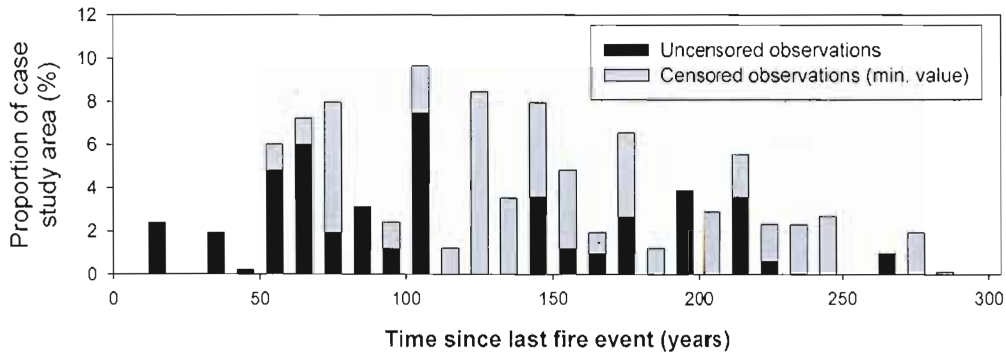


Figure 1.9 Age-class distribution of the case study area.

Table 1.1 Summary of simulation parameters.

Total size / pixel size of simulated landscape (ha)	1 596 100* / 1
Total length of simulation (years)	4000
Length of landscape initialization phase (years)	1000
Individual fire size distribution	Log-normal (fit from empirical records)
Simulated fire cycles (years)	75, 140, 253, and 539
Simulated sampling effort (random points)	10, 20, 30, 50, 75, 94*, 250
Time scopes used for quantifying temporal variations in fire activity (years)	5, 25, 50, 75, 100, 125, 150, 175, 200, 250, 300

* Same as empirical dataset from the case study area

Table 1.2 Summary statistics for the four simulated global FCs (excluding initialization phase when $t \leq 1000$). The true fire cycle values are calculated using several reference periods and the mean time since fire (TSF) is calculated from the entire virtual landscape (based on uncensored values for the 1 596 100 elements). Mean values are presented alongside with minimum and maximum values.

Simulated global fire cycle (years)	True fire cycle mean [min; max]			
	Reference period			Mean TSF
	Past 50 yrs.	Past 150 yrs.	Past 300 yrs.	
75	79 [40; 139]	76 [56; 100]	76 [62; 92]	75 [43, 98]
140	149 [65; 278]	141 [107; 207]	140 [108; 167]	139 [93, 175]
253	278 [104; 523]	263 [167; 371]	260 [190; 334]	254 [186, 304]
539	639 [130; 2810]	545 [268; 1038]	527 [346; 808]	500 [401, 566]

Table 1.3 Summary statistics for $residuals_{300}$ (Estimated FC – True FC_{300} based on the last 300 years) when sampling effort N=94.

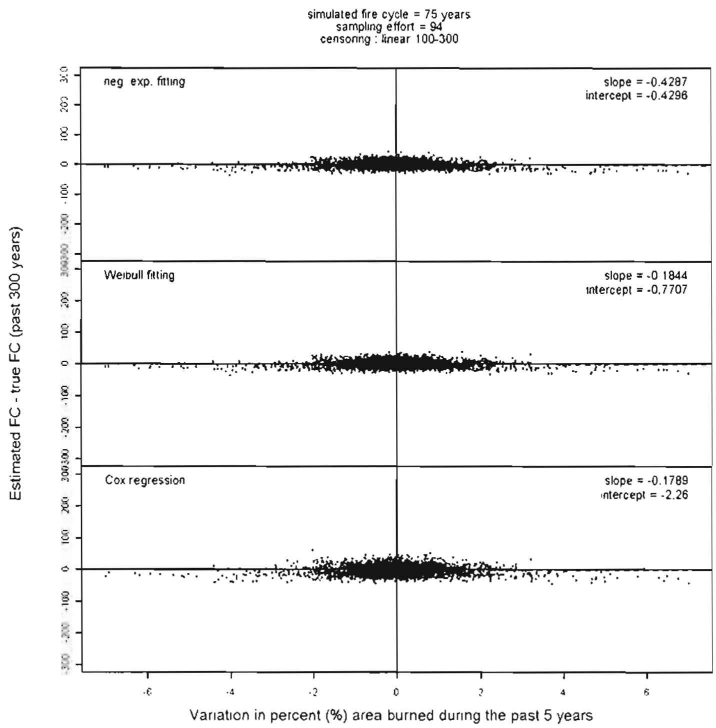
Global simulated fire cycle (yrs.)	Exponential fit mean	Exponential fit L95CI U95CI	Weibull fit mean	Weibull fit L95CI U95CI	Cox regression mean	Cox regression L95CI U95CI
75	-0.4	-21.0 22.8	-0.8	-20.8 21.3	-2.2	-30.1 28.5
140	1.1	-38.0 49.1	0.0	-37.8 53.9	-4.9	-52.4 48.3
253	2.5	-72.5 105.2	4.0	-83.5 172.6	-23.5	-102.2 80.0
539	16.4	-190.2 372.0	86.6	-285.8 1042.2	-75.5	-301.3 231.1

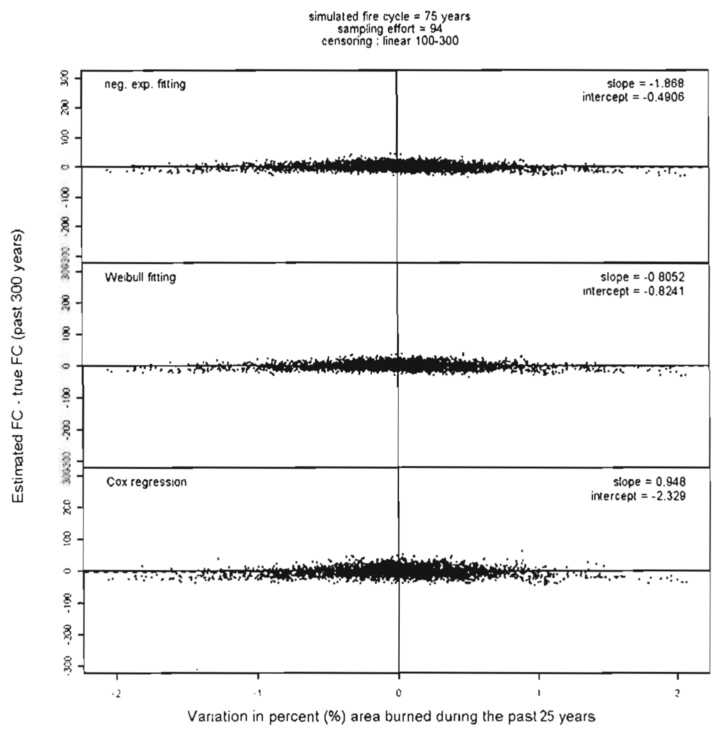
Table 1.4 Minimum and maximum variations in fire activity observed within several reference periods of varying lengths. Difference in fire activity is expressed in difference in the mean percent annual area burned in the recent reference period as compared with the previous one.

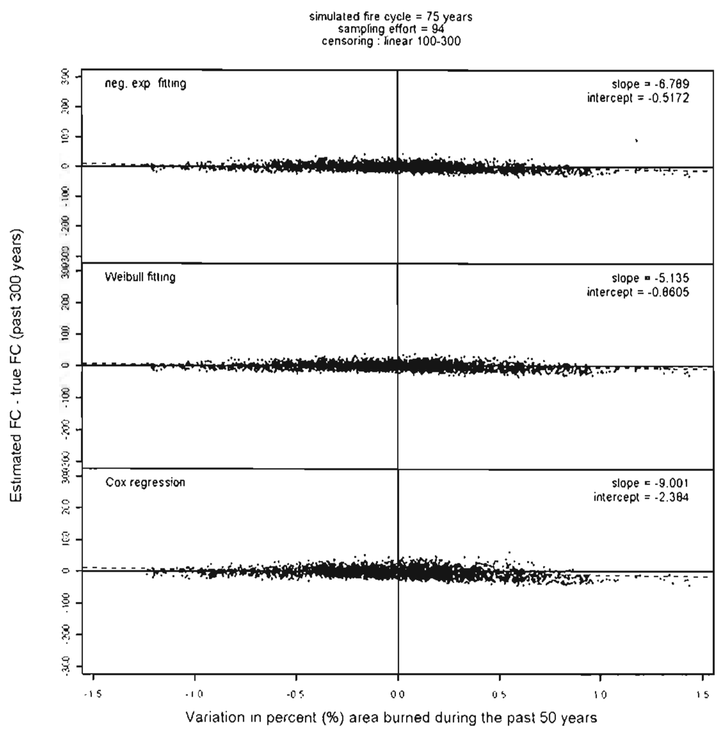
Length of reference period (years)	Difference in fire activity expressed in difference in the mean percent annual area burned — Simulated global fire cycle 75	140	253	539
5	-6.99; 7.01	-5.48; 5.25	-4.23, 4.02	-5.53; 5.58
25	-2.05; 2.06	-1.84; 1.65	-1.03; 1.00	-1.13, 1.13
50	-1.24; 1.44	-1.05; 1.00	-0.68; 0.65	-0.58; 0.65
75	-0.96, 0.91	-0.78; 0.68	-0.49; 0.42	-0.51; 0.51
100	-0.91; 0.77	-0.57; 0.50	-0.42; 0.36	-0.37; 0.40
125	-0.82; 0.62	-0.51; 0.37	-0.33; 0.30	-0.31; 0.32
150	-0.63; 0.53	-0.38; 0.33	-0.27; 0.23	-0.26; 0.25
175	-0.58; 0.52	-0.35; 0.35	-0.23; 0.21	-0.20; 0.19
200	-0.55; 0.47	-0.36; 0.37	-0.21; 0.19	-0.17; 0.18
250	-0.47; 0.39	-0.27; 0.35	-0.20; 0.17	-0.14; 0.14
300	-0.43; 0.36	-0.28; 0.18	-0.19; 0.18	-0.14; 0.13

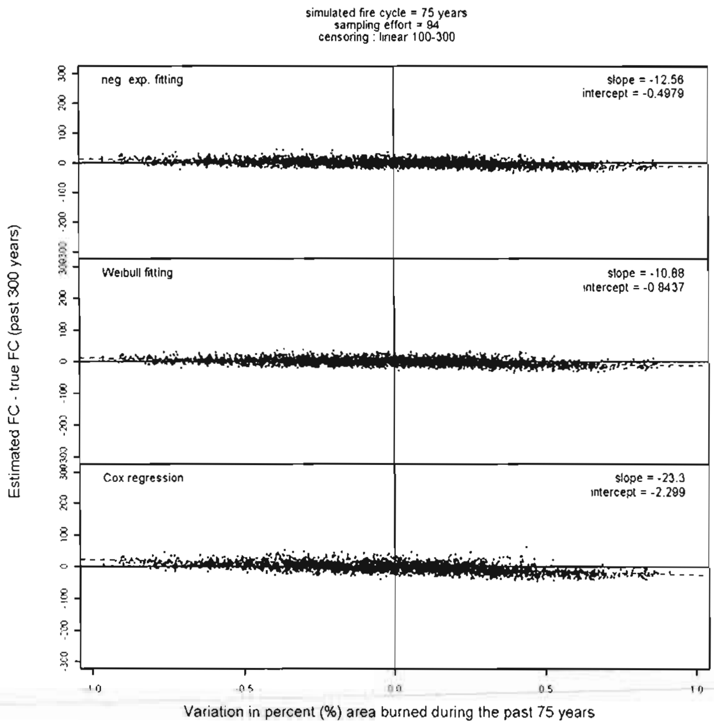
Appendix 1.1 $Residuals_{300}$ (estimated FC – true FC_{300} for the last 300 years) as a function of past variations in fire activity (calculated in percent annual area burned). FC was estimated from a constant sampling effort corresponding to the case study (N=94). Each plot illustrates this relationship using a different reference period for calculating past variations in fire activity (5, 25, 50, 75, 100, 125, 150, 175, 200, 150 and 300 years), which are all presented in sequence for global simulated FC of a) 75 years, b) 140 years, c) 253 years, and 539 years. Linear regressions parameters are indicated on each plot and slopes were compiled in figure 1.7.

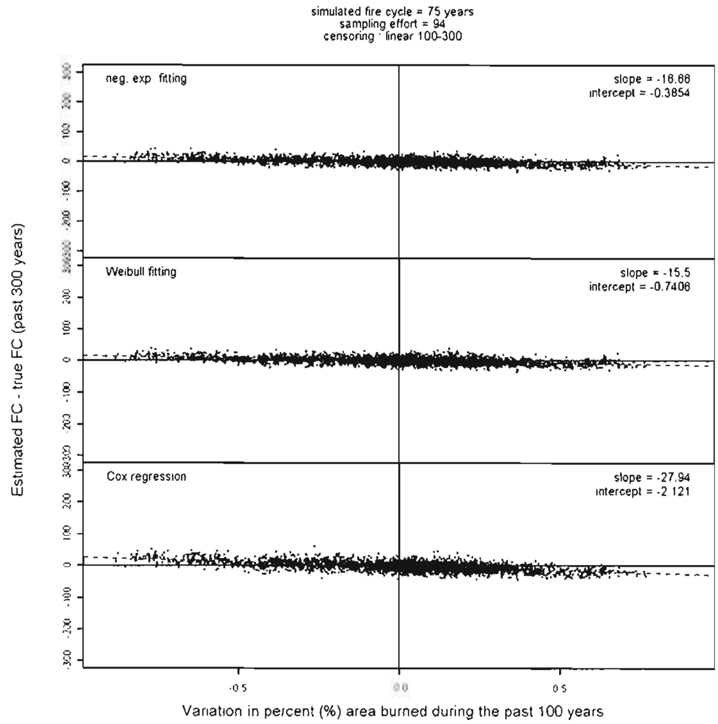
Appendix 1.1a (Global simulated FC = 75 years)

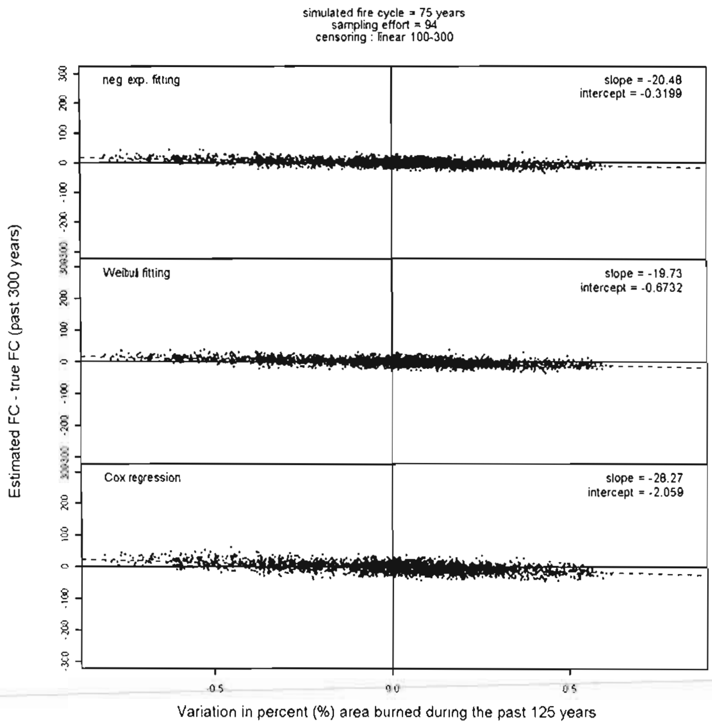


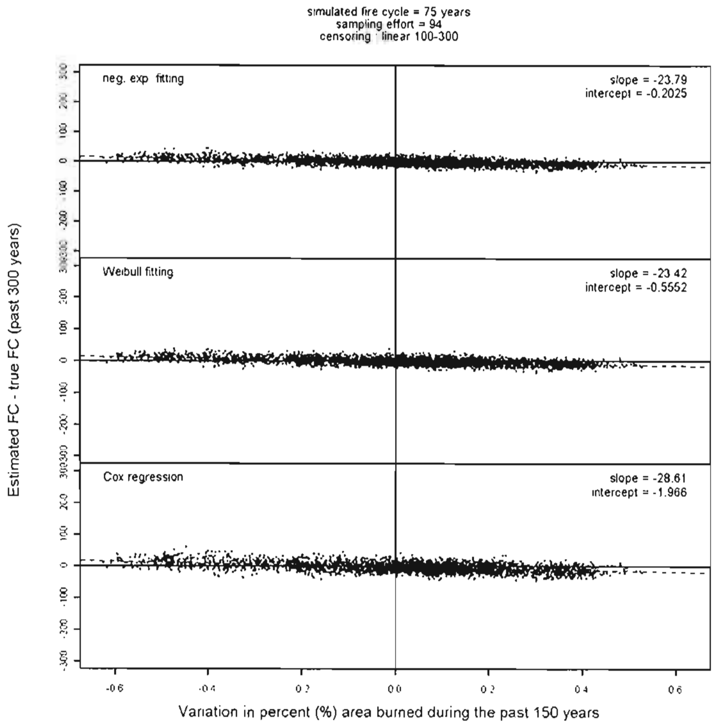

simulated fire cycle = 75 years
sampling effort = 94
censoring : linear 100-300
neg. exp. fitting
slope = -1.868
intercept = -0.4906
Weibull fitting
slope = -0.8052
intercept = -0.8241
Cox regression
slope = 0.948
intercept = -2.329
Estimated FC - true FC (past 300 years)
Variation in percent (%) area burned during the past 25 years

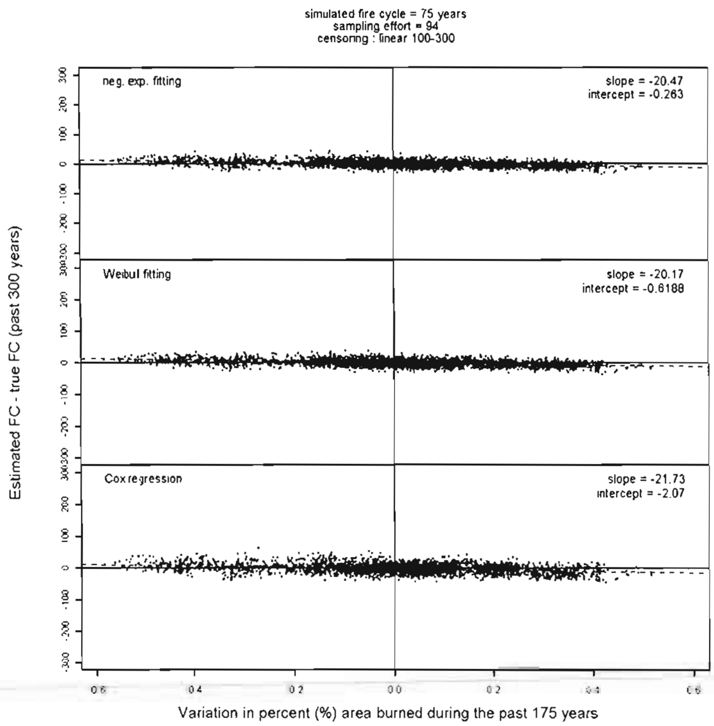

simulated fire cycle = 75 years
sampling effort = 94
censoring : linear 100-300
neg. exp fitting
slope = -6.789
intercept = -0.5172
Weibull fitting
slope = -5.135
intercept = -0.8605
Cox regression
slope = -9.001
intercept = -2.384
Estimated FC - true FC (past 300 years)
Variation in percent (%) area burned during the past 50 years

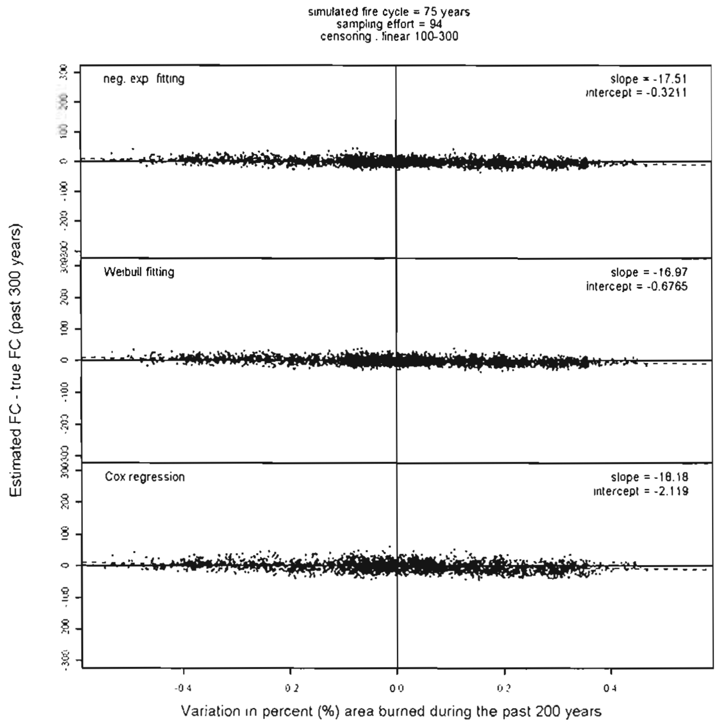

simulated fire cycle = 75 years
sampling effort = 84
censoring : linear 100-300
neg exp. fitting
slope = -12.56
intercept = -0.4979
Weibull fitting
slope = -10.88
intercept = -0.8437
Cox regression
slope = -23.3
intercept = -2.299
Estimated FC - true FC (past 300 years)
Variation in percent (%) area burned during the past 75 years

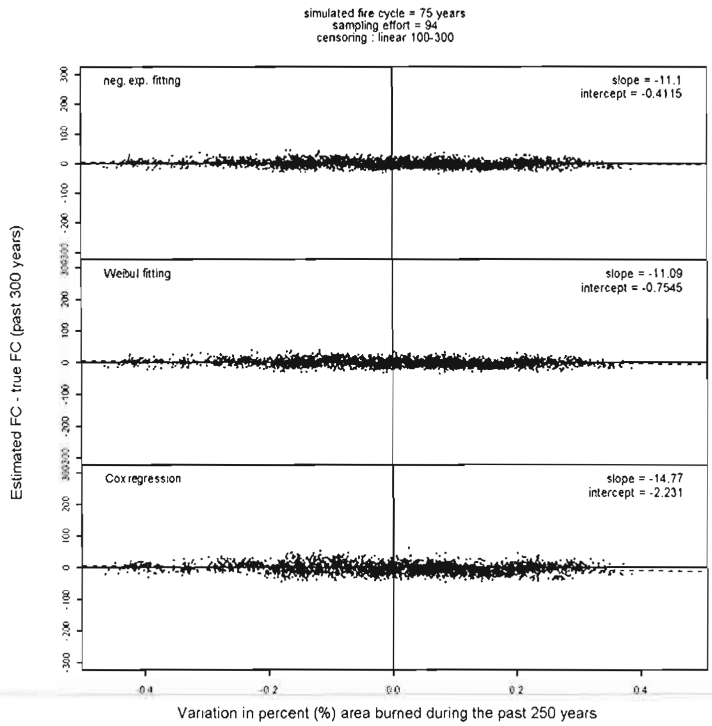

simulated fire cycle = 75 years
sampling effort = 94
censoring : linear 100-300
neg. exp fitting
slope = -16.66
intercept = -0.3854
Weibull fitting
slope = -15.5
intercept = -0.7406
Cox regression
slope = -27.94
intercept = -2.121
Estimated FC - true FC (past 300 years)
Variation in percent (%) area burned during the past 100 years

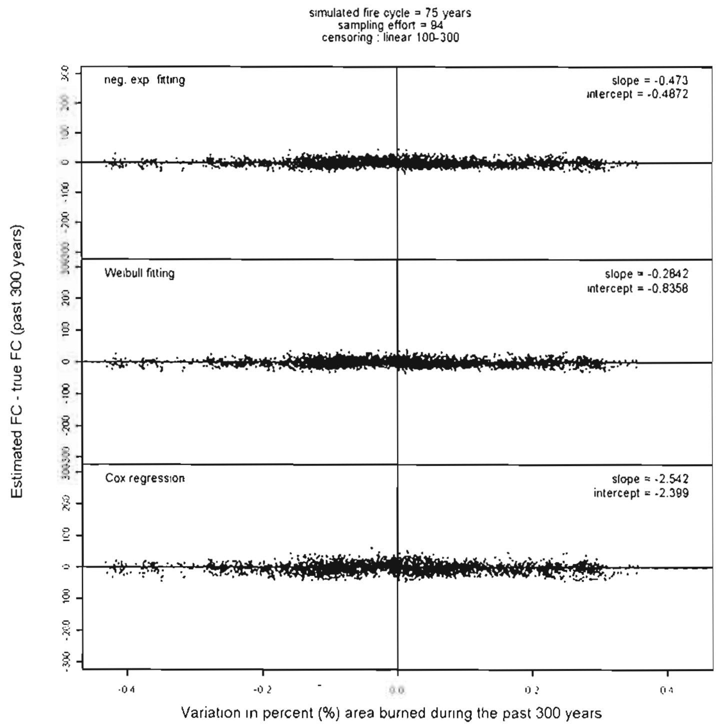

simulated fire cycle = 75 years
sampling effort = 94
censoring : linear 100-300
neg exp. fitting
slope = -20.48
intercept = -0.3199
Weibul fitting
slope = -19.73
intercept = -0.6732
Cox regression
slope = -28.27
intercept = -2.059
Estimated FC - true FC (past 300 years)
Variation in percent (%) area burned during the past 125 years


simulated fire cycle = 75 years
sampling effort = 94
censoring : linear 100-300
neg. exp fitting
slope = -23.79
intercept = -0.2025
Weibull fitting
slope = -23.42
intercept = -0.5552
Cox regression
slope = -28.61
intercept = -1.966
Estimated FC - true FC (past 300 years)
Variation in percent (%) area burned during the past 150 years

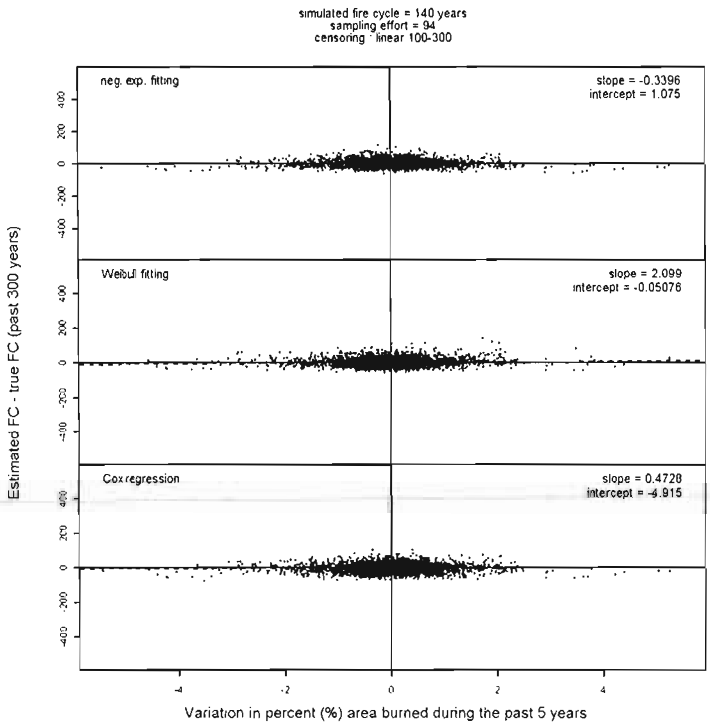

simulated fire cycle = 75 years
sampling effort = 94
censoring : linear 100-300
neg. exp. fitting
slope = -20.47
intercept = -0.263
Weibul fitting
slope = -20.17
intercept = -0.6188
Cox regression
slope = -21.73
intercept = -2.07
Estimated FC - true FC (past 300 years)
Variation in percent (%) area burned during the past 175 years

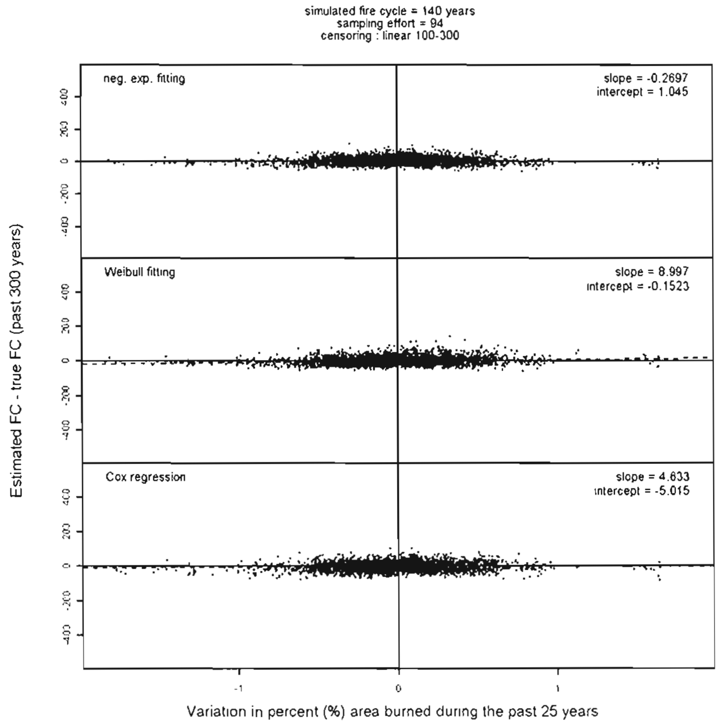

simulated fire cycle = 75 years
sampling effort = 94
censoring . linear 100-300
neg. exp fitting
slope = -17.51
intercept = -0.3211
Weibull fitting
slope = -16.97
intercept = -0.6765
Cox regression
slope = -18.18
intercept = -2.119
Estimated FC - true FC (past 300 years)
Variation in percent (%) area burned during the past 200 years

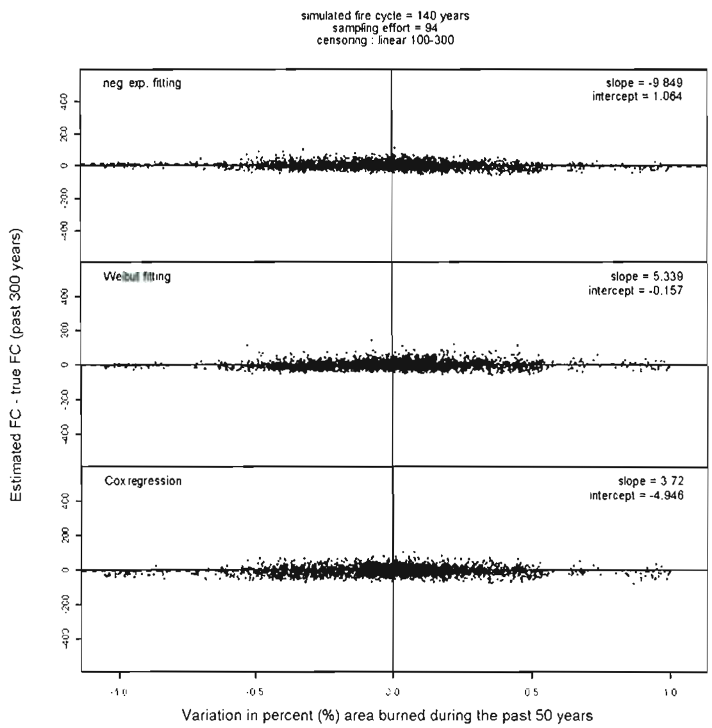

simulated fire cycle = 75 years
sampling effort = 94
censoring : linear 100-300
neg. exp. fitting
slope = -11.1
intercept = -0.4115
Weibul fitting
slope = -11.09
intercept = -0.7545
Cox regression
slope = -14.77
intercept = -2.231
Estimated FC - true FC (past 300 years)
Variation in percent (%) area burned during the past 250 years

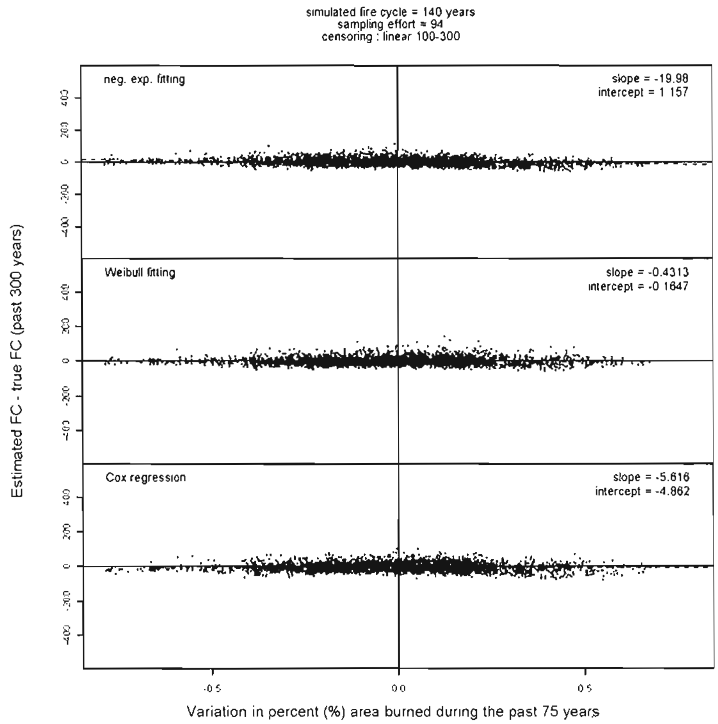

simulated fire cycle = 75 years
sampling effort = 94
censoring : linear 100-300
neg. exp fitting
slope = -0.473
intercept = -0.4872
Weibull fitting
slope = -0.2842
intercept = -0.8358
Cox regression
slope = -2.542
intercept = -2.399
Estimated FC - true FC (past 300 years)
Variation in percent (%) area burned during the past 300 years

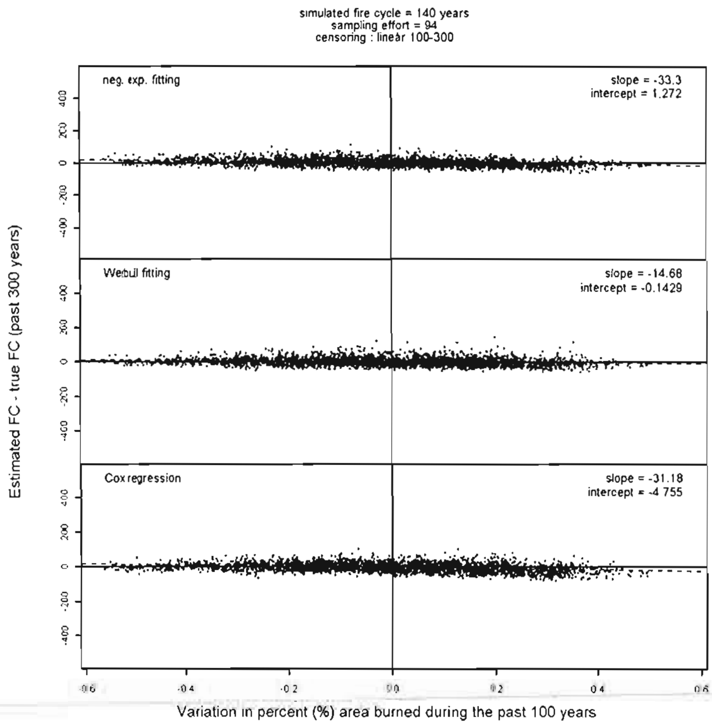
Appendix 1.1b (Global simulated FC = 140 year).



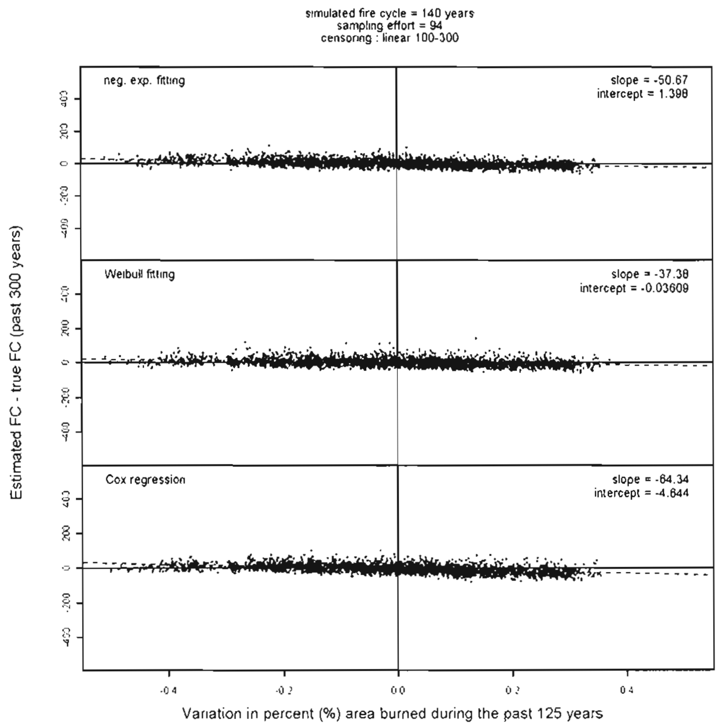

simulated fire cycle = 140 years
sampling effort = 94
censoring : linear 100-300
neg. exp. fitting
slope = -0.2697
intercept = 1.045
Weibull fitting
slope = 8.997
intercept = -0.1523
Cox regression
slope = 4.633
intercept = -5.015
Estimated FC - true FC (past 300 years)
Variation in percent (%) area burned during the past 25 years

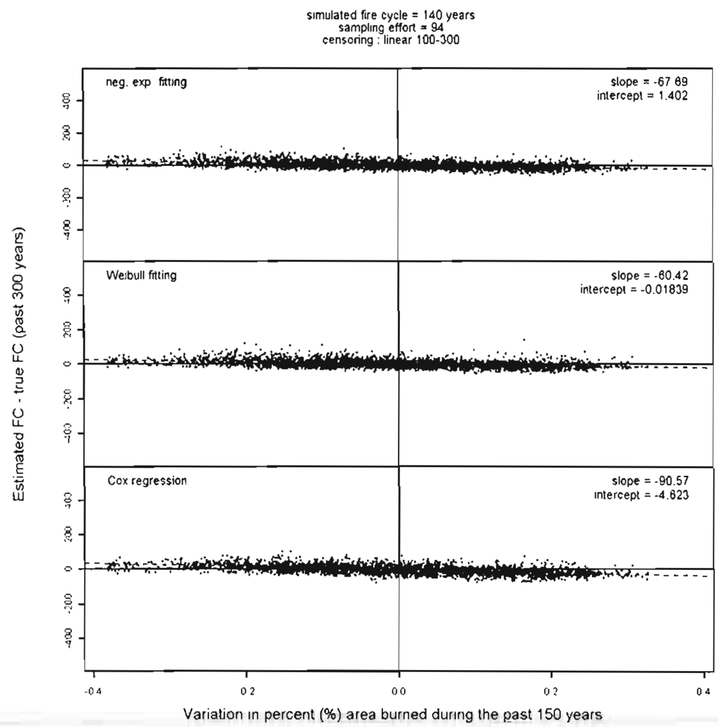

simulated fire cycle = 140 years
sampling effort = 94
censoring : linear 100-300
neg. exp. fitting
slope = -9.849
intercept = 1.064
Weibull fitting
slope = 5.339
intercept = -0.157
Cox regression
slope = 3.72
intercept = -4.946
Estimated FC - true FC (past 300 years)
Variation in percent (%) area burned during the past 50 years

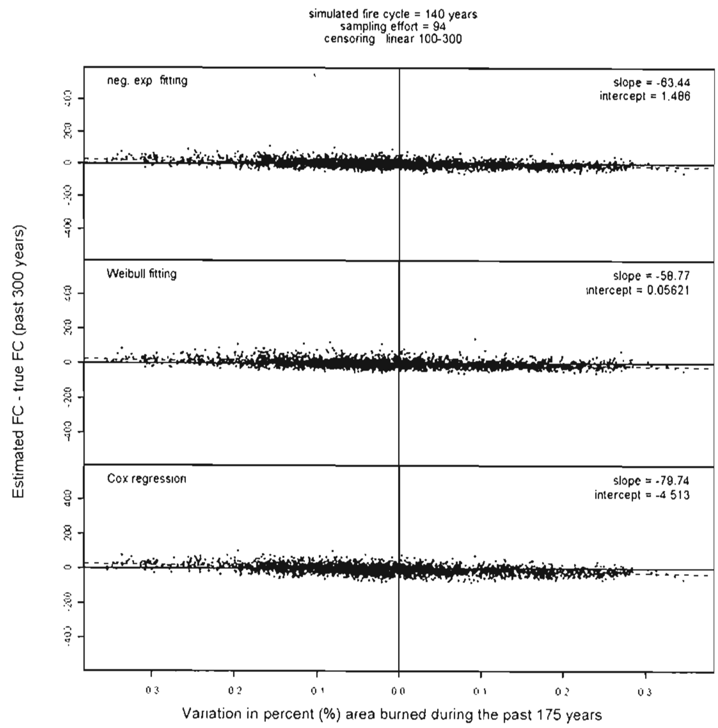

simulated fire cycle = 140 years
sampling effort = 94
censoring : linear 100-300
neg. exp. fitting
slope = -19.98
intercept = 1 157
Weibull fitting
slope = -0.4313
intercept = -0 1647
Cox regression
slope = -5.616
intercept = -4.862
Estimated FC - true FC (past 300 years)
Variation in percent (%) area burned during the past 75 years

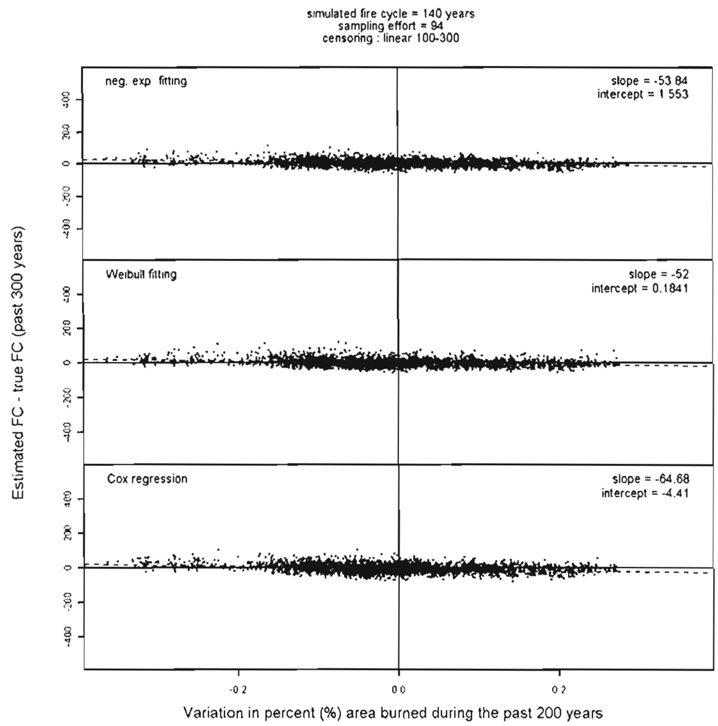


simulated fire cycle = 140 years
sampling effort = 94
censoring : linear 100-300
neg. exp. fitting
slope = -33.3
intercept = 1.272
Weibull fitting
slope = -14.68
intercept = -0.1429
Cox regression
slope = -31.18
intercept = -4.755
Estimated FC - true FC (past 300 years)
Variation in percent (%) area burned during the past 100 years

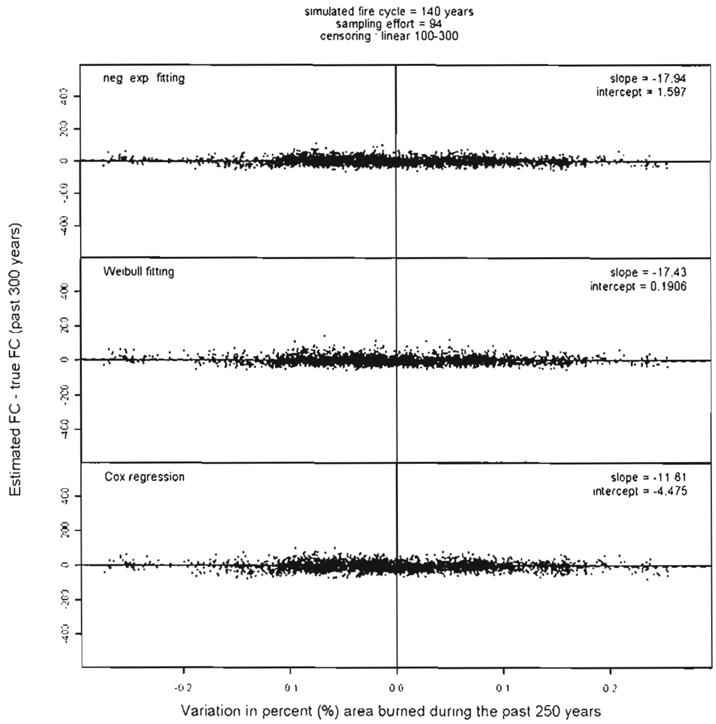

simulated fire cycle = 140 years
sampling effort = 94
censoring : linear 100-300
neg. exp. fitting
slope = -50.67
intercept = 1.398
Weibull fitting
slope = -37.38
intercept = -0.03609
Cox regression
slope = -64.34
intercept = -4.644
Estimated FC - true FC (past 300 years)
Variation in percent (%) area burned during the past 125 years

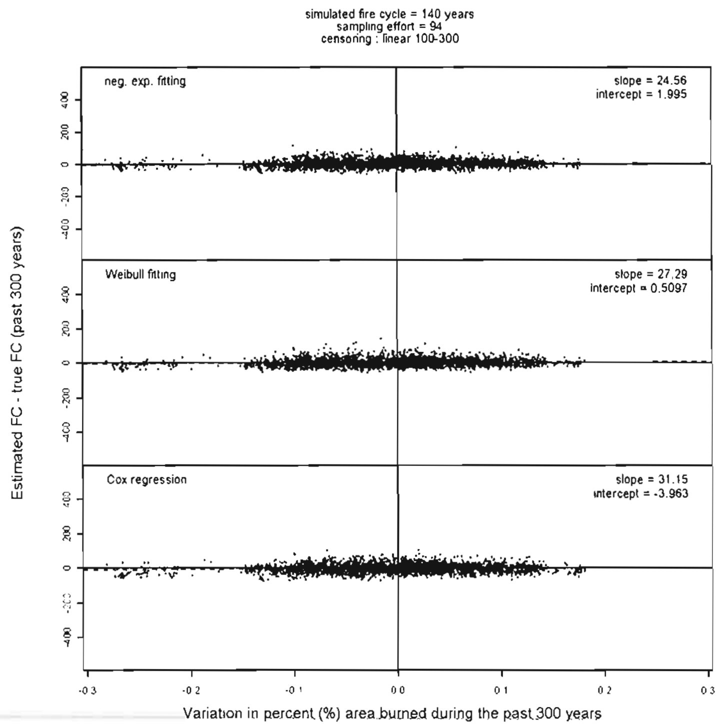

simulated fire cycle = 140 years
sampling effort = 94
censoring : linear 100-300
neg. exp fitting
slope = -67.69
intercept = 1.402
Weibull fitting
slope = -60.42
intercept = -0.01839
Cox regression
slope = -90.57
intercept = -4.623
Estimated FC - true FC (past 300 years)
Variation in percent (%) area burned during the past 150 years


simulated fire cycle = 140 years
sampling effort = 94
censoring linear 100-300
neg. exp fitting
slope = -63.44
intercept = 1.486
Weibull fitting
slope = -58.77
intercept = 0.05621
Cox regression
slope = -79.74
intercept = -4 513
Estimated FC - true FC (past 300 years)
Variation in percent (%) area burned during the past 175 years

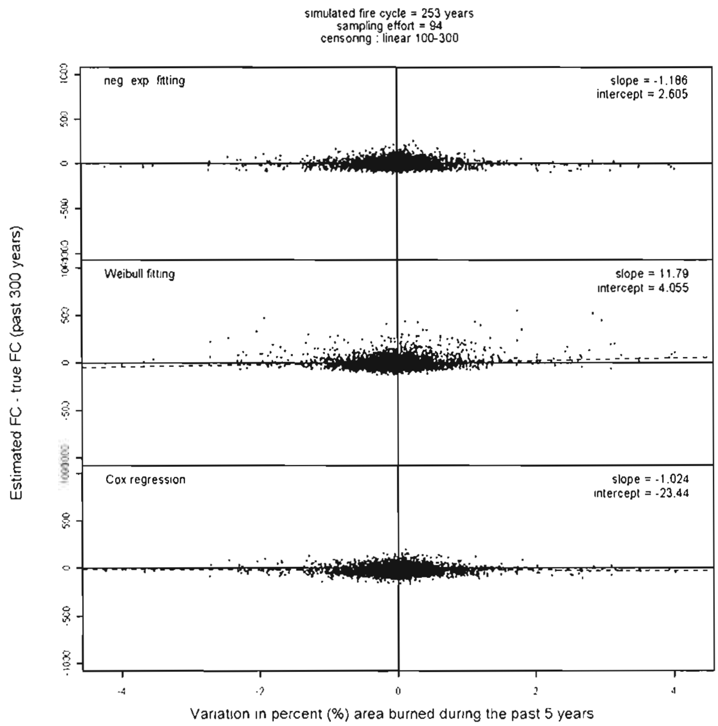


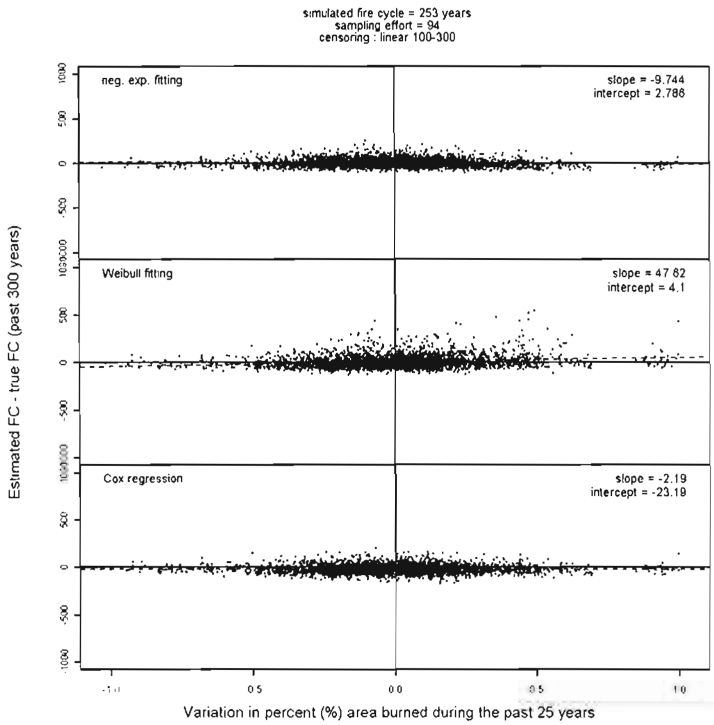
simulated fire cycle = 140 years
sampling effort = 94
censoring : linear 100-300
neg. exp fitting
slope = -53.84
intercept = 1.553
Weibull fitting
slope = -52
intercept = 0.1841
Cox regression
slope = -64.68
intercept = -4.41
Estimated FC - true FC (past 300 years)
-400
-200
0
200
400
-0.2
0.0
0.2
Variation in percent (%) area burned during the past 200 years

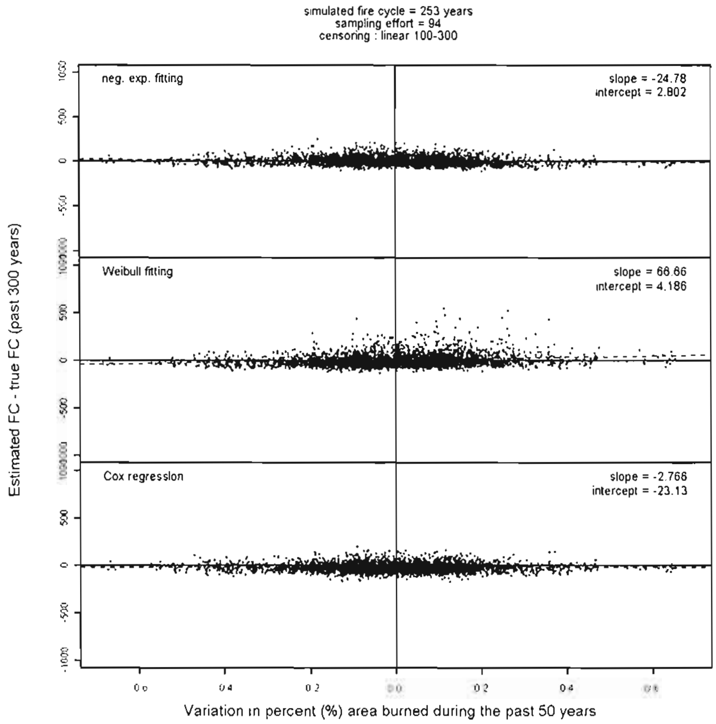

simulated fire cycle = 140 years
sampling effort = 94
censoring : linear 100-300
neg exp fitting
slope = -17.94
intercept = 1.597
Weibull fitting
slope = -17.43
intercept = 0.1906
Cox regression
slope = -11 61
intercept = -4.475
400
200
0
-200
-400
-0 2
0 1
0 0
0 1
0 2
Estimated FC - true FC (past 300 years)
Variation in percent (%) area burned during the past 250 years


simulated fire cycle = 140 years
sampling effort = 94
censoring : linear 100-300
neg. exp. fitting
slope = 24.56
intercept = 1.995
Weibull fitting
slope = 27.29
intercept = 0.5097
Cox regression
slope = 31.15
intercept = -3.963
Estimated FC - true FC (past 300 years)
Variation in percent (%) area burned during the past 300 years

Appendix 1.1c (Global simulated FC = 253 years).




simulated fire cycle = 253 years
sampling effort = 94
censoring : linear 100-300
neg. exp. fitting
slope = -9.744
intercept = 2.788
Weibull fitting
slope = 47.82
intercept = 4.1
Cox regression
slope = -2.19
intercept = -23.19
Estimated FC - true FC (past 300 years)
Variation in percent (%) area burned during the past 25 years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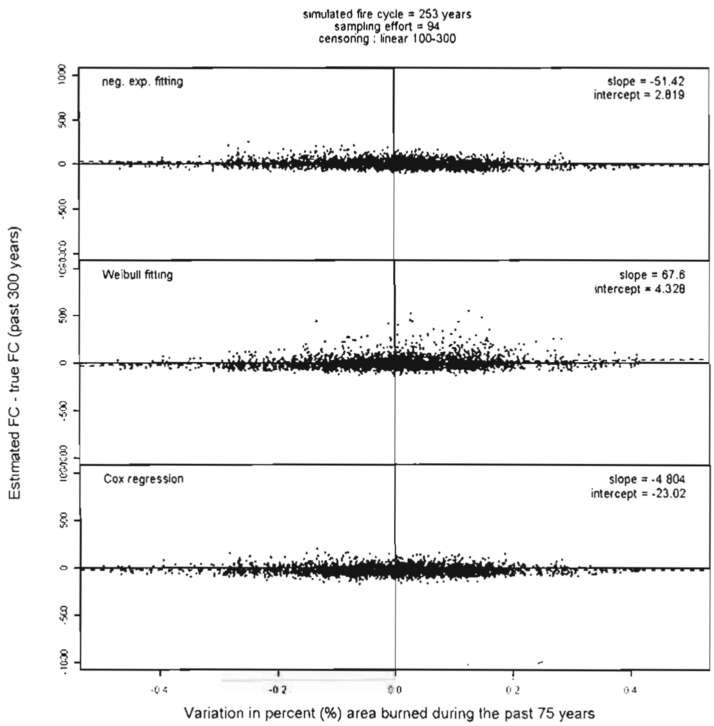
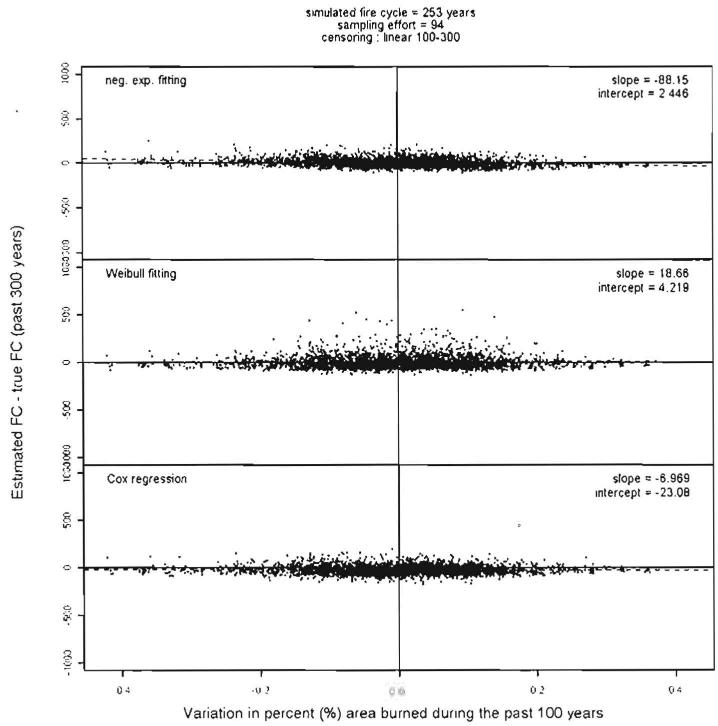
sampling effort = 94
censoring : linear 100-300
neg. exp. fitting
slope = -24.78
intercept = 2.802
Weibull fitting
slope = 66.66
intercept = 4.186
Cox regression
slope = -2.766
intercept = -23.13
Estimated FC - true FC (past 300 years)
Variation in percent (%) area burned during the past 50 years


simulated fire cycle = 253 years
sampling effort = 94
censoring : linear 100-300
neg. exp. fitting
slope = -51.42
intercept = 2.819
Weibull fitting
slope = 67.6
intercept = 4.328
Cox regression
slope = -4.804
intercept = -23.02
Estimated FC - true FC (past 300 years)
Variation in percent (%) area burned during the past 75 years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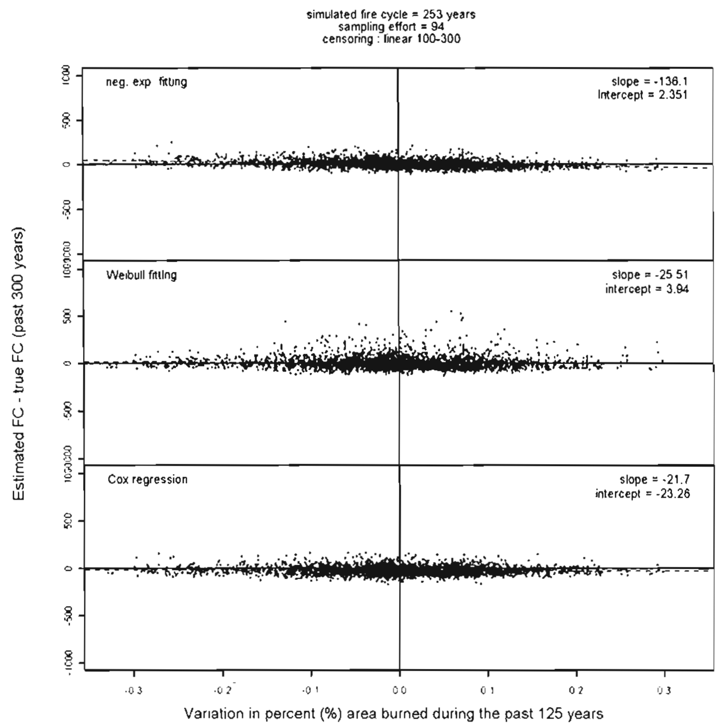
sampling effort = 94
censoring : linear 100-300
neg. exp. fitting
slope = -88.15
intercept = 2.446
Weibull fitting
slope = 18.66
intercept = 4.219
Cox regression
slope = -6.969
intercept = -23.08
Estimated FC - true FC (past 300 years)
Variation in percent (%) area burned during the past 100 years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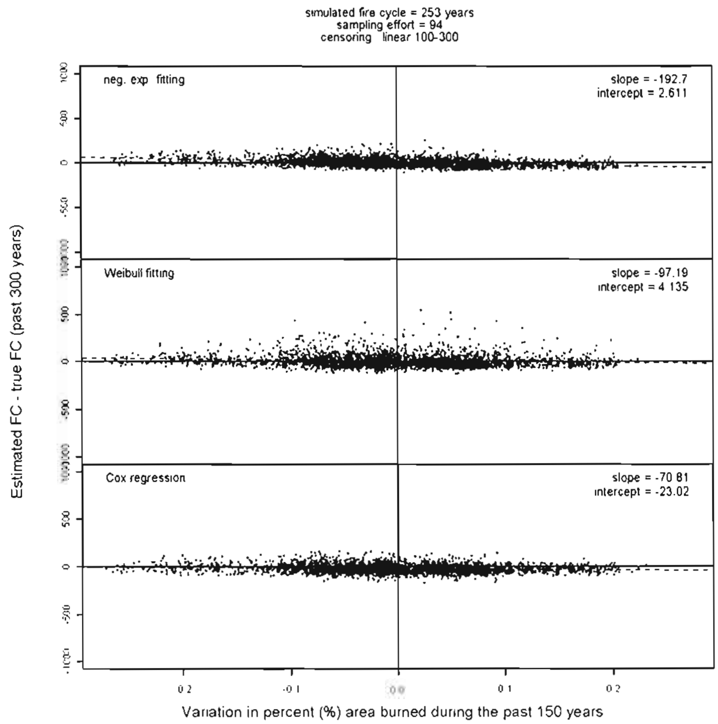
sampling effort = 94
censoring : linear 100-300
neg. exp fitting
slope = -136.1
Intercept = 2.351
Weibull fitting
slope = -25.51
intercept = 3.94
Cox regression
slope = -21.7
intercept = -23.26
Estimated FC - true FC (past 300 years)
Variation in percent (%) area burned during the past 125 years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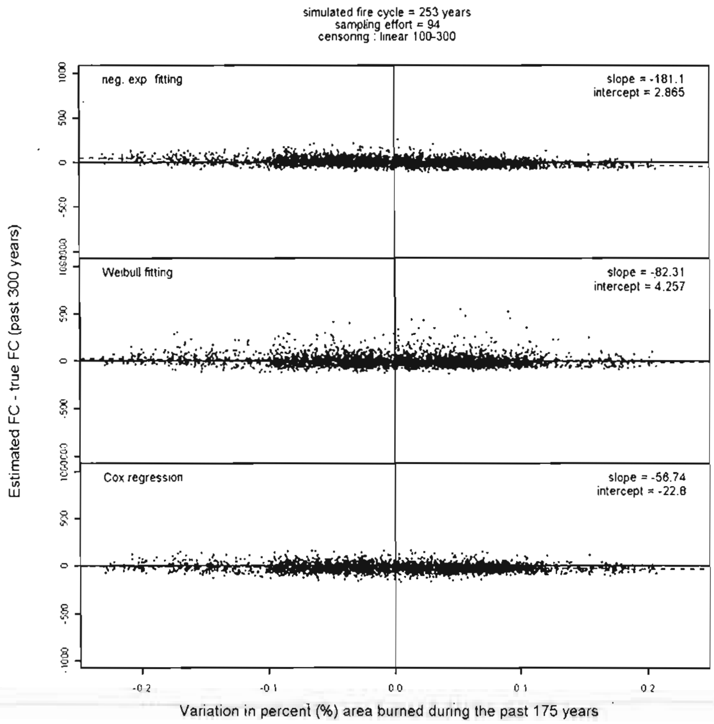
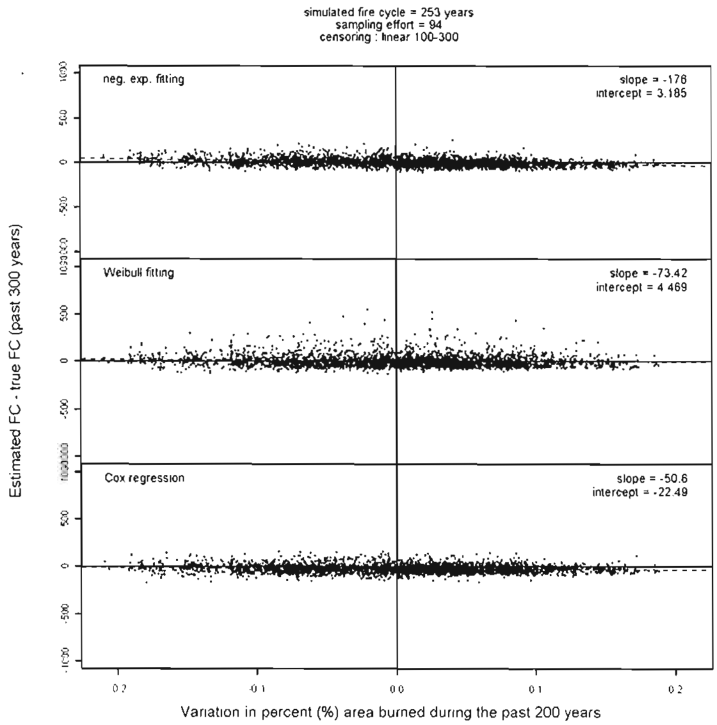
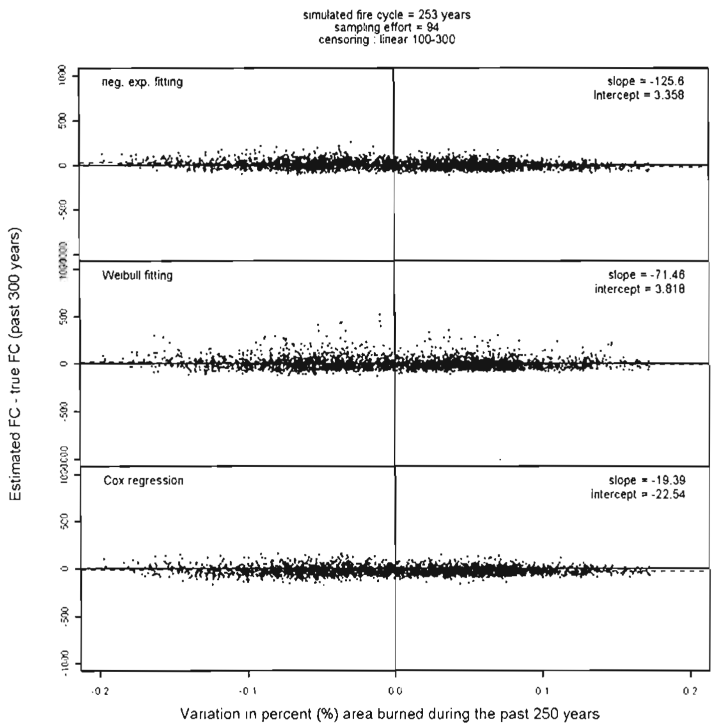
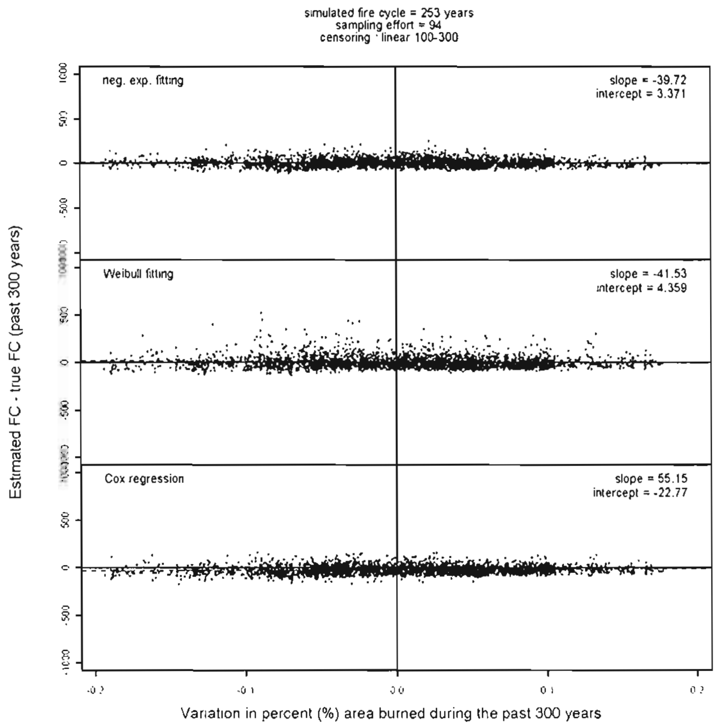
sampling effort = 94
censoring linear 100-300
neg. exp fitting
slope = -192.7
intercept = 2.611
Weibull fitting
slope = -97.19
intercept = 4 135
Cox regression
slope = -70 81
intercept = -23.02
Estimated FC - true FC (past 300 years)
Variation in percent (%) area burned during the past 150 years


simulated fire cycle = 253 years
sampling effort = 94
censoring : linear 100-300
neg. exp fitting
slope = -181.1
intercept = 2.865
Weibull fitting
slope = -82.31
intercept = 4.257
Cox regression
slope = -56.74
intercept = -22.8
Estimated FC - true FC (past 300 years)
Variation in percent (%) area burned during the past 175 years

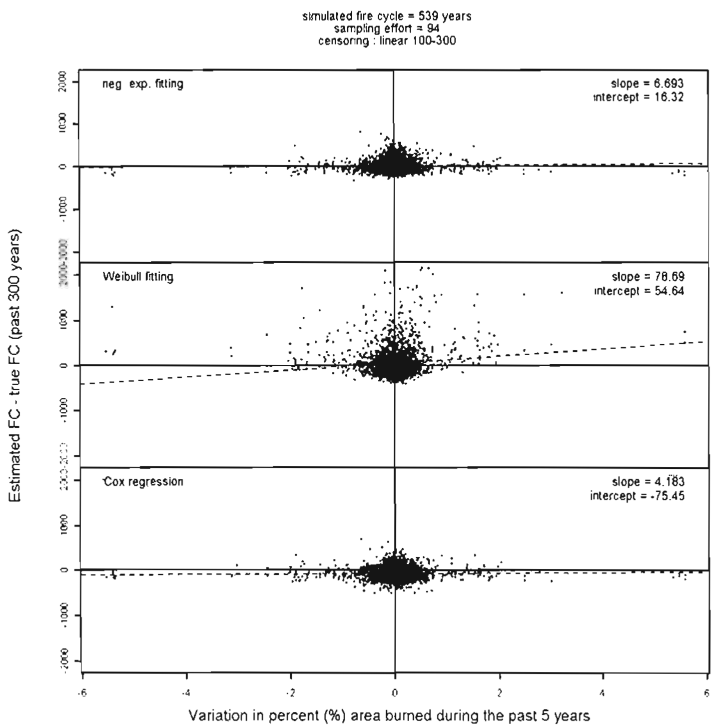

simulated fire cycle = 253 years
sampling effort = 94
censoring : linear 100-300
neg. exp. fitting
slope = -176
intercept = 3.185
Weibull fitting
slope = -73.42
intercept = 4.469
Cox regression
slope = -50.6
intercept = -22.49
Estimated FC - true FC (past 300 years)
Variation in percent (%) area burned during the past 200 years

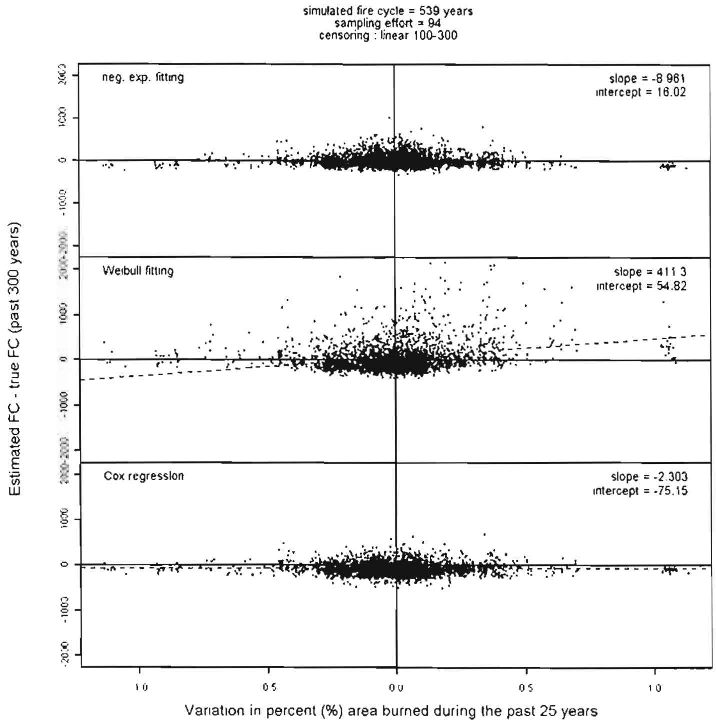

simulated fire cycle = 253 years
sampling effort = 94
censoring : linear 100-300
neg. exp. fitting
slope = -125.6
Intercept = 3.358
Weibull fitting
slope = -71.46
intercept = 3.818
Cox regression
slope = -19.39
intercept = -22.54
Estimated FC - true FC (past 300 years)
Variation in percent (%) area burned during the past 250 years

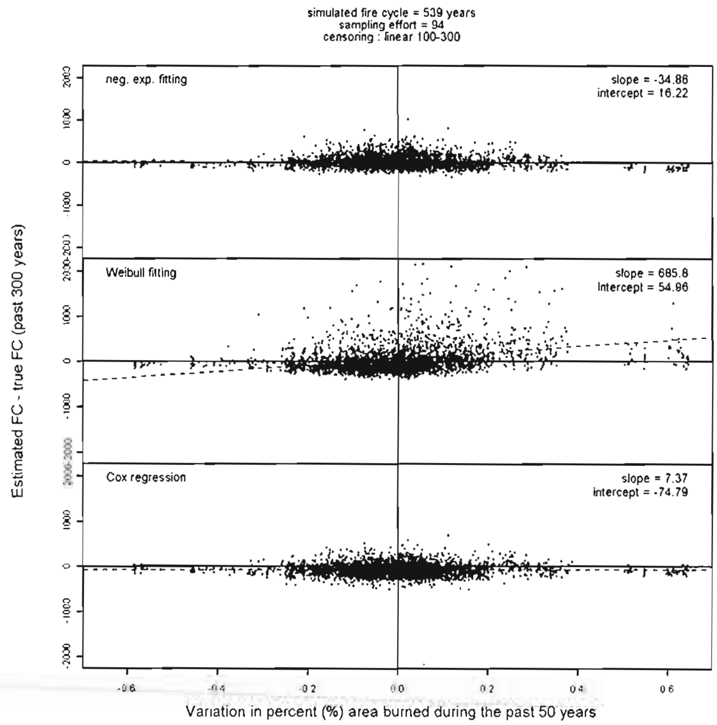


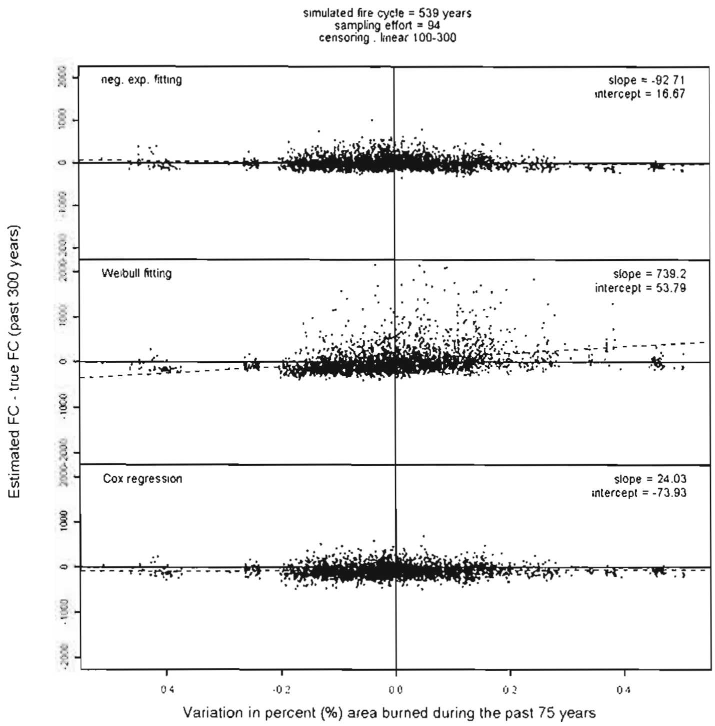
simulated fire cycle = 253 years
sampling effort = 94
censoring : linear 100-300
neg. exp. fitting
slope = -39.72
intercept = 3.371
Weibull fitting
slope = -41.53
intercept = 4.359
Cox regression
slope = 55.15
intercept = -22.77
Estimated FC - true FC (past 300 years)
Variation in percent (%) area burned during the past 300 years

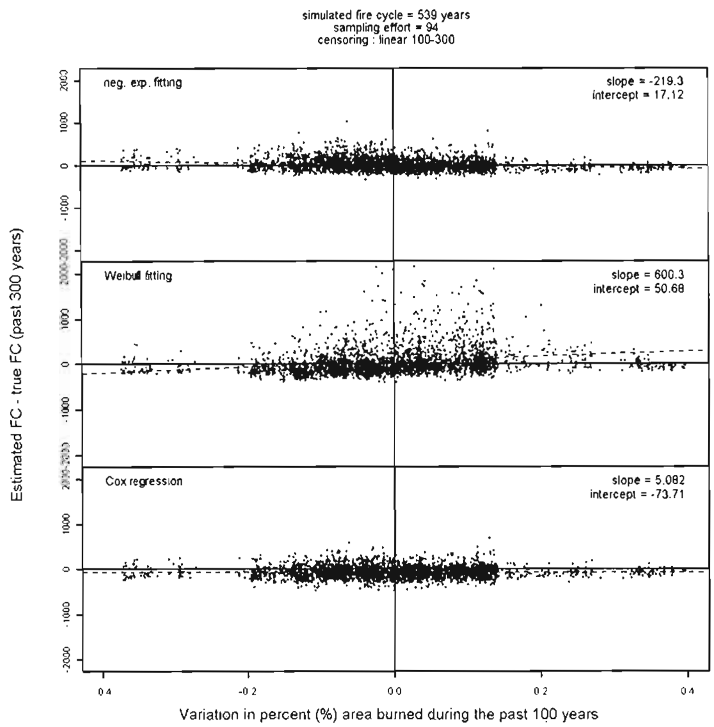
Appendix 1.1d (Global simulated FC = 539 years).

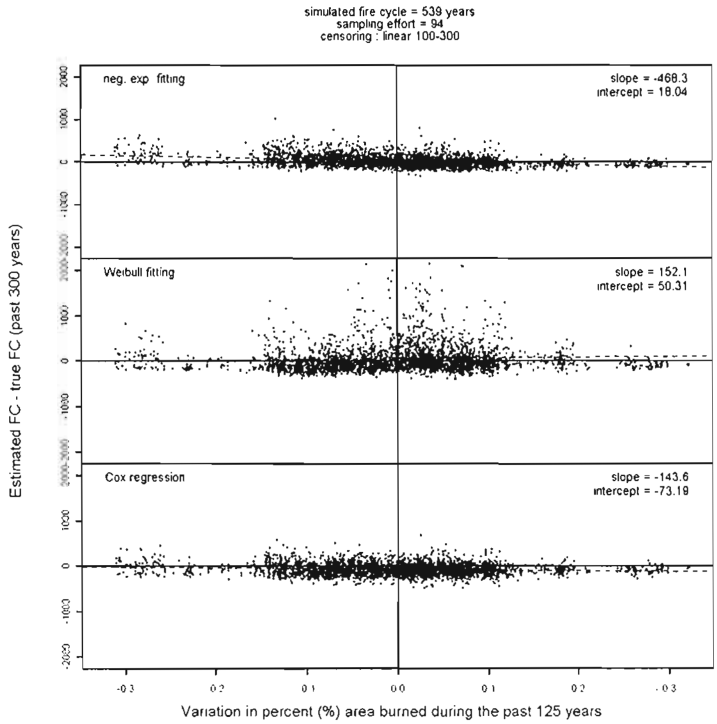


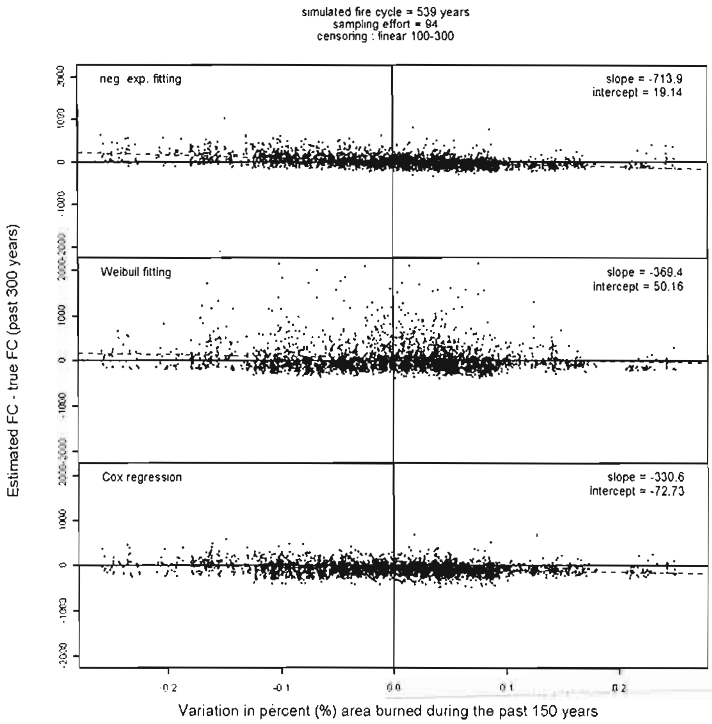

simulated fire cycle = 539 years
sampling effort = 94
censoring : linear 100-300
neg. exp. fitting
slope = -8.981
intercept = 16.02
Weibull fitting
slope = 411.3
intercept = 54.82
Cox regression
slope = -2.303
intercept = -75.15
Estimated FC - true FC (past 300 years)
Variation in percent (%) area burned during the past 25 years

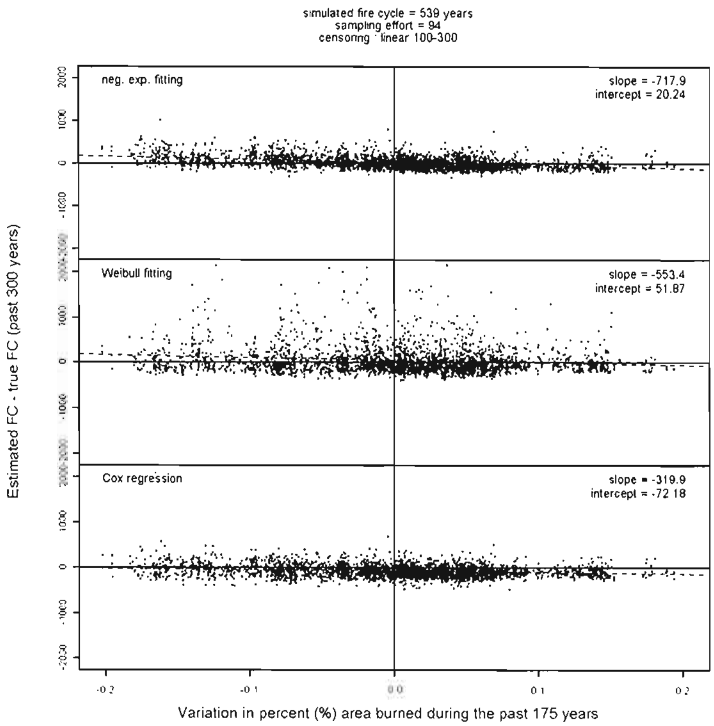

simulated fire cycle = 539 years
sampling effort = 94
censoring : linear 100-300
neg. exp. fitting
slope = -34.86
intercept = 16.22
Weibull fitting
slope = 685.8
Intercept = 54.96
Cox regression
slope = 7.37
intercept = -74.79
Estimated FC - true FC (past 300 years)
Variation in percent (%) area burned during the past 50 years

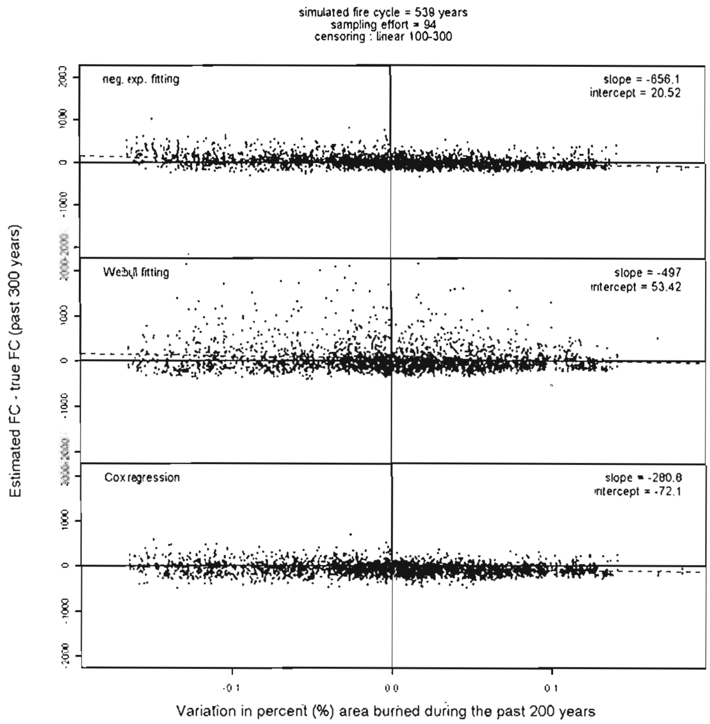

simulated fire cycle = 539 years
sampling effort = 94
censoring . linear 100-300
neg. exp. fitting
slope = -92 71
intercept = 16.67
Weibull fitting
slope = 739.2
intercept = 53.79
Cox regression
slope = 24.03
intercept = -73.93
Estimated FC - true FC (past 300 years)
0 4
-0 2
0 0
0 2
0 4
Variation in percent (%) area burned during the past 75 years

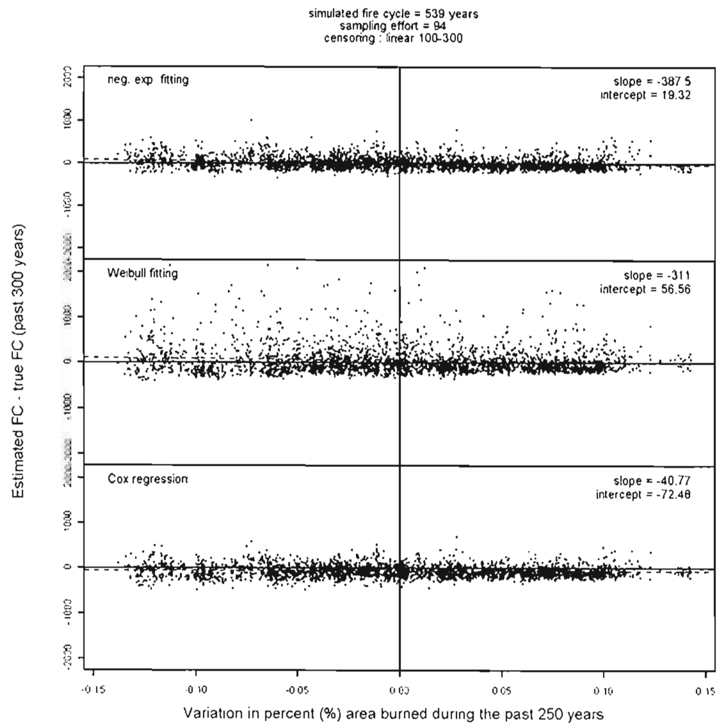

simulated fire cycle = 539 years
sampling effort = 94
censoring : linear 100-300
neg. exp. fitting
slope = -219.3
intercept = 17.12
Weibull fitting
slope = 600.3
intercept = 50.68
Cox regression
slope = 5.082
intercept = -73.71
Estimated FC - true FC (past 300 years)
Variation in percent (%) area burned during the past 100 years

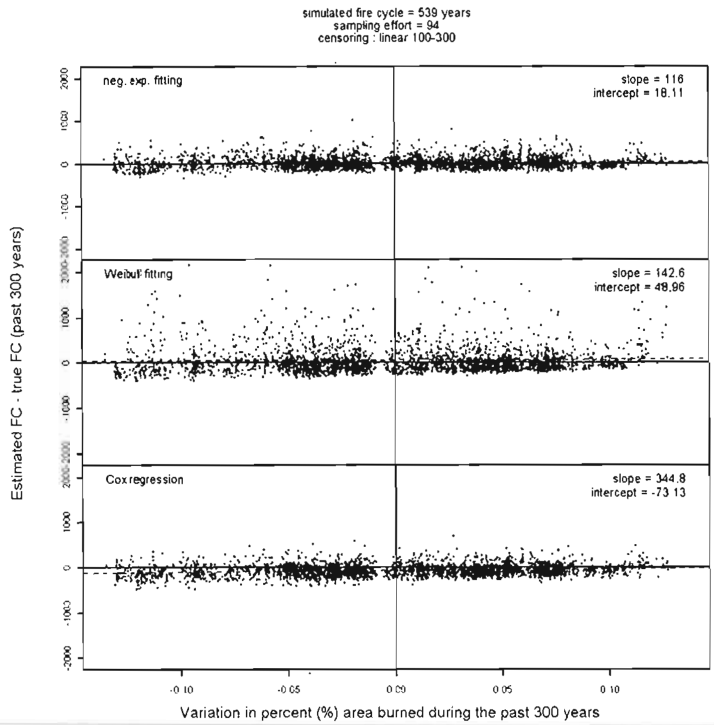

simulated fire cycle = 539 years
sampling effort = 94
censoring : linear 100-300
neg. exp fitting
slope = -468.3
intercept = 18.04
Weibull fitting
slope = 152.1
intercept = 50.31
Cox regression
slope = -143.6
intercept = -73.19
Estimated FC - true FC (past 300 years)
Variation in percent (%) area burned during the past 125 years


simulated fire cycle = 539 years
sampling effort = 94
censoring : linear 100-300
neg. exp. fitting
slope = -713.9
intercept = 19.14
Weibull fitting
slope = -369.4
intercept = 50.16
Cox regression
slope = -330.6
intercept = -72.73
Estimated FC - true FC (past 300 years)
Variation in percent (%) area burned during the past 150 years


simulated fire cycle = 539 years
sampling effort = 94
censoring : linear 100-300
neg. exp. fitting
slope = -717.9
intercept = 20.24
Weibull fitting
slope = -553.4
intercept = 51.87
Cox regression
slope = -319.9
intercept = -72.18
Estimated FC - true FC (past 300 years)
Variation in percent (%) area burned during the past 175 years


simulated fire cycle = 539 years
sampling effort = 94
censoring : linear 100-300
neg. exp. fitting
slope = -656.1
intercept = 20.52
Weibull fitting
slope = -497
intercept = 53.42
Cox regression
slope = -280.8
intercept = -72.1
Estimated FC - true FC (past 300 years)
Variation in percent (%) area burned during the past 200 years


simulated fire cycle = 539 years
sampling effort = 94
censoring : linear 100-300
neg. exp fitting
slope = -387.5
intercept = 19.32
Weibull fitting
slope = -311
intercept = 56.56
Cox regression
slope = -40.77
intercept = -72.48
Estimated FC - true FC (past 300 years)
Variation in percent (%) area burned during the past 250 years


simulated fire cycle = 539 years
sampling effort = 94
censoring : linear 100-300
neg. exp. fitting
slope = 116
intercept = 18.11
Weibull fitting
slope = 142.6
intercept = 48.96
Cox regression
slope = 344.8
intercept = -73.13
Estimated FC - true FC (past 300 years)
Variation in percent (%) area burned during the past 300 years

CHAPITRE II

SCALE-DEPENDANT DETERMINANTS OF HETEROGENEITY IN FIRE FREQUENCY IN A CONIFEROUS BOREAL FOREST OF EASTERN CANADA

2.1 Résumé

L'importance relative des portions déterministes et stochastiques de la variabilité spatiale intra-régionale de la fréquence des feux est très peu documentée en dépit de l'importance incontestée des feux en forêt boréale nord-américaine. Le principal objectif de cette étude est d'identifier les sources de variabilité spatiale de la fréquence des feux dans un paysage de la forêt boréale de l'est du Québec. Parmi les facteurs environnementaux pouvant influencer la fréquence des feux, la latitude, la longitude, les activités humaines et l'appartenance à un domaine bioclimatique donné sont associés à de larges échelles spatiales, tandis que la pente, la position sur la pente, l'exposition des versants, les dépôts de surface et le drainage sont associés à des échelles spatiales fines. La distance moyenne aux cours d'eau s'ajoutant à la liste de facteurs environnementaux considérés, celui-ci correspondant à une échelle spatiale intermédiaire. Dans un premier temps, nous avons recours à un modèle à risques proportionnels (régression de Cox), un type d'analyse de survie semi-paramétrique, afin d'évaluer l'influence potentielle de ces facteurs environnementaux sur la fréquence des feux. Dans un deuxième temps, nous utilisons un modèle numérique d'élévation afin d'évaluer l'exposition dominante au sein de voisinages de taille variable et nous incorporons ces nouvelles variables au modèle de survie. Nos résultats montrent que la longitude est associée significativement à la fréquence des feux, suggérant une influence maritime dans ce territoire côtier. De plus, les sites localisés sur les hauts de pente sont sujet à une fréquence des feux moindre que la moyenne. Enfin, l'exposition dominante au sein de voisinage circulaire de 4000 à 10000 m de rayon semble aussi affecter la fréquence des feux. Considérant l'influence de ces trois facteurs, certains sites s'avèrent sujet à des fréquences des feux 2 à 6 fois plus élevées que d'autres. L'influence du contexte topographique

(exposition des versants) est toutefois fortement dépendante de l'échelle spatiale considérée étant donnée la nature très contagieuse des feux de forêt. Il est en effet nécessaire de considérer des zones de quelques dizaines de km^2 afin de déceler cette influence réelle du contexte topographique. Une discussion portant sur les implications d'une telle hétérogénéité spatiale de la fréquence des feux sur la biodiversité ainsi que pour l'aménagement forestier est aussi présentée.

2.2 Abstract

Despite the recognized importance of fire in North American boreal forests, the relative importance of stochastic and deterministic portions of intra-regional spatial variability in fire frequency is still poorly understood. The first objective of this study is to identify sources of spatial variability in fire frequency in a landscape of eastern Quebec's coniferous boreal forest. Broad-scale environmental factors considered included latitude, longitude, human activities and belonging to a given bioclimatic domain, whereas fine-scale factors included slope, position on the slope, aspect, elevation, surficial deposit and drainage. The average distance to waterbodies was also considered as a potential intermediate-scale source of variability in fire frequency. In order to assess these environmental factors' potential influence, they were incorporated into a proportional hazard model, a semi-parametric form of survival analysis. We also used a digital elevation model in order to evaluate the dominant aspect within neighborhoods of varying sizes and successively incorporated these covariates into the proportional hazard model. We found that longitude significantly affects fire frequency, suggesting a maritime influence on fire frequency in this coastal landscape. We also found that position on the slope was related to fire frequency since hilltops and upperslopes were subject to a lower fire frequency. Dominant aspect was also related to fire frequency, but only when characterized within a neighborhood delimited by 4,000 to 10,000-m radii (5,027-31,416 ha). A 2-6-fold variation in fire frequency can be induced by geographic and topographic contexts, suggesting a substantial intra-regional heterogeneity in disturbance regime with potential consequences on forest dynamics and biodiversity patterns. Implications for forest management are also briefly discussed.

2.3 Introduction

Fire is one of the most important ecological processes in North American boreal forests (Johnson, 1992 ; Payette, 1992). Forest fire regimes, defined by fire frequency, size, intensity, seasonality, fire type and severity (Flannigan, 1993 ; Weber and Flannigan, 1997) have a significant influence on many boreal forest attributes. Fire regimes affect the distribution of species (Asselin *et al.*, 2003 ; Desponts and Payette, 1992 ; Flannigan and Bergeron, 1998 ; Le Goff and Sirois, 2004), age-class distribution of stands (Bergeron *et al.*, 2001), characteristics of wildlife habitats (Thompson *et al.*, 1998), vulnerability of forests to insect epidemics (Bergeron and Leduc, 1998), and net primary production and carbon balance (Peng and Apps, 2000). Fire regimes are even more important in boreal forests in that they have considerable spatial variation across several scales (Keane, Parsons and Rollins, 2004), thus helping to generate patterns of biological and ecosystem diversity on continental (Payette, 1992) and regional scales (Bergeron *et al.*, 2004 ; Heyerdahl, Brubaker and Agee, 2001) as well as within the perimeter of a single fire event, particularly in areas affected by fires of low or variable severity (Schimmel and Granstrom, 1996 ; Weisberg, 2004) but also where fire severity is usually high (Delong and Kessler, 2000 ; Kafka, Gauthier and Bergeron, 2001).

The spatial variability generated by fire regimes results from both the stochasticity inherent to forest fires (Lertzman, Fall and Dorner, 1998) and complex determinist interactions between vegetation, climate, physiography (Engelmark, 1987 ; Heyerdahl, Brubaker and Agee, 2001 ; Schulte *et al.*, 2005) as well as human activities (Lefort, Gauthier and Bergeron, 2003). The term heterogeneity will be used in the course of this paper to describe the determinist (explainable) portion of spatial variability (Lertzman, Fall and Dorner, 1998).

The environmental factors controlling the spatial heterogeneity of fire regimes are numerous and vary from one ecosystem to another. They also depend on the spatial scales being considered. We will talk about top-down controls when the fire regime is mainly affected by environmental factors that might be described on broad spatial scales. Climate and belonging to major vegetation and physiographical formations would be included in the top-down controls associated with fire regimes commonly reported in the literature (Johnson, 1992 ; Payette, 1992 ; Wein and MacLean, 1983). Environmental factors described on a local scale, such as stand type or stand age, density of vegetation, surficial deposits, drainage, slope gradient and aspect, to give but a few examples, are bottom-up controls (Heyerdahl, Brubaker and Agee, 2001 ; Lertzman and Fall, 1998). Bottom-up controls are frequently reported in Mediterranean-type ecosystems (Broncano and Retana, 2004 ; Mermoz, Kitzberger and Veblen, 2005 ; Moritz *et al.*, 2004), in temperate forests (Kushla and Ripple, 1998) or in landscapes with very complex topography (Dorner, Lertzman and Fall, 2002 ; Gavin, Brubaker and Lertzman, 2003). Although some bottom-up controls are sometimes mentioned in the case of coniferous boreal forests (Kafka, Gauthier and Bergeron, 2001), it seems that boreal fire regimes are mostly subject to the influence of extended droughts that produce the conditions favourable to fire spread over vast areas (Bessie and Johnson, 1995). Other environmental factors are more difficult to categorize within one of these two classes. Some studies indeed mention physiographical factors on intermediate spatial scales. They are usually environmental factors that influence the ignition or spread of fires within landscape units ranging in size from a few square kilometres to several hundred square kilometres; for example, proximity to surrounding firebreaks (Cyr *et al.*, 2005 ; Larsen, 1997), proportion of the area covered by wetlands or connectivity of forest blocks conducive to fire spread (Hellberg, Niklasson and Granström, 2004) or relative proportions of softwood and hardwood stands (Bergeron *et al.*, 2004 ; Krawchuck *et al.*, 2006).

Fire frequency, the characteristic of the fire regime on which we will focus, is defined as the burning probability of non-overlapping units of a landscape, per unit of time (Johnson and Gutsell, 1994). We are basing our study on the premise that fire frequency is potentially the fire regime dimension most likely to be influenced by both top-down and bottom-up controls. Moreover, it is certainly the fire regime dimension whose history is easiest to reconstruct.

The principal objective of this study is to highlight environmental factors responsible for the spatial variability of time elapsed since previous fires in a boreal forest landscape in eastern Canada. Our hypothesis is that the overall variability is partly determined by environmental factors inducing heterogeneity in fire frequency within the landscape concerned. We predict that fire frequency is mainly affected by top-down controls and that it is more the environmental factors described on broad spatial scales that are most likely to have an impact on fire frequency. However, we will test slightly more rigorously the assumption that topography, primarily aspect, usually classified among bottom-up controls, influences fire frequency within this landscape. According to this assumption, south-facing slopes have a higher fire frequency than north-facing slopes, owing to the drier conditions created by a greater input of solar radiations, whereas west-facing slopes may have a higher fire frequency than east-facing slopes because of the combined effects of prevailing wind direction and the fact that the maximum temperature is usually reached in the afternoon. However, the highly contagious nature of boreal forest fires suggests that the surrounding context plays an extremely significant role, perhaps even when the environmental factor concerned is usually considered a bottom-up type of control, such as topography. Consequently, a possible impact of topography would not necessarily be detected, if described on a local scale, but detected if described on a broader spatial scale.

2.4 Methods

2.4.1 Study area

The study area covers 15 961 km^2 of boreal forest in eastern Quebec, specifically in the North Shore region, between longitudes 67.00° W and 69.00° W and between latitudes 49.00° N and 50.25° N (Fig. 2.1). This region has a cold, maritime climate with an average annual temperature of 1.4°C and average precipitation of 1 018 mm, measured in Baie Comeau in the southwest corner of the study area. Precipitations are evenly distributed during the year, and occurs as 70% rain (Environment Canada, 1996). The topography is moderately uneven with high hills with rounded summits and many rocky escarpments. The highest hills, located in the northeastern part of the area, are just over 700-m high while other sparsely distributed hills reach above 500 m. The average elevation ranges within landscape subunits vary between 150 m and 200 m. Three of these landscape subunits, as described by Robitaille and Saucier (1998), make up for almost the totality of the whole study area. The average slope is 15%. The hydrography is complex with numerous small lakes and rivers of varying sizes, some of them very large. The configuration of the topography produces a drainage system with a mainly north-south orientation (Robitaille and Saucier, 1998). There are rocky outcrops on slightly more than a third of the total land area, while the rest of the land area consists mainly of thin tills on sloping areas and thick tills at the bottoms of slopes. To a lesser extent, there are glaciofluvial deposits on valley floors (Robitaille and Saucier, 1998).

The study area is divided almost equally between two bioclimatic domains: a balsam fir-white birch domain in the south and a black spruce–moss domain in the north (Robitaille and Saucier, 1998). The same tree species are found in both bioclimatic domains, only the proportions differ. Black spruce (*Picea mariana* (Mill.) BSP) and balsam fir (*Abies balsamea* (L.) Mill.) are the dominant species, along with white spruce (*Picea glauca* (Moench) Voss) and white birch (*Betula papyrifera* Marsh.). Also to be found in the region, but more sporadically, are trembling aspen (*Populus tremuloides* Michx.) and jack pine (*Pinus banksiana* Lamb.), mainly in recently burned areas. Tamarack (*Larix laricina* (Du Roi) K. Koch) can also be found along with black spruce on a few rare hydric sites in the region.

2.4.2 Fire history

Information from various sources has been used to compile the fire history of this area. All fires affecting a surface area of one or more hectares and occurring in the period since 1941 are listed in the SOPFEU's (*Société de protection des forêts contre les feux)* archives (http://www.sopfeu.qc.ca/), and aerial photographs dating back to 1931–32 were interpreted in order to map two older fires (1923 and 1896). In some areas, dendroecological surveys conducted for decadal forest inventories of the Quebec Department of Natural Resources and Wildlife (MRNFQ) were used to assess the amount of time elapsed since the most recent fires. In order to take full advantage of this available data and focus our efforts on ground sampling in the areas where the fire history was less well known, a preliminary time since fire map of the area was carried out. This rough demarcation included recently mapped fires and sections of the study area covered mainly by even-aged forests of black spruce, which were determined with the help of dendroecological surveys carried out during MRNFQ forest inventory campaigns.

Samples were then taken in the study area according to a systematic random plan (Fig. 2.1). The entire study area was subdivided into 80 sectors measuring 15 km by 15 km, within which two accessible points (less than 1 000 m away from roads) and covered with forest were randomly positioned and reached with the help of a GPS. One or two sites could be sampled, depending on time constraints during the field campaign, but were weighted accordingly to ensure that the sample was representative in the subsequent statistical analyses available. A total of 94 points made up the final sample. The SOPFEU map archives were used to directly assign a fire date to some recent fires, i.e. 12.8% of cases. Dendroecological analyses were used to estimate the time interval elapsed since the most recent fires for the rest of the sample, based on data gathered in the MRNFP decadal inventories (37.2%) and during the sample-gathering campaign carried out for this study (50%). The time intervals since the most recent fires, estimated with the help of the dendroecological surveys were inferred based on the conventional methods of Arno and Sneck (Arno and Sneck). Between 10 and 15 dominant trees were cut at root collar and dated at each site. Fire dates were deemed sufficiently reliable if they concerned even-aged stands of a pioneer species commonly establishing itself after a fire. A minimum age (censored data) was assigned to uneven-aged stands, i.e. where a 20-year interval included less than 60% of the sampled dominant trees. However, a visual examination of each stand's age structure suggested that this 20-year interval was too restrictive in the case of some of the older stands that seemed in fact even-aged, probably because of an increasing imprecision of dating with stand age, we thus chose to extend it to 30 years for stands older than 200 years. A minimum age was also assigned to stands consisting primarily of one species that usually does not establish itself after fire such as balsam fir, independently of their age structure.

2.4.3 Survival analyses

Survival analyses are a statistical tool used to take censored data into consideration (Allison, 1995). Such consideration is particularly important in a region such as the North Shore where, because of a relatively long fire cycle, there is a high percentage of old-growth and uneven-aged stands to which only a minimum age corresponding to the age of the oldest tree can be assigned. The influence of environmental variables on fire frequency was estimated using a proportional hazard model, more commonly known as the Cox regression model (Cox, 1972). The Cox regression model belongs to a category of semi-parametric regressions, which gives it a high level of robustness given that the baseline hazard of burning function does not have to be specified beforehand, as in the case of parametric regressions (Allison, 1995), because it is derived from the empirical time-since-fire distribution obtained from dendroecological sampling and archival data (see Johnson and Gutsell, 1994, for details related to the equivalence of these distributions). This allows for control of the temporal variability in fire frequency caused by climate change or human activities in the area and furthermore, allows to test for the influence of spatial variables that might cause departures from the baseline hazard of burning function. As stated by Johnson and Gutsell (Johnson and Gutsell), it should be noted that the term *hazard of burning* refers to the statistical notion of *hazard rate, i.e* the instantaneous probability of fire, and must not be mistaken for *fire hazard* which, for the foresters, rather refers to the potential of fire based on fuel load, structure and phenology. Finally, any significant influence of an environmental factor revealed by the Cox regression will be interpreted as one on *fire frequency*, which is an averaged quantification of hazard of burning over a given period of time (see also Reed *et al.*). The term fire frequency, therefore, will exclusively be used in the rest of this paper for the sake of clarity.

The Cox regressions were conducted using the PHREG procedure of the SAS software (v9.1; SAS Institute Inc, 2003), which estimates the parameters of the model through partial likelihood. Independent variables integrated into the model were chosen by stepwise selection. Table 2.1 shows the environmental variables that were taken into consideration to develop the initial survival model. Even though it has been shown to be an important determinant of fire frequency in other regions (Kasischke, Williams and Barry, 2002 ; Larsen, 1997), stand type was not considered in the survival model since aspen (*Populus tremuloides*) is an early successional species (Lesieur, Gauthier and Bergeron, 2002), generally replaced during the fire-free intervals typical of this region. Its presence would thus probably be related to short fire-free intervals even though it is very unlikely to be a causal factor leading to short fire frequency because of its assumed lower flammability.

Nominal variables were coded as sets of dummy variables while aspect, which varies within a circular scale, had to be converted into a couple of coordinates (x, y) in order to be incorporated in the linear context of the Cox regression. Each aspect class (north, north-east, east, south-east, south, south-west, west and north-west) was thus positioned on a trigonometric circle of radius 1 centered at the origin where the angle corresponds to the azimuth of the dominant aspect of the surrounding slopes. The horizontal axis (x) therefore corresponds to the west-east axis, while the vertical axis (y) corresponds to south-north axis. Sites located within a topographical context where west, east, south and north slopes predominated were assigned the coordinates of (-1,0), (1,0), (0,-1) and (0,1), respectively, while sites located within a topographical context where south-west, north-west, south-east and north-east slopes predominated were assigned the coordinates (-0.7071,-0.7071), (-0.7071, 0.7071), (0.7071,-0.7071) and (0.7071, 0.7071), respectively ($\sin(45^{\circ})=\cos(45^{\circ})\approx 0.7071$). It should be noted that aspect is only characterized at the station level in this initial model. In order to assess the importance of collinearity among all the variables in the data set, we computed Spearman's nonparametric correlations. This allowed us to evaluate whether some of them should be discarded or interpreted more carefully should they reveal a significant effect on fire interval. We paid a particular attention to eventual collinearities with stand type, which was not considered in the survival model for the above-mentioned reasons, but could still introduce a confounding bias should it be closely related to another covariate. Many variables that went into the stepwise selection are significantly correlated, although most of these correlations are not very strong (Spearman's *Rho* between 0.2 and 0.35), except for a few that are closely related by nature (Appendix 2.1). A particular attention has been paid to the stand type, which is in some systems a key determinant of fire frequency that was voluntarily discarded from this model for the reasons stated above. The mixed stands of this area, which represent less than 5% of our sample, seem to occur a little more frequently in the southern part, while resinous stands seem to be slightly excluded from locations close to waterbodies, although the correlations are weak at 0.214, just above the 5% probability threshold. As most correlations are either weak, easily explainable or seemingly irrelevant with regards to fire behaviour, we decided to submit our original dataset to the stepwise selection procedure without any modifications.

The initial model was then improved through a multiscale examination of aspect as a potential source of spatial heterogeneity in fire frequency. A geographic information system (ArcView GIS 3.2a ESRI Inc. 2000) was used to determine the dominant aspect around each pixel of the digital elevation model (93-m resolution). A series of contextual variables corresponding to the **dominant aspect** within a circular area with a radius varying between 93 m and 15 000 m (3.1 ha to 70 685.8 ha); Fig. 2.2) were successively incorporated into the regression model obtained after the stepwise selection described above. Each of these contextual variables was tested individually and a Bonferroni correction for 20 simultaneous tests was applied to the 5% significance threshold. Spearman's correlations among this second set of variables were also computed and suggested no confounding bias (Appendix 2.2). Of course, dominant aspects at varying spatial scales are correlated among them, but should not interfere with each other since they are incorporated individually into the second survival model.

2.5 Results

2.5.1 First survival model

In the first group of variables considered in the Cox regression model, only longitude and hilltop/upperhill were significantly related to fire frequency (Table 2.2). Longitude entered first into the regression model and maintained most of its contribution after the hilltop/upperhill category was incorporated during the second round of the stepwise selection. No other variables could be included into the model after these two rounds of stepwise selection.

The fire frequency ratios resulting from the Cox regressions (called *hazard ratios* or *risk ratios* in statistical literature) can be used to quantify the influence of each variable on fire frequency (Allison, 1995). The fire frequency ratio associated with longitude (0.5200; Table 2.2) indicates a decreasing gradient in fire frequency from west to east, because a one-degree increase in longitude corresponds to a decrease in fire frequency of nearly half the original fire frequency. On the other hand, hilltops and upperhills, characterized by a fire frequency ratio of 0.4710, thus seem to burn roughly half as much as sites on other positions on the slope. Median fire-free intervals (Table 2.3) are indeed longer in the eastern portion (>191) of the study area than in the western part of it (179), although it is impossible to obtain a precise estimate in the western part because of the preponderance of stands for which only a minimum age is known. At a more local scale, sites on hilltops or upperslopes are characterized by a longer median fire-free interval (214) than sites on other positions on the slope (175).

2.5.2 Second survival model

After taking longitude and hilltop and upperhill into consideration, it is possible to detect a statistically significant relationship between dominant aspect of surrounding slopes and fire frequency, but at certain spatial scales only (Fig. 2.3). The strength of the statistical relationship between fire frequency and dominant aspect was indeed above the 5% threshold when determined within a radius of between 4 000 m and 10 000 m with a peak at 8 750 m, the only scale at which the relationship remains significant after a Bonferroni correction for 20 simultaneous tests.

The individual fire frequency ratios corresponding to each of the x and y coordinates (not shown), associated respectively with the east-west and south-north axes, were combined to evaluate the direction and amplitude of the influence of dominant aspect. Each vector presented in Fig. 2.4 illustrates a fire frequency gradient related to dominant aspect at a single spatial scale, the fire frequency being at its maximum where slopes predominantly face the azimuth corresponding to the direction of the vector (thus, at its minimum in the opposite direction). Moreover, the length of each vector indicates the amplitude of this gradient in the form of a ratio. In more concrete terms, the vector associated with the 8750-m scale indicates that sites that are located in environments dominated by south-west facing slopes burn about 3 times more often than the average site, controlling for other covariates (longitude and hilltop/upperhill). Because a linear relationship between the independent variables and the criterion variable is assumed in the Cox regressions (Allison, 1995), these results also indicate that the areas where north and north-east slopes predominate are about 3 times less likely to burn than the average site, with a linear gradient between these two extremes. These results are reflected in the median fire-free intervals (Table 2.3) of the various longitudinal and topographical contexts characterized at the 8 750-m scale (the spatial scale where the statistical relationship is maximized) and in the percentage of stands for which only a minimum age is known (% censored).

2.6 Discussion

2.6.1 Intra-regional longitudinal gradient

The inter-regional variability of fire frequency in North American boreal forests is already well documented, particularly because of the growing number of regional long-term fire history reconstructions carried out in recent years (Bergeron *et al.*, 2006 ; Bergeron *et al.*, 2004 ; Bergeron *et al.*, 2001 ; Grenier *et al.*, 2005 ; Heinselman, 1973 ; Johnson and Larsen, 1991 ; Lesieur, Gauthier and Bergeron, 2002 ; Masters, 1990). In the case of eastern Canada's boreal forests, a decreasing gradient in fire frequency from west to east has been observed (Gauthier *et al.*, 2001), which is mostly related to a precipitation gradient caused by the gradual transition of a continental climate to one under increasing maritime influence (Grondin, 1996). The longitudinal gradient detected in our study suggests the same kind of phenomenon at a smaller spatial scale. The explanation of this longitudinal gradient is indeed likely related to climate since longitude varies independently of other covariates (Appendix 2.1), except elevation, which never comes close to the significance threshold in the stepwise selection (Table 2.2), and distance from the shore, which is in this case a variable of very similar nature that would have led to the same kind of hypothesis. For these reasons, and even though we cannot completely discard the possibility of collinearity with another environmental factor that was not considered in this study, we think that the climate-related hypothesis remains the most plausible. As a matter of fact, similar fire frequency gradients correlated with longitude were observed in Alaska (Dissing and Verbyla, 2003) and in the James Bay region of Quebec (Parisien and Sirois, 2003) and were attributed to climate-related phenomena. This latter study, conducted in an area of similar size, attributes this to the sea breeze effect, which consists of moist cold air blown inland. A notable difference between Parisien and Sirois' study and the present one is the direction of this possible sea breeze effect which would be, in this case, in the opposite direction of the prevailing winds during the fire season. Dissing and Verbyla (2003) also suggest that the cool and more stable atmospheric conditions typical of maritime climates may suppress convective activity generated by heterogeneity in albedo of large landscape features, such as recently burned areas and large inland waterbodies within a matrix of coniferous forest, that is sometime sufficient to increase lightning strike activity (Knowles, 1993)The survival model indicates that this possible maritime influence is substantial because, within this area, each degree of longitude from west to east would correspond to a decrease in fire frequency by a factor of almost 2.

2.6.2 Broad-scale and local-scale physiographic determinants of fire frequency

Many studies have highlighted the impact of topography described at a local scale on fire frequency, particularly aspect (Beaty and Taylor, 2001 ; Broncano and Retana, 2004 ; Clark, 1990 ; Heyerdahl, Brubaker and Agee, 2001 ; Kushla and Ripple, 1998 ; Mermoz, Kitzberger and Veblen, 2005 ; Vazquez and Moreno, 2001). Even though aspect sometimes exerts a strong control over the distribution of fuel types, e.g. when a significantly larger proportion are found on southern slopes (Kasischke, Williams and Barry, 2002), slopes with more direct exposure to solar radiation and prevailing winds usually are more vulnerable to fire because of the generally favourable influence of these two factors on the quality of fuels. However, this influence of aspect on fire frequency usually seems much greater in systems subject to small but frequent fire events, such as Mediterranean-type ecosystems, or in mountainous systems. Although they exist, there are not many references to the influence of aspect on fire frequency in continental coniferous boreal forests despite the large number of available studies of fire regimes. In fact, topography is acknowledged to have a more important influence on fire severity than on fire frequency *per se* (Kushla and Ripple, 1998). The continuity of quality fuels in coniferous boreal forests, which fosters the development of high-intensity crown fires, especially in prolonged drought periods during which most major fire events occur, probably explains to a large degree the modest influence of topography on fire frequency when described at a local scale.

Nonetheless, based on the results of this study, it seems that topography can have a significant influence on fire frequency in this non-mountainous yet rather hilly boreal landscape. However, it is necessary to describe the topography more contextually and to include a rather large area with a radius of between 4 000 m and 10 000 m. Because fire frequency responds to a gradient running from areas with predominant south-west aspects, where fire frequency is highest, to areas with predominant north-east aspects, where fire frequency is lowest, we assume that mechanisms underlying these results are indeed related to the quantity of solar radiation and possibly, to a lesser degree, to the direction of the prevailing winds. Collinearity with other significant covariates doesn't seem to be an issue (Appendix 2.2).

There are two hypotheses that, because they are not mutually exclusive, may explain the influence of dominant exposure on fire frequency. Areas with greater exposure to solar radiation and prevailing winds can either be subject to a greater **ignition probability** or can facilitate **fire spread**. We believe it is not very likely for dominant aspect to have a significant influence on the occurrence of lightning, although it is possible that slopes with the greatest exposure to solar radiation and prevailing winds also contain combustibles more conducive to ignition. However, we assume that such variability would be observable on spatial scales of a few dozen metres, or a few hundred metres at most, which leads us to assign this hypothesis to second place, because such spatial scales do not correspond at all to the effective scales highlighted in our analyses. The second hypothesis concerning fire spread seems more plausible, because it is compatible with the effective spatial scales detected in our analyses (radius of between 4 000 m and 10 000 m). It has also been demonstrated in the past that certain physiographical factors influencing fire spread, which are observable on comparable spatial scales, have a significant influence on fire frequency. The proximity of potential firebreaks (Cyr *et al.*, 2005 ; Larsen, 1997) and the connectivity of forest stands more conducive to fire spread (Hellberg, Niklasson and Granström, 2004) are good examples of environmental factors with an impact on fire frequency. Moreover, fire spread is probably facilitated earlier in the season in areas with predominantly southern exposure as snow melts earlier and faster on these slopes, creating heterogeneity in terms of the length of the fire season within the study area.

Moreover, hilltops and upperslopes are subject to a lower fire frequency than other positions on the slopes, suggesting that at least one local-scale environmental factor may participate in creating spatial heterogeneity in fire frequency. Both edaphic and microclimatic conditions typical of higher positions on the slope may explain this lower fire frequency. The range of elevation in this area is not sufficient to considerably limit vegetation growth but the thinner soils, more frequent rocky outcrops and escarpments, and perhaps, stronger winds, induce fuel discontinuity that may significantly slow down fire spread. Furthermore, the lower fire frequency detected on hilltops and upperslopes may or may not interact with the broad-scale influence of dominant aspect. One could indeed expect to find more of these high positions on the slope at the transitions between large topographic units, thus creating a concentration of partial fire-breaks that may decrease the probability of a fire spreading from one fire-prone topographic unit to one characterized by a lower fire frequency. A meticulous analysis of the correspondence between single fire events boundaries and topographic features would be necessary to confirm of infirm this hypothesis. This is, however, beyond the scope of this study.

2.6.3 Relative importance of top-down and bottom-up controls on fire frequency

Cox regression models are estimated by partial likelihood and, therefore, do not allow for a rigorous estimation of the relative contribution of each independent variable to the survival since there is no partitioning of the variance. Nevertheless, the nature of the selected variables and the order of entry into the model in the course of a stepwise selection procedure can provide indications. Following this rationale, fire frequency in this region seems to respond more to top-down controls, such as longitude and broad-scale topographic context, than to bottom-up control such as the position on the slope.

As a general rule, coniferous boreal forests are subject to large-area fire regimes. In the case of the study area, the average surface area of forest fires since the SOPFEU began to keep records is over 5 000 ha. This does not compare in any way with studies carried out in ecosystems other than boreal forests, such as Mediterranean-type, pyrophilous plant formations where topography has a particularly marked influence on fire frequency even on a very local scale. In fact, the average surface area covered by fires is in direct relation with their level of contagiousness and could be used as a rule of thumb for evaluating the relative importance of bottom-up and top-down controls in a given system. In the present case, the architecture of boreal conifers, such as black spruce, fir and white spruce, which cover the vast majority of the area, is rather conducive to high-intensity crown fires (Wein and MacLean, 1983). It is not surprising therefore that fire frequency is more subject to top-down controls since typical fires in North American boreal forests mainly occur in relatively infrequent, extreme weather conditions (Flannigan and Harrington, 1988), depending on the region, that are conducive to the occurrence of intense fires fed by abundant high-quality combustibles (Johnson, 1992). In such systems, where fires are typically highly contagious, very local environmental factors are subordinated to more contextual environmental factors.

2.6.4 Conclusions

The amplitude of the intraregional heterogeneity in fire frequency highlighted in our results is considerable. It is also likely permanent, since it is related to the physical environment. This suggests many potential implications. Strictly from a management perspective, a better understanding of the intraregional heterogeneity of fire frequency and effective spatial scales can increase our capacity to predict future fire occurrences within managed landscapes. This knowledge could be used in the development of bio-economical risk analyses that may be useful for forest management planning in general and for fire management specifically (Bonazountas *et al.*, 2005 ; Brillinger, Preisler and Benoit, 2003 ; Hirsh *et al.*, 2001). On the other hand, the ecological implications of such a heterogeneity are also numerous. Such heterogeneity in fire frequency indeed affects time-since-fire distributions at the landscape level, stands' attribute and spatial distribution throughout the landscape, as well as potentially promotes different successional pathways (Frelich and Reich, 1995). This leads us to believe that areas which are relatively geographically close to one another may be home to distinct biological legacies left by distinct disturbance regimes.

Considerable attention has been given to the inter-regional variability of fire regimes in boreal forests in recent years (Bergeron *et al.*, 2006 ; Flannigan and Bergeron, 1998 ; Lefort *et al.*, 2004 ; Stocks *et al.*, 2003) largely in reaction to the widespread application of consistent management practices over vast areas which results in a standardization of boreal forest that may have serious impacts on ecosystemic diversity. It has indeed been suggested that we should diversify our forest management practices based on the inter-regional variability of natural disturbance regimes in order to preserve this diversity (Attiwill, 1994 ; Gauthier, Leduc and Bergeron, 1996) and apply a coarse filter, or in other words, a pragmatic conservation biology-based approach that recognizes the impossibility of taking the specific needs of each species into account (Franklin, 1993 ; Hunter, Jacobson and Webb, 1988 ; Noss, 1987). We suggest that the intraregional heterogeneity of fire frequency may be an additional level of variability that could be considered through forest management based on the natural dynamics of boreal forest disturbances.

Moreover, forest zoning is often suggested in order to meet the multiples objectives inherent to sustainable development (Andison, 2003 ; D'eon, Hebert and Viszlay, 2004 ; Seymour and Hunter, 1999). This involves spatialization of the various types of forest management where spatial patterns in large scale natural disturbance must be taken into consideration (Angelstam, 1998 ; Baker, 1992 ; Le Goff *et al.*, 2005). In fact, fire frequency heterogeneity could be considered beforehand in order to optimize such zoning according to the desired objectives.

Lastly, we believe that the findings of this study demonstrate once again the importance of correctly identifying spatial scales related to the ecological processes being studied. We therefore encourage the use of research tools and experimental design allowing the exploration of multiple spatial scales so that valid hypotheses are not rejected solely because the effective scales have not been targeted.

2.7 References

Allison, P.D. (1995). Survival analysis using the SAS system: A practical guide. Cary, North Carolina, SAS Institute Inc.

Andison, D.W. 2003. «Tactical forest planning and landscape design». In *Towards Sustainable Management of the Boreal Forest,* P.J. Burton, C. Messier, D.W. Smith et W.L. Adamovicz, p. 433-480. Ottawa: NRC Research Press.

Angelstam, P.K. 1998. «Maintaining and restoring biodiversity in European boreal forests by developing natural disturbance regimes.». *Journal of Vegetation Science*, vol. 9, p. 593-602.

Arno, S.F., and K.M. Sneck (1977). A method for determining fire history in coniferous of the mountain west, USDA Forest Service

Asselin, H., S. Payette, M. J. Fortin and S. Vallee. 2003. «The Northern Limit of Pinus Banksiana Lamb. In Canada: Explaining the Difference Between the Eastern and Western Distributions». *Journal of Biogeography*, vol. 30, no 11, p. 1709-1718.

Attiwill, Peter M. 1994. «The disturbance of forest ecosystems: The ecological basis for conservative management.». *Forest Ecology and Management*, vol. 63, no 2-3, p. 247-300.

Baker, W.L. 1992. «The landscape ecology of large disturbances in the design and management of nature reserves». *Landscape Ecology*, vol. 7, no 3, p. 191-194.

Beaty, R. M., and A. H. Taylor. 2001. «Spatial and Temporal Variation of Fire Regimes in a Mixed Conifer Forest Landscape, Southern Cascades, California, Usa». *Journal of Biogeography*, vol. 28, no 8, p. 955-966.

Bergeron, Y., D. Cyr, C.R. Drever, M. Flannigan, S. Gauthier, D. Kneeshaw, E. Lauzon, A. Leduc, H. Le Goff, D. Lesieur and K. Logan. 2006. «Past, current, and future fire frequencies in Quebec's commercial forests: Implications for the cumulative effects of harvesting and fire on age-class structure and natural disturbance-based management». *Canadian Journal of Forest Research*, vol. 36, no 11, p. 2737-2744.

Bergeron, Y., S. Gauthier, M. Flannigan and V. Kafka. 2004. «Fire regimes at the transition between mixedwood and coniferous boreal forest in northwestern Quebec». *Ecology*, vol. 85, no 7, p. 1916-1932.

Bergeron, Yves, Sylvie Gauthier, Victor Kafka, Patrick Lefort and Daniel Lesieur. 2001. «Natural fire frequency for the eastern Canadian boreal forest: Consequences for sustainable forestry.». *Canadian Journal of Forest Research*, vol. 31, no 3, p. 384-391.

Bergeron, Yves, and Alain Leduc. 1998. «Relationships between change in fire frequency and mortality due to spruce budworm outbreak in the southeastern Canadian boreal forest.». *Journal of Vegetation Science*, vol. 9, no 4, p. 493-500.

Bessie, W C, and E A Johnson. 1995. «The relative importance of fuels and weather on fire behavior in subalpine forests.». *Ecology*, vol. 76, no 3, p. 747-762.

Bonazountas, M., D. Kallidromitou, P. A. Kassomenos and N. Passas. 2005. «Forest Fire Risk Analysis». *Human and Ecological Risk Assessment*, vol. 11, no 3, p. 617-626.

Brillinger, D. R., H. K. Preisler and J. W. Benoit. 2003. «Risk Assessment: a Forest Fire Example». In *Science and Statistics: A Festschrift for Terry Speed*, p. 177-196. Beachwood, Ohio: Institute of Mathematical Statistics.

Broncano, M. J., and J. Retana. 2004. «Topography and Forest Composition Affecting the Variability in Fire Severity and Post-Fire Regeneration Occurring After a Large Fire in the Mediterranean Basin». *International Journal of Wildland Fire*, vol. 13, no 2, p. 209-216.

Clark, J S. 1990. «Fire and climate change during the last 750 yr in Northwestern Minnesota (USA).». *Ecological Monographs*, vol. 60, no 2, p. 135-160.

Cox, D.R. 1972. «Regression models and life-tables (with discussion)». *Journal of The Royal Statistical Society B*, vol. 34, p. 187-220.

Cyr, D., Y. Bergeron, S. Gauthier and A. Larouche. 2005. «Are the Old-Growth Forests of the Clay Belt Part of a Fire-Regulated Mosaic?». *Canadian Journal of Forest Research*, vol. 35, no 1, p. 65-73.

D'eon, R.G., D. Hebert and S.L. Viszlay. 2004. «An ecological rationale for sustainable forest management concepts at Riverside Forest Products, south central British Columbia». *The Forestry Chronicle*, vol. 80, no 3, p. 341-348.

Delong, S. C., and W. B. Kessler. 2000. «Ecological Characteristics of Mature Forest Remnants Left by Wildfire». *Forest Ecology and Management*, vol. 131, no 1-3, p. 93-106.

Desponts, M, and S Payette. 1992. «Recent dynamics of jack pine at its northern distribution limit in northern Quebec». *Canadian Journal of Botany*, vol. 70, no 6, p. 1157-1167.

Dissing, D., and D. L. Verbyla. 2003. «Spatial Patterns of Lightning Strikes in Interior Alaska and Their Relations to Elevation and Vegetation». *Canadian Journal of Forest Research*, vol. 33, no 5, p. 770-782.

Dorner, B., K. Lertzman and J. Fall. 2002. «Landscape Pattern in Topographically Complex Landscapes: Issues and Techniques for Analysis». *Landscape Ecology*, vol. 17, no 8, p. 729-743.

Engelmark, O. 1987. «Fire history correlations to forest type and topography in northern Sweden». *Annales Botanici Fennici*, vol. 24, p. 317-324.

Environment Canada. 1996. *Canadian climate normals 1947-1996*: Canadian Climate Program. Environment Canada. Atmospheric Environment Service.

Flannigan, M D, and Y Bergeron. 1998. «Possible role of disturbance in shaping the northern distribution of Pinus resinosa.». *Journal of Vegetation Science*, vol. 9, no 4, p. 477-482.

Flannigan, M.D. 1993. «Fire regime and the abundance of red pine». *International Journal of Wildland Fire*, vol. 3, p. 241-247.

Flannigan, M.D., and J.B. Harrington. 1988. «A Study of the Relation of Meteorological Variables to Monthly Provincial Area Burned by Wildfire in Canada (1953–80)». *Journal of Applied Meteorology*, vol. 27, no 4, p. 441-452.

Franklin, J.F. 1993. «Preserving biodiversity: species, ecosystems, or landscapes». *Ecological Applications*, vol. 3, p. 202-205.

Frelich, Lee E, and Peter B Reich. 1995. «Spatial patterns and succession in a Minnesota southern-boreal forest.». *Ecological Monographs*, vol. 65, no 3, p. 325-346.

Gauthier, S., A. Leduc, B. Harvey, Y. Bergeron and P. Drapeau. 2001. «Les perturbations naturelles et la diversité écosystémique». *Le Naturaliste Canadien*, vol. 125, p. 10-17.

Gauthier, Sylvie, Alain Leduc and Yves Bergeron. 1996. «Forest dynamics modelling under natural fire cycles: A tool to define natural mosaic diversity for forest management.». *Environmental Monitoring and Assessment*, vol. 39, no 1-3, p. 417-434.

Gavin, D.G., L.B. Brubaker and K.P. Lertzman. 2003. «An 1800-year record of the spatial and temporal distribution of fire from the west coast of Vancouver Island, Canada.». *Canadian Journal of Forest Research*, vol. 33, p. 573-586.

Grenier, D. J., Y. Bergeron, D. Kneeshaw and S. Gauthier. 2005. «Fire Frequency for the Transitional Mixedwood Forest of Timiskaming, Quebec, Canada». *Canadian Journal of Forest Research*, vol. 35, no 3, p. 656-666.

Grondin, P. 1996. «Écologie forestière». In *Manuel de foresterie,* J.A. Bérard et M. Côté, p. 133-279. Québec: Les Presses de l'Université Laval.

Heinselman, M.L. 1973. «Fire in the virgin forests of the Boundary Waters Canoe area, Minnesota». *Quaternary Research*, vol. 3, p. 329-382.

Hellberg, E., M. Niklasson and A. Granström. 2004. «Influence of landscape structure on patterns of forest fires in boreal forest landscapes in Sweden». *Canadian Journal of Forest Research*, vol. 34, p. 332-338.

Heyerdahl, E. K., L. B. Brubaker and J. K. Agee. 2001. «Spatial Controls of Historical Fire Regimes: a Multiscale Example From the Interior West, Usa». *Ecology*, vol. 82, no 3, p. 660-678.

Hirsh, K., V. Kafka, C. Tymstra, R. McAlpine, B. Hawkes, H. Stegehuis, S. Quintilio, S. Gauthier and K. Peck. 2001. «Fire-smart forest management: A pragmatic approach to sustainable forest management in fire-dominated ecosystems.». *The Forestry Chronicle*, vol. 77, no 2, p. 357-363.

Hunter, M L JR, G J JR Jacobson and T III Webb. 1988. «Paleoecology and the coarse-filter approach to maintaining biological diversity». *Conservation Biology*, vol. 2, no 4, p. 375-385.

Johnson, E A, and C P S Larsen. 1991. «Climatically induced change in fire frequency in the southern Canadian Rockies.». *Ecology*, vol. 72, no 1, p. 194-201.

Johnson, E.A. (1992). Fire and vegetation dynamics: Studies from the North American boreal forest. New York, Cambridge University Press

Johnson, E.A., and S.L. Gutsell. 1994. «Fire frequency models, methods and interpretations.». *Advances in Ecological Research*, vol. 25, p. 239-287.

Kafka, V., S. Gauthier and Y. Bergeron. 2001. «Fire Impacts and Crowning in the Boreal Forest: Study of a Large Wildfire in Western Quebec». *International Journal of Wildland Fire*, vol. 10, no 2, p. 119-127.

Kasischke, E. S., D. Williams and D. Barry. 2002. «Analysis of the Patterns of Large Fires in the Boreal Forest Region of Alaska». *International Journal of Wildland Fire*, vol. 11, no 2, p. 131-144.

Keane, R.E., R. Parsons and M.G. Rollins. 2004. «Predicting fire regimes across multiple scales». In *Emulating Natural Disturbances; Concepts and Techniques*, A. Perera, p. 88-94. UK: Cambridge University Press.

Knowles, J.B. 1993. «The influence of forest fire induced albedo differences on the generations of mesoscale circulations.». Fort Collins, U.S., Colorado State University.

Krawchuck, M.A., S.G. Cumming, M.D. Flannigan and R.W. Wein. 2006. «Biotic and abiotic regulation of lightning fire initiation in the mixedwood boreal forest». *Ecology*, vol. 87, no 2, p. 458-468.

Kushla, J. D., and W. J. Ripple. 1998. «Assessing Wildfire Effects With Landsat Thematic Mapper Data». *International Journal of Remote Sensing*, vol. 19, no 13, p. 2493-2507.

Larsen, C P S. 1997. «Spatial and temporal variations in boreal forest fire frequency in northern Alberta.». *Journal of Biogeography*, vol. 24, no 5, p. 663-673.

Le Goff, H., A. Leduc, Y. Bergeron and M. Flannigan. 2005. «The adaptative capacity of forest management to changing fire regimes in the boreal forest of Quebec». *The Forestry Chronicle*, vol. 81, no 4, p. 582-592.

Le Goff, H., and L. Sirois. 2004. «Black Spruce and Jack Pine Dynamics Simulated Under Varying Fire Cycles in the Northern Boreal Forest of Quebec, Canada». *Canadian Journal of Forest Research*, vol. 34, no 12, p. 2399-2409.

Lefort, P., A. Leduc, S. Gauthier and Y. Bergeron. 2004. «Recent fire regime (1945-1998) in the boreal forest of western Quebec». *Ecoscience*, vol. 11, no 4, p. 433-445.

Lefort, Patrick, Sylvie Gauthier and Yves Bergeron. 2003. «The influence of fire weather and land use on the fire activity of the lake Abitibi Area, Eastern Canada.». *Forest Science.*, vol. 49, no 4, p. 509-521.

Lertzman, K., and J. Fall. 1998. «From forest stands to landscapes: spatial scales and the role of disturbance». In *Ecological scale: Theory and applications*, D.L. Peterson et T. Parker, p. 339-367. New York: Columbia University Press.

Lertzman, K., J. Fall and B. Dorner. 1998. «Three kinds of heterogeneity in fire regimes: at the crossroads of fire history and landscape ecology». *Northwest Science*, vol. 72, p. 4-23.

Lesieur, D., S. Gauthier and Y. Bergeron. 2002. «Fire frequency and vegetation dynamics for the south-central boreal forest of Quebec, Canada». *Canadian Journal of Forest Research*, vol. 32, p. 1996-2008.

Masters, A.M. 1990. «Changes in forest fire frequency in Kootenay National Park, Canadian Rockies». *Canadian Journal of Botany*, vol. 68, p. 1763-1767.

Mermoz, M., T. Kitzberger and T. T. Veblen. 2005. «Landscape Influences on Occurrence and Spread of Wildfires in Patagonian Forests and Shrublands». *Ecology*, vol. 86, no 10, p. 2705-2715.

Moritz, M.A., J.E. Keeley, E.A. Johnson and A.A. Schaffner. 2004. «Testing a basic assumption of shrubland fire management: how important is fuel age?». *Frontiers in Ecology and the Environment*, vol. 2, no 2, p. 67-72.

Noss, R.F. 1987. «From plant communities to landscape in conservation inventories: a look at the nature conservancy». *Biological Conservation*, vol. 41, p. 11-37.

Parisien, M. A., and L. Sirois. 2003. «Distribution and Dynamics of Tree Species Across a Fire Frequency Gradient in the James Bay Region of Quebec». *Canadian Journal of Forest Research*, vol. 33, no 2, p. 243-256.

Payette, S. 1992. «Fire as a controling process in the North American boreal forest». In *A system analysis of the global boreal forest*, H.H. Shugart, R. Leemans et G.B. Bonan, p. 144-169. New York: Cambridge University Press.

Peng, Chang hui , and Michael J Apps. 2000. «Simulating global soil-CO2 flux and its response to climate change.». *Journal of Environmental Sciences (China)*, vol. 12, no 3, p. 257-265.

Reed, W J, C P S Larsen, E A Johnson and G M MacDonald. 1998. «Estimation of temporal variations in historical fire frequency from time-since-fire map data.». *Forest Science*, vol. 44, no 3, p. 465-475.

Robitaille, A, and J.P. Saucier (1998). Paysages régionaux du Québec méridional. Québec, Les Publications du Québec

Saucier, JP. 1994. *Le point d'observation écologique : normes techniques*. Quebec: Ministère des Ressources Naturelles et de la Faune - Direction des inventaires forestier.

Schimmel, Johnny, and A. Granstrom. 1996. «Fire severity and vegetation response in the boreal swedish forest». *Ecology*, vol. 77, no 5, p. 1436-1450.

Schulte, L. A., D. J. Mladenoff, S. N. Burrows, T. A. Sickley and E. V. Nordheim. 2005. «Spatial Controls of Pre-Euro-American Wind and Fire Disturbance in Northern Wisconsin (Usa) Forest Landscapes». *Ecosystems*, vol. 8, no 1, p. 73-94.

Seymour, R. S., and M.L. Jr Hunter. 1999. «Principles of ecological forestry». In *Maintaining biodiversity in forest ecosystems,* M.L. Hunter, p. 22-61. Cambridge: Cambridge University Press.

Stocks, B.J., J.A. Mason, J.B. Todd, E.M. Bosch, B.M. Wotton, B.D. Amiro, M.D. Flannigan, K.G. Hirsch, K.A. Logan, D.L. Martell and W.R. Skinner. 2003. «Large forest fires in Canada, 1959-1997». *Journal of Geophysical Research*, vol. 108, p. doi:10.1029/2001JD000484.

Thompson, Ian D, Michael D Flannigan, B Michael Wotton and Roger Suffling. 1998. «The effects of climate change on landscape diversity: An example in Ontario Forests.». *Environmental Monitoring and Assessment*, vol. 49, no 2-3, p. 213-233.

Vazquez, A., and J. M. Moreno. 2001. «Spatial Distribution of Forest Fires in Sierra De Gredos (Central Spain)». *Forest Ecology and Management*, vol. 147, no 1, p. 55-65.

Weber, M.G., and M.D. Flannigan. 1997. «Canadian boreal forest ecosystem structure and function in a changing climate: impact on fire regime». *Environmental Reviews*, vol. 5, p. 145-166.

Wein, R.W., and D.A. MacLean (1983). The role of fire in northern circumpolar ecosystems. Toronto, Canada, John Wiley & Sons Ltd.

Weisberg, P. J. 2004. «Importance of Non-Stand-Replacing Fire for Development of Forest Structure in the Pacific Northwest, Usa». *Forest Science*, vol. 50, no 2, p. 245-258.

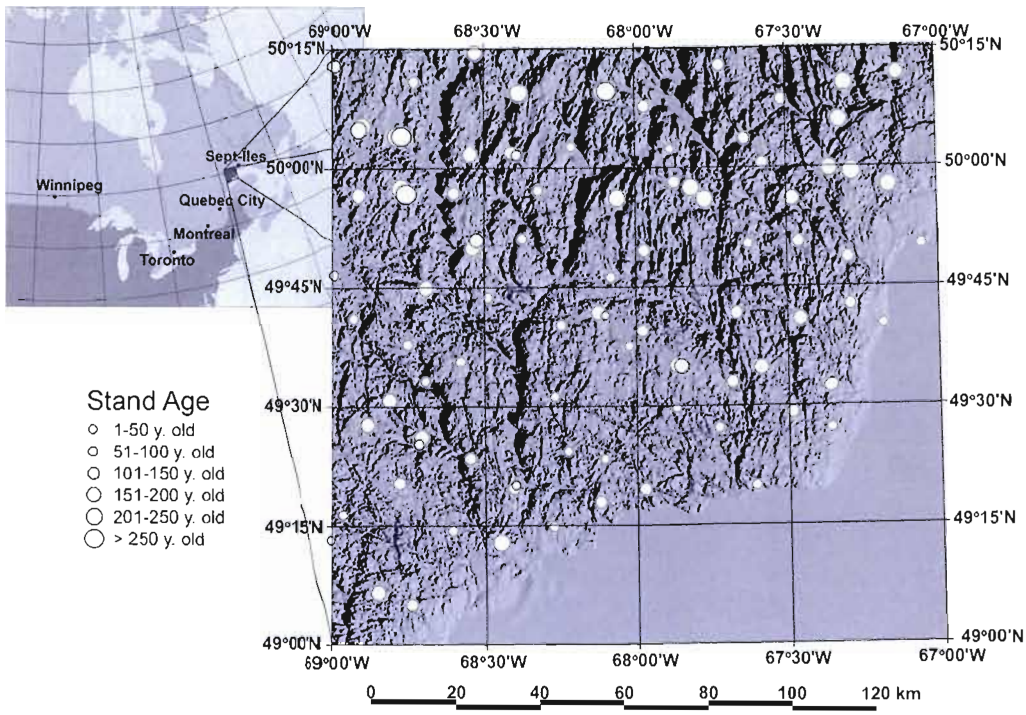


Figure 2.1 Study area - Topography and spatial distribution of sampled stands (elevation amplified 10 times).

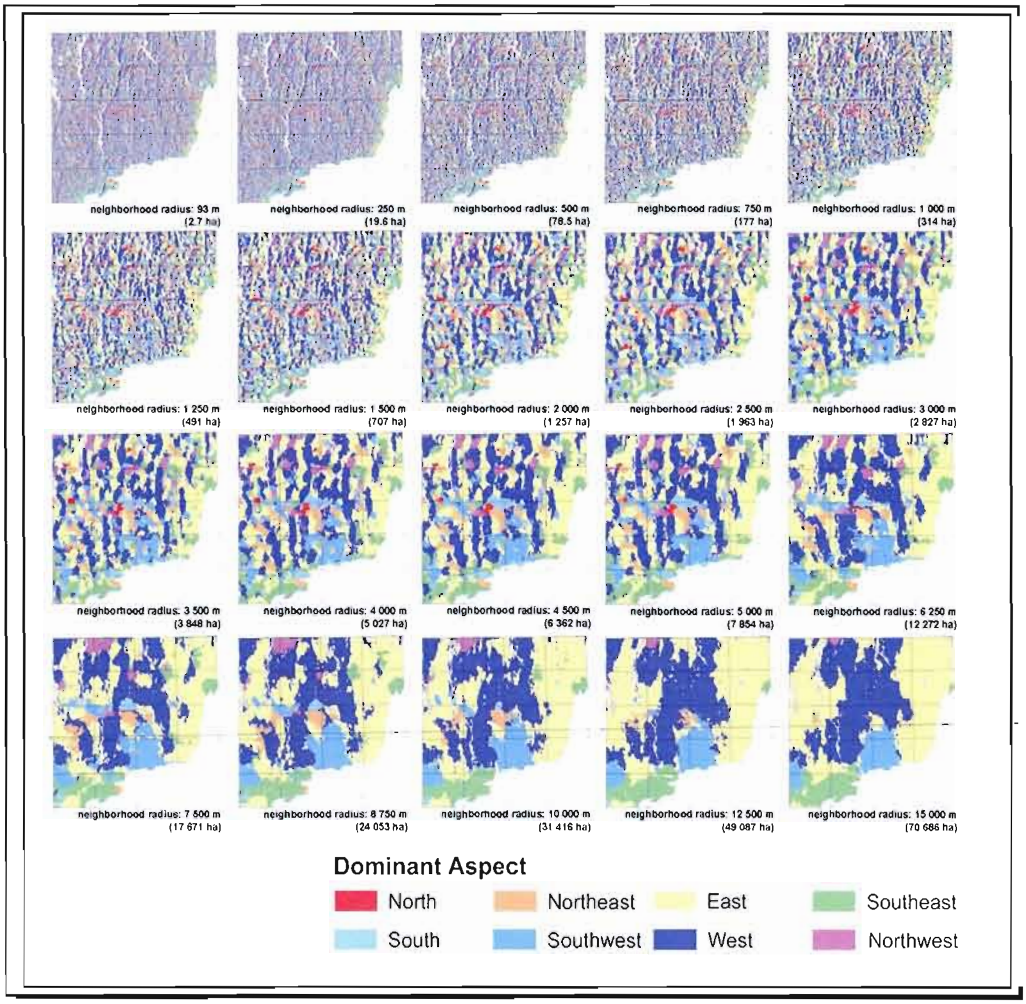


Figure 2.2 Dominant aspect (for all elevations) considering various neighbourhood sizes.

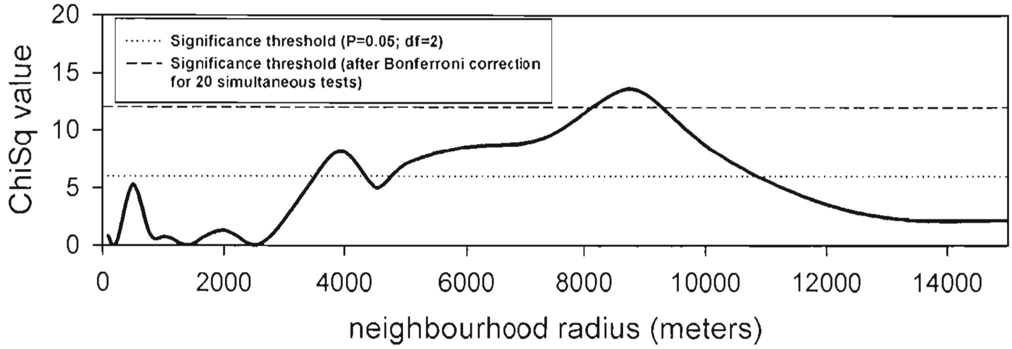


Figure 2.3 Strength of statistical relationship between dominant aspect and fire frequency as a function of the neighbourhood radius considered.

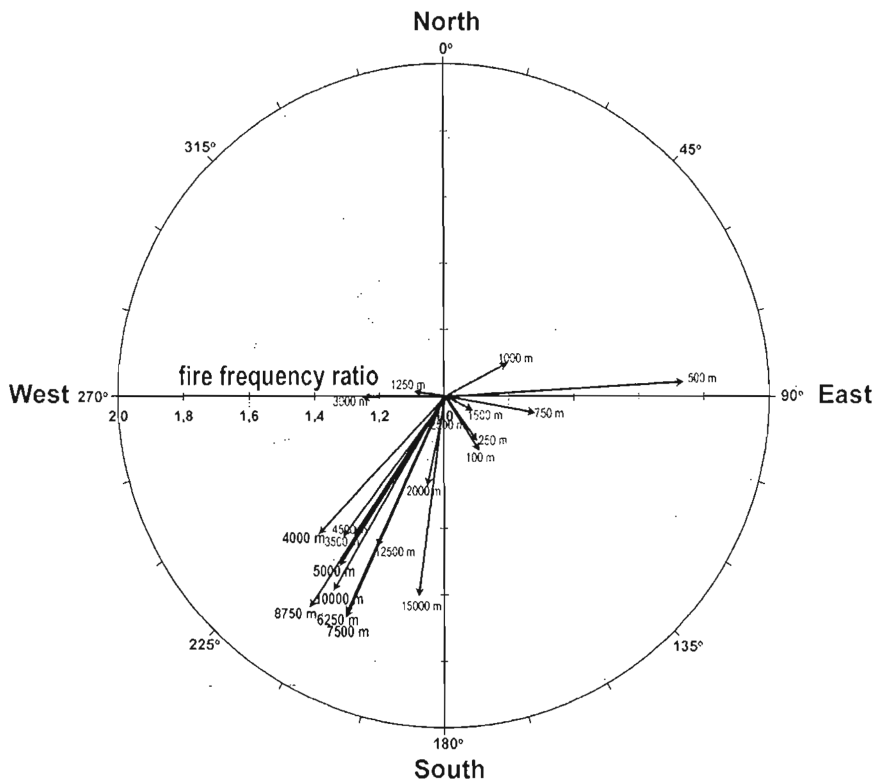


Figure 2.4 Fire frequency gradients as a function of dominant aspect and neighbourhood radius considered. Radial axis indicates the amplitude of the gradient while the angular axis represents the direction in which the fire frequency is at its maximum, e.g., a vector of length 3 pointing in a south-south-west direction indicates that sites located in areas dominated by slopes facing this azimuth burn three times as much as the average site and that sites located in areas dominated by slopes facing the opposite azimuth (north-north-east) burn three times less often than the average site, with a linear gradient between these extremes. Neighbourhood radii corresponding to significant spatial scales are in bold characters.

Table 2.1 Details of environmental variables considered in the initial survival model.

Vegetation	Stand type[a]	Mixed	local scale	nominal
		Coniferous	local scale	
	Bioclimatic domain[b]	balsam fir - white birch	broad scale	nominal
		black spruce - pleurozium	broad scale	
Geography	Longitude		broad scale	continuous (decimal degrees)
	Latitude		broad scale	continuous (decimal degrees)
	Distance from Saint-Lawrence River		broad scale	continuous (meters)
Physiography and Topography	Surficial deposit[c]	rocky outcrop	local scale	nominal
		thin till	local scale	
		thick till	local scale	
		glaciofluvial	local scale	
	Slope aspect[c]	west-east axis (x)	local scale	continuous (x,y)
		south-north axis (y)	local scale	
	Position on the slope[c]	hilltop/upperslope	local scale	nominal
		midslope	local scale	
		depression/lowerslope	local scale	
		flat	local scale	
	Mean waterbreak distance[d]		intermediate	continuous (meters)
	Drainage[c]		local scale	ordinal; from 1(excessive) to 6 (organic)
	Elevation		local scale	continuous (meters)

[a] Stands composed of 25-50% of either decidous or resinous trees (basal area) were characterized as mixed while stands. with over 75% of resinous trees were characterized as resinous. Our sample included no stands with more than 75% of decidous trees. Collinearity with other variables was evaluated, but stand type was not submitted to the stepwise selection.

[b] From Robitaille and Saucier (1998).

[c] Evaluated following the protocol used in Quebec's provincial forest inventories (Saucier, 1994).

[d] The mean waterbreak distance considered the eight nearest waterbodies in all cardinal directions and their intermediates represented on a 1 : 250 000 topographic map (Larsen, 1997).

Table 2.2 Summary of stepwise selection of independent variables of the initial survival model.

covariates	1st round			2nd round			final model (no other covariates added)				
	-2 log L	ChiSq[a]	prob > ChiSq	-2 log L	ChiSq[a]	prob > ChiSq	-2 log L	parameter estimate	Fire frequency ratio[b]	ChiSq[a]	prob > ChiSq
Longitude	**286.6100**	**4.7780**	**0.0288**	[c]	**4.7157**	**0.0299**	[c]	**-0.6537**	**0.5200**	**4.7157**	**0.0299**
Latitude	288.8650	2.5230	0.1122	285.4970	1.1130	0.2914	280.8070	-0.5392	0.5830	1.1330	0.2871
Distance to St-Lawrence River	290.4470	0.9410	0.3320	286.5510	0.0590	0.8081	281.8500	0.0000	1.0000	0.0900	0.7642
Balsam fir - white birch domain	288.2630	3.1250	0.0771	284.4550	2.1550	0.1421	280.3190	0.4360	1.5470	1.6210	0.2030
Black spruce - *Pleurozium* domain	288.2630	3.1250	0.0771	284.4550	2.1550	0.1421	280.3190	-0.4360	0.6470	1.6210	0.2030
Rocky outcrop	290.5970	0.7910	0.3738	286.3180	0.2920	0.5889	281.6590	0.1765	1.1930	0.2810	0.5960
Thin till	289.9990	1.3890	0.2386	285.6430	0.9670	0.3254	281.6430	-0.2076	0.8130	0.2970	0.5858
Thick till	291.3170	0.0710	0.7899	286.5740	0.0360	0.8495	281.7250	-0.2076	0.6501	0.2150	0.6429
Glacio-fluvial	290.8770	0.5110	0.4747	285.6950	0.9150	0.3388	281.6400	0.3144	1.3690	0.3000	0.5839
Aspect (west-east axis)	291.1980	0.1900	0.6629	286.4910	0.1190	0.7301	281.9400	0.0020	1.0020	0.0000	1.0000
Aspect (south-north axis)	291.3550	0.0330	0.8559	286.6100	0.0000	0.9975	281.9000	0.0502	1.0520	0.0400	0.8415
Hilltop/upperslope	287.0090	4.3790	0.0364	**281.9400**	**4.6700**	**0.0307**	[c]	**-0.7521**	**0.4710**	**4.6700**	**0.0307**
Midslope	290.1240	1.2640	0.2609	284.9650	1.6450	0.1996	281.8420	0.1207	0.7534	0.0980	0.7542
Depression/lowerslope	287.8080	3.5800	0.0585	283.6480	2.9620	0.0852	280.9910	0.3222	1.4890	0.9490	0.3300
Flat	290.9940	0.3940	0.5302	286.3160	0.2940	0.5877	279.8960	-0.6883	0.5020	2.0440	0.1528
Mean Waterbreak Distance	288.6920	2.6960	0.1006	284.3430	0.1551	0.6937	279.8990	-0.0004	1.0000	2.0410	0.1531
Drainage	290.5944	0.7936	0.3730	284.5890	2.0210	0.1551	280.7613	-0.5037	0.6040	1.1787	0.2776
Elevation	291.3220	0.0660	0.7973	286.3910	0.2190	0.6398	281.6420	-0.0008	0.9990	0.2980	0.5851
without covariates	**291.388**										
with longitude added to the model				**286.6100**							
with longitude and hilltop/upperslope added to the model							**281.94**				

[a] The Chi^2 values listed above come from log-likelihood ratio tests described in Allison (1995). These tests, which compare survival models with or without the variable concerned, produce a Chi^2 with a degree of freedom corresponding to the number of differing variables between the two compared models.

[b] In the case of a continuous variable (longitude, for instance) the fire frequency ratio corresponds to the proportion of the original hazard of burning maintained after a one-unit increase of this given variable, likewise for a dummy (binary) variable such as hilltop/upperslope, to which only the values 0 or 1 can be attributed.

[c] Covariate's contribution included in the model.

Table 2.3 Median fire-free intervals as a function of geographic and physiographic context.

	Median fire-free interval (years)	N	% censored[a]
East (longitude > -68°)	>191[b] (1st quartile = 157)	40	69.2
West (longitude ≤ -68°)	179 (1st quartile = 90)	54	41.3
Hilltop/upperslope	214	32	62.5
Other (flat, depression/lowerslope, midslope)	175	62	46.9
Fire-prone topographic context[c]	108	32	29.7
Intermediate topographic context[c]	169	8	15.2
Fire-resistant topographic context[c]	269	54	72.3
Global	191	94	53.2

[a] "% censored" corresponds to the percentage of stands to which only a minimum age was attributed. These stands were either uneven-aged or consisting of a species that generally doesn't establish after a fire (e.g. balsam fir).
[b] Only an underestimation of the median fire-free interval is available since we only know the minimum age of the older stands (censored data). The first quartile has been added for comparison purposes.
[c] Topographic context characterized within a 8750-m radius. Fire-prone topographic contexts are dominated by south, south-west or west facing slopes. Intermediate topographic contexts are dominated by south-east or north-west facing slopes. Fire-resistant topographic contexts are dominated by north, north-east or east facing slopes.

Appendix 2.1 Nonparametric correlations (Spearman's *Rho*) among covariates tested in the initial survival model. Correlations significant under the 5% threshold are in light grey while correlations significant after Bonferroni correction are in dark grey.

				var #	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
Vegetation	Stand type[a] (nominal)	Mixed	local scale	1	1.000																			
		Coniferous	local scale	2	-0.310	1.000																		
	Bioclimatic domain[b] (nominal)	balsam fir - white birch	broad scale	3	0.214	-0.199	1.000																	
		black spruce - pleurozium	broad scale	4	-0.214	0.199	-1.000	1.000																
Geography	Longitude (continuous, decimal degrees)		broad scale	5	0.110	-0.019	-0.041	0.041	1.000															
	Latitude (continuous, decimal degrees)		broad scale	6	-0.248	0.243	-0.860	0.860	0.152	1.000														
	Distance from Saint-Lawrence River (continuous, meters)		broad scale	7	-0.252	0.193	-0.631	0.631	-0.546	0.663	1.000													
Physiography and Topography	Surficial deposit[c] (nominal)	rocky outcrop	local scale	8	-0.048	-0.008	0.002	-0.002	-0.173	-0.008	0.030	1.000												
		thin till	local scale	9	0.103	-0.082	0.180	-0.180	0.056	-0.175	-0.185	-0.467	1.000											
		thick till	local scale	10	-0.099	0.147	-0.251	0.251	0.057	0.186	0.165	-0.359	-0.296	1.000										
		glaciofluvial	local scale	11	0.041	-0.044	0.041	-0.041	0.093	0.026	0.012	-0.346	-0.286	-0.220	1.000									
	Slope aspect[c] (continuous, [x,y])	west-east axis (x)	local scale	12	-0.004	-0.008	-0.023	0.023	0.033	0.038	0.042	-0.054	-0.001	0.034	0.035	1.000								
		south-north axis (y)	local scale	13	-0.061	0.102	-0.175	0.175	-0.072	0.118	0.180	0.171	-0.194	0.048	-0.037	-0.121	1.000							
	Position on the slope[c] (nominal)	hilltop/upperslope	local scale	14	-0.018	0.032	-0.162	0.162	-0.057	0.087	0.030	0.137	0.163	-0.129	-0.079	0.036	0.094	1.000						
		midslope	local scale	15	0.091	-0.196	0.088	-0.088	-0.009	-0.105	-0.185	0.119	0.047	-0.080	-0.123	0.161	-0.053	-0.416	1.000					
		depression/lowerslope	local scale	16	-0.096	0.132	0.096	-0.096	0.004	-0.029	0.165	0.105	-0.044	-0.011	-0.070	-0.224	0.027	-0.294	-0.301	1.000				
		flat	local scale	17	0.006	0.058	-0.007	0.007	0.067	0.047	0.012	-0.368	-0.184	0.233	0.444	-0.011	-0.067	-0.355	-0.364	-0.257	1.000			
	Mean waterbreak distance[d] (continuous, meters)		intermediate	18	0.019	0.214	-0.038	0.038	0.080	-0.102	-0.166	0.056	0.122	0.080	-0.295	0.035	0.142	0.141	-0.101	0.042	-0.078	1.000		
	Drainage[c] (ordinal: from 1(excessive) to 6 (organic))		local scale	19	0.078	0.245	0.021	-0.021	0.016	0.033	0.077	-0.274	0.077	0.170	0.036	0.083	0.081	-0.243	-0.232	-0.043	0.176	0.084	1.000	
	Elevation (continuous, meters)		local scale	20	-0.130	0.130	-0.357	0.357	-0.309	0.424	0.661	0.189	0.032	-0.054	-0.222	0.100	0.216	0.142	-0.004	-0.048	-0.103	-0.058	0.198	1.000

[a] stands composed of 25-50% of either decidous or resinous tree (basal area) were characterized as mixed while stands with over 75% of resinous trees were characterized as resinous.Our sample included no stands with more than 75% of decidous trees.

[b] Robitaille and Saucier (1998)

[c] Evaluated following the protocol used in Quebec's provincial forest inventories (Saucier et al. 1994)

[d] The mean waterbreak distance considered the eight nearest waterbodies represented on a 1 : 250 000 topographic map (Larsen 1997)

Appendix 2.2 Nonparametric correlations (Spearman's *Rho*) among covariates[a] of the second survival model. Correlations significant under the 5% threshold are in light grey while correlations significant after Bonferroni correction are in dark grey.

Variable	longitude	hilltop/upperslope	x93	x250	x500	x750	x1000	x1250	x1500	x2000	x2500	x3000	x3500	x4000	x4500	x5000	x6250	x7500	x8750	x10000	x12500	x15000
longitude	1.000																					
hilltop/upperslope	-0.059	1.000																				
x93	-0.047	0.108	1.000																			
x250	-0.034	0.159	0.921	1.000																		
x500	0.123	0.155	0.610	0.686	1.000																	
x750	0.094	0.103	0.453	0.506	0.717	1.000																
x1000	-0.078	-0.022	0.337	0.387	0.499	0.700	1.000															
x1250	0.016	0.105	0.311	0.352	0.445	0.618	0.812	1.000														
x1500	0.034	0.002	0.290	0.287	0.404	0.580	0.661	0.831	1.000													
x2000	-0.005	0.082	0.206	0.139	0.247	0.312	0.463	0.637	0.650	1.000												
x2500	0.050	0.125	0.155	0.153	0.297	0.323	0.398	0.573	0.616	0.822	1.000											
x3000	-0.025	0.115	0.201	0.214	0.221	0.297	0.310	0.436	0.403	0.561	0.553	1.000										
x3500	-0.060	0.104	0.186	0.164	0.150	0.220	0.241	0.376	0.332	0.590	0.512	0.864	1.000									
x4000	-0.014	-0.030	0.006	0.008	0.044	0.128	0.181	0.301	0.298	0.504	0.603	0.628	0.669	1.000								
x4500	-0.024	0.059	0.053	0.049	0.089	0.120	0.145	0.219	0.286	0.350	0.519	0.478	0.550	0.769	1.000							
x5000	-0.024	0.041	0.060	0.012	0.040	0.075	0.097	0.171	0.230	0.422	0.471	0.480	0.619	0.786	0.931	1.000						
x6250	-0.012	-0.060	0.104	0.084	-0.004	0.017	0.086	0.112	0.176	0.311	0.315	0.225	0.316	0.494	0.521	0.587	1.000					
x7500	0.001	-0.047	0.057	0.035	0.031	0.012	0.028	0.074	0.091	0.211	0.250	0.256	0.272	0.346	0.367	0.412	0.709	1.000				
x8750	0.062	0.097	0.078	0.117	0.112	0.095	0.123	0.207	0.230	0.280	0.325	0.355	0.353	0.423	0.418	0.413	0.607	0.739	1.000			
x10000	0.057	0.002	-0.017	0.029	0.061	0.063	0.126	0.107	0.152	0.145	0.198	0.161	0.116	0.244	0.297	0.244	0.342	0.461	0.606	1.000		
x12500	0.189	0.068	0.032	0.047	0.074	0.063	0.136	0.110	0.075	0.174	0.220	0.124	0.107	0.169	0.200	0.147	0.372	0.466	0.492	0.616	1.000	
x15000	0.168	0.090	0.152	0.172	0.108	0.123	0.156	0.121	0.088	0.144	0.160	0.061	0.097	0.147	0.154	0.105	0.304	0.279	0.378	0.469	0.745	1.000
y93	-0.239	-0.014	-0.066	-0.087	-0.154	-0.185	-0.119	-0.126	-0.131	-0.044	-0.129	0.020	0.048	-0.093	-0.110	-0.104	-0.095	-0.191	-0.098	0.004	-0.070	-0.140
y250	-0.160	-0.049	-0.055	-0.055	-0.087	-0.141	-0.113	-0.129	-0.068	-0.082	-0.055	0.049	0.028	-0.087	-0.011	-0.057	-0.094	-0.203	-0.078	0.034	-0.015	-0.091
y500	-0.091	-0.005	-0.082	-0.071	-0.053	-0.116	-0.116	-0.138	-0.095	-0.146	-0.098	-0.006	-0.111	-0.182	-0.096	-0.140	-0.093	-0.147	-0.125	0.078	0.048	-0.012
y750	-0.088	0.011	-0.108	-0.135	-0.135	-0.048	-0.091	-0.113	-0.069	-0.162	-0.146	0.002	-0.127	-0.207	-0.139	-0.186	-0.127	-0.142	-0.126	0.110	0.079	0.055
y1000	-0.028	0.092	-0.077	-0.134	-0.084	-0.048	-0.026	-0.076	-0.046	-0.023	-0.080	-0.015	-0.102	-0.211	-0.151	-0.183	-0.191	-0.200	-0.169	0.067	0.054	0.009
y1250	-0.037	0.153	-0.232	-0.252	-0.195	-0.183	-0.139	-0.028	-0.008	-0.001	-0.009	-0.053	-0.091	-0.131	-0.055	-0.077	-0.221	-0.222	-0.142	0.068	0.064	-0.023
y1500	-0.034	0.115	-0.255	-0.237	-0.185	-0.171	-0.200	-0.078	-0.049	-0.040	-0.037	-0.152	-0.169	-0.154	-0.062	-0.096	-0.266	-0.299	-0.210	0.062	0.084	-0.031
y2000	0.036	0.168	-0.166	-0.217	-0.240	-0.150	-0.149	-0.044	-0.007	0.006	-0.010	0.051	-0.016	-0.032	-0.051	-0.066	-0.271	-0.201	-0.122	-0.092	-0.082	-0.135
y2500	0.009	0.136	-0.085	-0.126	-0.133	-0.101	-0.141	-0.082	-0.017	0.008	0.035	0.100	-0.014	-0.089	-0.112	-0.086	-0.268	-0.228	-0.155	-0.201	-0.104	-0.147
y3000	-0.129	0.048	0.031	-0.022	-0.120	-0.153	-0.208	-0.175	-0.100	-0.027	0.034	0.053	-0.010	-0.057	-0.134	-0.140	-0.267	-0.216	-0.160	-0.179	-0.099	-0.122
y3500	-0.063	0.016	-0.010	-0.055	0.068	-0.134	-0.213	-0.187	-0.136	-0.074	-0.112	0.038	0.054	-0.012	-0.055	-0.066	-0.163	-0.094	-0.048	-0.062	-0.106	-0.085
y4000	-0.071	-0.017	-0.213	-0.254	-0.297	-0.302	-0.242	-0.228	-0.143	-0.104	-0.107	0.036	0.020	0.074	0.131	0.103	-0.077	-0.016	0.048	0.033	-0.105	-0.145
y4500	-0.079	0.021	-0.117	-0.178	-0.210	-0.218	-0.223	-0.177	-0.093	-0.048	-0.045	0.065	0.003	0.014	0.068	0.046	-0.155	-0.091	-0.033	-0.016	-0.209	-0.188
y5000	-0.082	0.030	-0.115	-0.176	-0.216	-0.224	-0.218	-0.171	-0.095	-0.049	-0.046	0.007	0.005	0.014	0.067	0.048	-0.149	-0.086	-0.027	-0.017	-0.211	-0.191
y6250	0.036	-0.035	-0.061	-0.107	-0.159	-0.094	-0.063	-0.048	0.014	0.006	0.031	0.134	0.140	0.118	0.166	0.154	0.049	0.119	0.138	0.108	-0.064	-0.102
y7500	-0.064	0.094	0.016	-0.032	-0.198	-0.150	-0.131	-0.116	-0.093	-0.069	-0.020	0.067	0.120	0.076	0.149	0.089	-0.024	0.052	-0.003	-0.033	-0.138	-0.151
y8750	-0.090	0.025	-0.028	-0.062	-0.148	-0.096	-0.075	-0.031	-0.006	-0.113	-0.053	-0.022	0.035	0.046	0.135	0.075	-0.053	0.046	0.110	0.128	-0.031	-0.026
y10000	-0.013	-0.031	-0.010	-0.031	-0.054	0.003	-0.035	-0.012	0.052	-0.011	-0.017	0.041	0.105	0.074	0.155	0.131	-0.062	-0.007	0.086	0.134	-0.030	0.010
y12500	0.118	-0.040	-0.052	-0.058	-0.044	0.041	-0.021	0.013	0.113	0.071	0.034	0.034	0.058	0.045	0.158	0.132	-0.088	0.003	0.104	0.115	0.087	0.111
y15000	0.072	-0.006	0.064	0.057	-0.019	0.057	0.009	0.089	0.138	0.032	0.011	0.079	0.097	0.12[illegible]	0.217	0.182	-0.018	0.063	0.167	0.161	0.032	0.177

Variable	y93	y250	y500	y750	y1000	y1250	y1500	y2000	y2500	y3000	y3500	y4000	y4500	y5000	y6250	y7500	y8750	y10000	y12500	y15000
y93	1.000																			
y250	0.904	1.000																		
y500	0.749	0.854	1.000																	
y750	0.666	0.743	0.869	1.000																
y1000	0.510	0.545	0.685	0.785	1.000															
y1250	0.450	0.450	0.537	0.610	0.689	1.000														
y1500	0.377	0.345	0.407	0.472	0.593	0.891	1.000													
y2000	0.236	0.182	0.214	0.327	0.408	0.586	0.600	1.000												
y2500	0.280	0.253	0.296	0.391	0.396	0.528	0.497	0.716	1.000											
y3000	0.265	0.207	0.203	0.272	0.362	0.289	0.328	0.481	0.661	1.000										
y3500	0.258	0.197	0.148	0.205	0.311	0.192	0.235	0.399	0.434	0.754	1.000									
y4000	0.211	0.155	0.113	0.194	0.271	0.315	0.330	0.557	0.522	0.553	0.716	1.000								
y4500	0.208	0.173	0.126	0.190	0.280	0.243	0.265	0.525	0.484	0.562	0.708	0.902	1.000							
y5000	0.215	0.179	0.132	0.197	0.283	0.243	0.258	0.519	0.477	0.560	0.707	0.901	0.999	1.000						
y6250	0.090	0.074	0.047	0.078	0.086	0.118	0.130	0.384	0.325	0.355	0.496	0.598	0.601	0.607	1.000					
y7500	0.112	0.099	0.019	0.022	0.084	0.011	0.013	0.308	0.240	0.373	0.545	0.601	0.601	0.607	0.799	1.000				
y8750	0.117	0.083	-0.012	0.039	0.070	0.159	0.165	0.344	0.237	0.271	0.454	0.545	0.531	0.535	0.633	0.721	1.000			
y10000	0.102	0.089	0.019	0.073	0.130	0.187	0.228	0.377	0.290	0.259	0.453	0.537	0.556	0.550	0.646	0.655	0.847	1.000		
y12500	0.168	0.225	0.146	0.195	0.194	0.279	0.285	0.392	0.361	0.194	0.268	0.370	0.328	0.319	0.432	0.392	0.568	0.651	1.000	
y15000	0.003	0.070	0.036	0.057	0.037	0.067	0.084	0.231	0.154	0.118	0.281	0.315	0.336	0.326	0.387	0.396	0.480	0.501	0.716	1.000

[a]The name of the covariates related to dominant aspect are coded using the prefix *x* or *y*, which respectively indicate the south-north and the south-north axis, and a numeric suffix which indicates the radius of the surrounding neighbourhood, in meter, that was considered.

CHAPITRE 3

THE INFLUENCE OF LANDSCAPE-LEVEL HETEROGENEITY IN FIRE FREQUENCY ON CANOPY COMPOSITION IN THE BOREAL FOREST OF EASTERN CANADA

3.1 Résumé

De grandes portions de paysage ($\approx 10^5$-10^6 ha) ont été préalablement associées à des fréquences de feux variant d'un facteur 3 dans un paysage boréal de l'est du Canada. L'objectif principal de cette étude était donc d'évaluer si cette hétérogénéité de la fréquence des feux génère des patrons observables au niveau de la composition forestière et de la dynamique de la végétation et, plus spécifiquement, de voir si elle influence l'abondance relative des principales espèces en fonction de leur statut successionnel. Nous avons visité 160 placettes circulaires situées en forêt fermée dans un paysage de 1.5 M-ha à l'intérieur desquelles nous avons mesuré la composition de la végétation, l'historique locale des feux (temps écoulé depuis le dernier feu) ainsi que les conditions édaphiques. Nous avons effectué des analyses multivariées (*NMDS, multi-response permutation procedure*) et des comparaisons appariées pour évaluer si la composition de la canopée différait entre les portions de paysage affectées par des fréquences de feux contrastantes, et ce, avant et après avoir extrait la variance expliquée par les facteurs environnementaux locaux incluant le temps depuis le dernier feu. Même si les facteurs environnementaux locaux demeurent prédominants en tant que déterminant de la composition locale des peuplements, nous avons observé des différences significatives au niveau de d'abondances relatives des principales espèces d'arbre. Dans les vieux peuplements, *Picea mariana* est l'espèce la plus abondante dans les zones de forte fréquence des feux tandis qu'*Abies balsamea* est la plus abondante dans les zone de faible fréquence des feux, et ce, avant comme après avoir extrait la variance expliquée par les variables environnementales locales incluant le temps depuis le dernier feu. Les jeunes peuplements ne diffèrent pas au niveau de l'abondance relative des espèces lorsque considérées individuellement, mais présentent une plus grande variabilité dans les zones de faible fréquence des feux. Les zones de faible fréquence des feux permettent donc au principal spécialiste de fin de succession, *A. balsamea*, de supplanter l'omniprésente *P. mariana* en raison du temps depuis le dernier feu généralement plus long. L'influence de l'hétérogénéité de la fréquence des feux à l'échelle du paysage influence donc principalement la structure du paysage en agrégeant les jeunes et les vieux peuplements entre eux, avec de possibles répercussions sur le renouvellement et la répartition spatiale d'habitats d'autres espèces qui leur sont associées. Nos résultats suggèrent aussi que la succession de *P. mariana* vers *A. balsamea* peut se produire longtemps après ce qui est généralement couvert par les reconstitutions dendroécologiques de l'historique des feux dans ce type de paysages boréaux (>200-300 ans).

3.2 Abstract

The objective of this study is to assess whether a 3-fold variation in fire frequency among large patches ($\approx 10^5$-10^6 ha) of boreal forest generates differences canopy composition and vegetation dynamics and, more specifically, whether it influences the relative abundance of species with regard to their typical position along the succession. We sampled 160 circular plots in closed-canopy forest in a 1.5 M-ha landscape located in the boreal forest of eastern Canada (Quebec) in which we measured canopy vegetation composition, local fire history (time since last fire), and edaphic conditions. We conducted multivariate analyses (NMDS, multi-response permutation procedure) and pairwise comparisons to assess whether there were differences in canopy composition between areas of contrasting fire frequency before and after controlling for the influence of local environmental factors. Although local environmental factors remain important determinants of local canopy composition, there are significant differences between areas of contrasting fire frequency in terms of relative species abundance. In old stands, *Picea mariana* is the most abundant species in high fire frequency areas while *Abies balsamea* is the most abundant species in low fire frequency areas both before and after controlling for local environmental factors, including time since fire. Young stands do not differ in terms of individual species relative abundance but show more variability among stands in low fire frequency areas. The low fire frequency areas allow late-successional specialist *A. balsamea* to take dominance over ubiquitous successional generalist *P. mariana* because of the typically longer time elapsed since the last fire. The influence of landscape-level heterogeneity in fire frequency therefore mainly contributes to the landscape structure by aggregating young and old stands throughout the landscape, which may reflect on other species' habitat turnover and spatial distribution. Our results also suggest that succession from *P. mariana* to *A. balsamea* can occur long after what is typically covered by dendroecologically reconstructed fire history in this type of boreal landscapes (>200-300 years).

3.3 Introduction

Natural disturbances are among the most important drivers of the natural dynamics of the boreal forest (Payette, 1992). At every spatial scale, natural disturbance regimes influence species composition and structure. Forest fires, which are usually considered to be the primary disturbance in coniferous boreal forest, set up the foundations of a landscape mosaic within which other processes interact, hence playing a crucial role in structuring communities in space and time (Burton *et al.*, 2008 ; Johnson, 1992). Fire severity, fire type, seasonality, size distribution and fire frequency are all aspects of fire regimes that influence vegetation dynamics in the boreal forest. Fire frequency, which we define as the proportion of the area burned per unit of time, or the reciprocal of the mean fire return interval (Baker, 1995 ; Li, Corns and Yang, 1999 ; Turner *et al.*, 1994), is especially important as it determines the proportions and importance of stands age-classes in the landscape and, in turn, influences the composition and structural attributes that are associated with these age-classes (Brassard *et al.*, 2008 ; De Grandpré, Morissette and Gauthier, 2000 ; Harper *et al.*, 2005). Although there is a large part of stochasticity in all fire regimes, several determinants of fire frequency were singled out in past studies conducted in the boreal forest and range from broad scale factors such as climate, dominant vegetation or land use (Bergeron *et al.*, 2004 ; Bridge, 2001 ; Girardin *et al.*, 2009 ; Lefort, Gauthier and Bergeron, 2003 ; Wein and MacLean, 1983 ; Weir, Johnson and Miyanishi, 2000) to others that are effective at finer scales such as surficial geology (Bergeron *et al.*, 2004 ; Mansuy *et al.*, 2010), position on the slope (Cyr, Gauthier and Bergeron, 2007) or aspect (Gavin, Brubaker and Lertzman, 2003), to name a few. Other physiographic determinants of fire frequency are described at intermediate scales such as distance to firebreaks (Cyr *et al.*, 2005 ; Larsen, 1997), the proportion of wetland (Hellberg, Niklasson and Granström, 2004) or dominant aspect in the surroundings (Cyr, Gauthier and Bergeron, 2007). All of these factors partly explain spatio-temporal variations in frequency and/or size of fires. Considering the importance of local fire history on stands attributes and structure, these determinants are crucial to the understanding of where and when boreal species can be found.

Vegetation communities present prior to a fire partly determine the composition of the post-fire initial cohort as well as the subsequent development of the stand through succession, hence generating ecological feedback from long-term *in situ* fire history (Foster, Knight and Franklin, 1998 ; McCune and Allen, 1985 ; Motzkin *et al.*, 1999). For instance, many species can resprout under some conditions (Perala, 1990 ; Safford, Bjorkbom and Zasada, 1990) or benefit from aerial seedbanks accumulated in serotinous cones that are released after the fire (Rudolph and Laidly, 1990 ; Viereck and Johnson, 1990). These strategies are often used by early-successional specialists and allow them to have a greater chance to re-establish when successive fires occur within short intervals. On the other hand, variable fire severity in the canopy often allows some trees to survive within recently burned areas (Eberhart and Woodard, 1987 ; Kafka, Gauthier and Bergeron, 2001 ; Madoui *et al.*, 2010). If the previous fire-free interval was long, the likelihood of these trees belonging to fire-sensitive, late-successional species is increased, and so is the likelihood of them influencing early development and rate of succession after fire (Johnstone and Chapin Iii, 2006 ; Keeton and Franklin, 2005 ; Wimberly and Spies, 2002).

Using survival analyses, Cyr et al. (2007) showed spatial heterogeneity in fire frequency within a landscape of 15 000 km^2 that is comparable in magnitude to the heterogeneity that is generally observed from one such large landscape to another. A 2-6-fold variation in fire frequency was indeed observed and related to topographic and geographic features. Dominant aspect within a neighbourhood of 4 000 m to

10 000 m was found to generate a fire frequency gradient where areas dominated by south west facing slopes burned up to three times more often than areas dominated by north east facing slopes, with intermediate values in between. Such landscape level heterogeneity in fire frequency, which is independent of fine-scale, bottom-up types of controls, creates a landscape mosaic made up of patches of several thousands of hectares in which the fire regimes differ substantially (Fig. 3.1). This heterogeneity is also most likely permanent despite changes in fire activity that might have occurred in the past since it is caused by permanent features of the physical environment.

The general objective of this study is to assess whether this landscape-level heterogeneity in fire frequency generates discernible patterns in canopy composition. Substantial differences in the age structure at the landscape level are expected because it is the most direct repercussion of any variation in fire frequency. Based on this premise and given the importance of time since fire as one determinant of canopy composition, we first want to assess whether the relative abundance of the dominant tree species differs between contrasting portions of the landscape in terms of fire frequency, especially with regard to the proportions of early- and late-successional specialists. The typically longer fire-free intervals in low fire frequency areas should indeed favour late-successional specialists, and vice versa for the early-successional specialists in a high fire frequency areas, while successional generalists should show a relatively constant abundance among high and low fire frequency areas. Second, we want to evaluate whether this heterogeneity in fire frequency influences the vegetation dynamics itself, i.e. whether differences in composition are primarily due to the fact that the last local fire-free intervals differ or if the **consistently** longer fire-free intervals, repeated over time, may have amplified the differences between these portions of the landscape.

3.4 Methods

3.4.1 Study area and main tree species

The study area covers 15,961 km^2 of boreal forest in eastern Quebec, specifically in the North Shore region, between longitudes 67° W and 69° W and between latitudes 49° N and 50.25° N (Fig. 3.1}. This region has a cold, maritime climate with an average annual temperature of 1.4°C and average precipitation of 1,018 mm, measured in Baie Comeau in the southwest corner of the study area. Precipitation is evenly distributed during the year, and is about 70% rain (Environment Canada, 1996). The topography is moderately rugged with high hills with rounded summits and many rocky escarpments. The highest hills, located in the northeastern part of the area, are just over 700-m high while other sparsely distributed hills reach above 500 m. There are rocky outcrops on slightly more than a third of the total land area, while the rest of the land area consists mainly of shallow tills on sloping areas and deep tills at the bottom of slopes. To a lesser extent, there are sandy glaciofluvial deposits on valley floors (Robitaille and Saucier, 1998).

Black spruce (*Picea mariana* (Mill.) B.S.P.) and balsam fir (*Abies balsamea* (L.) Mill.) are the dominant species, along with white spruce (*Picea glauca* (Moench) Voss) and white birch (*Betula papyrifera* Marsh.). Trembling aspen (*Populus tremuloides* Michx.) and jack pine (*Pinus banksiana* Lamb.) can also be found but in lower abundance. Tamarack (*Larix laricina* (Du Roi) K. Koch) can be found along with *P. mariana* in a few rare hydric stations in the region. The six most common tree species, i.e. all of the above-mentioned species but tamarack, were classified on the basis of their typical position along the successional gradient in this region. This classification is mainly based on their adaptations to fire, shade tolerance, and ability to regenerate under a closed canopy. *Betula papyrifera* and *P. tremuloides* were classified as early-successional specialists because of their ability to disperse over long distances and to use vegetative reproduction in open sites (Perala, 1990 ; Safford, Bjorkbom and Zasada, 1990), as was *P. banksiana* because of its serotinous cones that allow it to successfully re-establish after a fire when already present on a site (Gauthier, Bergeron and Simon, 1993 ; Rudolph and Laidly, 1990). These three species are also shade-intolerant (Humbert *et al.*, 2007), which considerably limits their ability to re-establish under closed canopy. It must be noted however that *B. papyrifera* seems to benefit more often than the others from the gaps created by secondary disturbances to maintain itself as a small component of older stands (Gauthier *et al.*, 2010). When these early-successional specialists make up for the largest part of a young stand, they are typically replaced by *P. mariana, P. glauca* or *A. balsamea* when the initial cohort starts breaking up (Bergeron, 2000 ; De Grandpré, Morissette and Gauthier, 2000). *A. balsamea* is the main late-successional specialist in this system (De Grandpré, Morissette and Gauthier, 2000). It is poorly adapted to fire and is among the most shade-tolerant tree species of the boreal forest (Bakusis and Hansen, 1965). Consequently, it is generally abundant in stands that have not burned for a long time. *P. mariana* is the archetypal generalist on many levels, and is also one from the perspective of succession. Its semi-serotinous cones allow it to re-establish after a fire, and its ability to reproduce vegetatively through layering assure regeneration even in the harshest conditions (Viereck and Johnson, 1990). In late succession stages, *P. mariana* often maintains dominance or at least a strong presence alongside *A. balsamea* in this region (Bouchard, Pothier and Gauthier, 2008 ; De Grandpré, Morissette and Gauthier, 2000 ; Pham *et al.*, 2004), even on mesic sites where *A. balsamea* is considered more competitive (Bakusis and Hansen, 1965). Finally, we also classified *P. glauca* as a generalist from the perspective of succession. It is not particularly well adapted to fire since as its reestablishment depends on surviving seed sources but is nevertheless known to successfully regenerate after a fire especially if it can benefit from a mast year

(Peters, Macdonald and Dale, 2005). It possesses an intermediate shade-tolerance (Humbert *et al.*, 2007) and is usually found as a minor component of stands, alongside any of the above-mentioned species (Galipeau, Kneeshaw and Bergeron, 1997).

3.4.2 Data acquisition

One hundred and sixty 400-m^2 circular plots showing no sign of past anthropogenic disturbance were sampled for canopy vegetation. We did not sampled recently burned sites, i.e. the most recently burned site was burned 47 years prior to the field campaign, or sites that showed signs of past harvesting. All trees with a diameter at breast height (DBH) of 1 cm or more were measured (DBH and height) and species determined. The geographic location, edaphic conditions and local fire history were noted for each station (cf Table 3.1 for complete listing of environmental covariates) and considered as covariates, which may partly explain species composition. We make an important distinction between local fire history and fire frequency areas. Through the analysis described below, we tried to control for the influence of the number of years elapsed since the last fire, as a local determinant of canopy composition, and areas of contrasting fire frequency, as a potential broader-scale determinant of canopy composition. Our main focus in this study is therefore the fire frequency areas while time since fire is considered as a covariate of which we want to control the influence along with that of other local environmental determinants of vegetation composition. This allow us to know whether the differences in composition are only due to the fact that the local fire-free intervals differ or if the **consistently** longer fire-free intervals, repeated over time, may have amplified the differences between these portions of the landscape.

For each plot that was sampled for quantifying canopy vegetation, we also attempted to date the last fire event by counting the rings of 10-15 of the dominant trees that were found outside but in close vicinity to the sampled plot (less than 30 m) using either cores or cross-sections. For that specific purpose, we favoured the species that were more likely to originate from a fire event. In decreasing order of preference, we selected *P. banksiana*, *P. tremuloides*, *B. papyrifera*, *P. mariana*, *P. glauca* and *A. balsamea*. The age of the oldest tree at each location was used as an indication of the time since fire. This indicator was deemed sufficiently reliable and considered as a known fire-free interval if a 20-year interval included at least 60% of the trees, especially if the growth patterns suggested open canopy conditions at establishment dates, while only a minimum time since fire was assigned when these conditions were not met. However, a visual examination of each stand's age structure suggested that a 20-year interval was too restrictive in the case of some of the older stands that seemed in fact even-aged, probably because of an increasing imprecision of dating with stand age (DesRochers and Gagnon, 1997 ; Parent, Morin and Messier, 2000). We thus chose to extend it to 30 years for stands where the older tree age was over 200 years. A minimum age was also assigned to stands where the only trees that could be dated were primarily of one species that usually does not establish themselves directly after a fire such as *A. balsamea*, independently of their age structure.

Stands were then classified as young/old based on whether they were younger or older than 150 years old, which roughly corresponds to the age at which stands break up (De Grandpré *et al.*, 2009 ; Gauthier *et al.*, 2010). The age-class distribution at the landscape level was also assessed.

Cyr et al. (2007) showed an influence of dominant aspect on fire frequency when characterized within a neighbourhood delimited by 4 000 to 10 000-m radii (5 027 - 31 416 ha) as well as an influence of longitude. Although the estimation of mean fire interval (1 / mean fire frequency) for the entire landscape under study is 226 years (Cyr, 2011), a 2 to 6-fold fold variation in fire frequency induced by these environmental factors (Cyr, Gauthier and Bergeron, 2007) creates a mosaic of landscape subunits with distinct fire regimes. The peak statistical association with dominant aspect was observed when characterized within an 8 750-m neighbourhood radius. For the purpose of the present study, we therefore used the survival model obtained in Cyr et al. (2007) to assign a relative fire frequency to each location based on the dominant aspect within an 8 750-m neighbourhood radius and on longitude, therefore providing an estimate that is independent of present vegetation. Then, we partitioned the landscape into two classes delimited by the average value of fire frequency for the entire landscape (Fig. 3.1). Using this map, the belonging to an above- or below-average fire frequency regime, referred to as high and low fire frequency areas, was determined. The mean fire intervals for high and low fire frequency areas are 164 and 521 years, respectively.

3.4.3 Data analysis

As a contextual preliminary analysis, we compared the age-class distribution at the landscape level between areas of contrasting fire frequency, both visually and by means of a chi-square contingency analysis testing for differences in the proportion of stands for which only a minimum estimate of the time elapsed since last fire is known (censored intervals).

To describe canopy composition and compare among areas of contrasting fire frequency and age-classes, we performed a non-metric multidimentional scaling ordination [NMDS, (Kruskal, 1964)] based on Bray-Curtis distance matrix (Legendre and Legendre, 1998) between sampled plots (n=161). The distance matrix was calculated from relative basal area of stems with DBH larger than 1 cm. We used relative basal area to control for variations in absolute basal area that are related to time since last fire. NMDS was performed with R version 2.9.0 (R Development Core Team 2009) using the metaMDS function in the VEGAN package (Oksanen *et al.*, 2009). It was determined that a number of three dimensions provided the best compromise between a low stress factor (k) and the interpretability of the visual output. Aside from the number of dimensions, which was determined manually, metaMDS initiated the iterative process at random starts, and selected among similar solutions with smallest stresses after submitting the raw data and/or the dissimilarity matrix to the most appropriate transformations (e.g. scaling and rotation). We used the multi-response permutation procedure (MRPP), also in the VEGAN package to test for differences in composition between fire frequency areas using each age-class (young/old) as strata within which permutations are restricted. A series of ANOVA-like permutation tests were subsequently performed on each species to compare the relative abundance of individual species. Local environmental covariates, including time since the last fire, were fitted as vectors or centroids depending on whether they were continuous or nominal covariates, respectively. Only significant associations under the 0.05 probability threshold are displayed on the ordination, which were also assessed based on random permutations.

To control for collinearity between fire frequency areas and local environmental covariates, we extracted the variance explained by a matrix of all local environmental covariates using a multiple linear regression within each age-class and analyzed the residuals between fire frequency areas by means of another series of ANOVA-like permutation tests. No variable selection was performed during these regressions as the objective was to control for the most locally induced variability possible (cf Appendix 3.1 for details). All permutation-based tests were based on 10 000 random permutations and the significance thresholds for all series of univariate ANOVA-like permutation tests were adjusted for multiple comparisons using Holm's procedure (Holm, 1979).

3.5 Results

3.5.1 Age-class distribution at the landscape level

An approximately 3-fold variation in mean fire-free intervals between areas of contrasting fire frequency produced considerable differences in age-class distribution at the landscape level (Fig. 3.2). The relative proportion of young stands indeed seems substantially higher in high fire frequency areas when compared with low fire frequency areas, and inversely for the proportions of old stands. This general appearance of the distributions, however, must be complemented by a comparison of the proportions of stands for which only a minimum age is known. This comparison confirms a significant difference between fire frequency areas as the proportion of stands for which only a minimum age is known is about 22% higher in low fire frequency areas ($chi^2 = 4.585$; $P = 0.0323$; $df = 1$) than in high fire frequency areas.

3.5.2 Comparison of canopy composition among fire-frequency areas and age-class groups

The NMDS ordination (Fig. 3.3) shows a relatively clear distinction between the canopy tree composition of young and old stands located in either high or low fire frequency areas. The 50% confidence interval ellipses show that the fire frequency areas can be better deciphered along the first axis of the ordination, while the age-classes and most other local environmental factors are more related to the second axis. Differences between fire frequency areas are confirmed by the multi-response permutation procedure conducted using age-classes as strata constraining random permutations ($P<0.0001$). While the old stands' 50% confidence interval ellipses distinguish themselves both on the basis of their location (composition) and spread (variability in composition) in the coordinate system, the difference relative to fire frequency areas in young stands appears to be more related to the variability in stand composition as the ellipses largely overlap and mostly differ in size.

Picea mariana and *A. balsamea* are the dominant species in this landscape. All species are present in young stands while there is an almost complete exclusion of *P. banksiana* and *P. tremuloides* in old stands (Fig. 3.4a). Young and old stands located in high fire frequency areas are more similar than their counterparts located in low fire frequency areas (Fig. 3.3a). *Picea mariana* maintains a strong presence in all groups while *A. balsamea* is mostly confined to old stands.

The first series of non-parametric ANOVA-like comparisons of the relative abundance of individual species within each age-class revealed that significant differences between fire frequency areas could only be detected in old stands. *Abies balsamea* could indeed be found in greater relative abundance in low fire frequency areas and so was *P. Glauca,* although it made up only a minor part of the forest landscape, while *P. mariana* had greater abundance in the high fire frequency areas (Fig. 3.4, and Appendix 3.2 for detailed results).

The coordinate system of the NMDS, however, is significantly correlated with local environmental covariates that are known to affect species composition. The first ordination axis was negatively correlated with slope and deep tills, and positively correlated with glaciofluvial deposits, while the second axis was positively correlated with latitude, elevation, the age of the oldest tree and censorship. A second series of non-parametric ANOVA-like permutations on residual values of species' relative abundances was thus conducted after controlling for the influence of local environmental covariates, including time since last fire. It confirmed a significantly lower proportion of *P. mariana* in old stands located in low fire frequency areas, while *A. balsamea* is more abundant in old forests located in low fire frequency areas (Fig. 3.4; Appendix 3.2). No significant difference in the relative abundance of *P. glauca* could be detected after controlling for the influence of local environmental covariates.

No significant differences in the relative abundances of individual species were detected in young stands either before or after controlling for the influence of local environmental covariates (Fig. 3.4), despite significant differences in overall composition (Fig. 3.3). The most notable trend between young stands of contrasting fire frequency, however, is that *P. mariana* seems more likely to be found in high fire frequency areas, which appears to affect the variability in stand composition, as suggested by the size of the 50% confidence interval ellipses (Fig. 3.3).

3.6 Discussion

The first and most obvious repercussion of contrasting fire frequency at this intermediate scale is observed on the age structure at the landscape level. As the fire-free intervals are generally longer in low fire frequency areas, the proportion of old stands is much higher. Considering the number of stands for which only a minimum age is known, the actual tail of the distribution is longer than it appears and thus contrasts even more with the one observed in high fire frequency areas. This may explain in large part the differences between high and low fire frequency areas that were observed in old stands even after controlling for local environmental factors.

3.6.1 Species' relative abundance in old stands – Stands exceeding 150 years of age make up the vast majority of this landscape. This explains why the most abundant species in this landscape are those that have the ability to thrive in late succession: *A. balsamea* and *P. mariana*. While *A. balsamea* is without contest the main late-successional specialist in this region of the boreal forest, mainly because of the ability of its seedlings to withstand the heaviest shade conditions in order to take the opportunity to fill the gaps that are eventually created in the canopy, the archetypal boreal generalist *P. mariana* is even more abundant as it can grow on a wider variety of conditions. Our results as well as results from previous studies (Bouchard, Pothier and Gauthier, 2008 ; De Grandpré, Morissette and Gauthier, 2000) suggest that late succession stands of this region usually converge towards either *P. mariana* or *A. balsamea* dominated stands or a mixture of both (Gauthier *et al.*, 2010). Whether an old stand will be dominated by *P. mariana* or *A. balsamea* appears to be largely determined by edaphic conditions (De Grandpré, Morissette and Gauthier, 2000), which is confirmed in our study by a strong association of *A. balsamea* with deep tills. However, the generally longer fire-free intervals that characterize low fire frequency areas appear to be an additional determinant of this species' relative abundance in old forest.

We currently do not have a very clear understanding of what happens in old stands as the time since fire exceeds what can typically be measured by dendroecological dating of fire events (200-300 years), which of course limits our knowledge of stand dynamics in the tail of such a long chronosequence. However, we know that the influence of smaller scale disturbances such as insects and windthrows become very important in stand dynamics and influence species' dominance (Bouchard, Pothier and Gauthier, 2008 ; De Grandpré, Morissette and Gauthier, 2000 ; Gauthier *et al.*, 2010). Pham et al. (2004) showed in a study on gap dynamics in this region that self-replacement of these two species is most common in old stands when they dominate. Reciprocal replacement, however, is common when both species are present, with a slight advantage to *A. balsamea*. At the stand level, relatively shorter fire-free intervals in high fire frequency areas may truncate succession on some sites where *A. balsamea* would normally become dominant, allowing a higher relative abundance of *P. mariana*. This supports the idea of a generally increasing proportion of *A. balsamea* as stands get older, although this process is not irreversible and might follow a "two-steps forward, one step back" kind of dynamics. A succession from *P. mariana* towards *A. balsamea* can therefore require many successive cohorts and could occur gradually and slowly, long after what is covered by typical dendroecological analyses.

3.6.2 Species' relative abundance in young stands - In the case of old forest stands, the late successional specialist *A. balsamea* showed it is favoured by a generally longer time since fire. However, the reverse hypothesis suggesting that early succession species, i.e. *P. tremuloides*, *B. papyrifera* and *P. banksiana*, would be favoured by higher fire frequency at this intermediate spatial scale is not supported. No clear trends in relative abundance of early successional specialists could be detected. This result shows that the availability of propagules for the early successional tree species is not limited by the scarcity of other young stands in low fire frequency areas, at least not more that in high fire frequency areas. Long-distance, massive seed dispersal certainly explains this in large part for intolerant hardwood species such as *P. tremuloides* and *B. papyrifera* (Perala, 1990 ; Safford, Bjorkbom and Zasada, 1990). The same mechanism cannot be invoked in the case of *P. banksiana* because it is known to disperse only over relatively short distances (Rudolph and Laidly, 1990). Its strong association with sandy deposits possibly made it the least likely to be affected by landscape-level heterogeneity in fire frequency, especially considering that anecdotal observations of multiple fire scars in such stands (personal observations) may indicate that a distinct, less severe but more frequent fire regime may be at work in some exceptional stands (see also Smirnova, Bergeron and Brais, 2008)

Although we could not detect significant differences in individual species' relative abundance in young stands between areas of contrasting fire frequency, the **overall** species composition differs, but mainly in terms of variability. The fact that relatively shorter fire-free intervals in high fire frequency areas may favour *P. mariana* in sites where *A. balsamea* would normally become dominant by truncating succession may also increase the likelihood of *P. mariana* reestablishment after a fire event. Pre-fire composition indeed influences the outcome of early establishment in recently burned stands (McCune and Allen, 1985 ; Motzkin *et al.*, 1999), hence explaining the stronger similarity in stand composition between young and old stands in high fire frequency areas than in low fire frequency areas (e.g. Greene *et al.*, 1999). *P. mariana* indeed benefits more often from local aerial seed banks provided by its semi-serotinous cones. Comparatively, *A. balsamea* is more common in low fire frequency areas but is poorly adapted to fire and almost never successfully re-establishes right after one, hence leaving an open site for early successional species. Furthermore, Gauthier et al. (2010) showed that stands that start succession with intolerant hardwoods seem to be more prone to a faster reestablishment and future dominance of *A. balsamea*. It is also possible that in the unlikely situation where successive fire events should occur in low fire frequency areas, a higher proportion of hardwoods might be favourable to the survival of some *A. balsamea* individuals by decreasing fire severity in the canopy (Kafka, Gauthier and Bergeron, 2001), which could also contribute to a faster reestablishment of this late-successional specialist (Bergeron *et al.*, 2004).

3.6.3 Conclusions

The landscape-level heterogeneity in fire frequency influences the distribution and relative importance of the two main tree species in this landscape, i.e. *P. mariana* and *A. balsamea*. We suggest that the higher relative importance of *A. balsamea* in low fire frequency areas can be in large part explained by the typically longer local fire-free intervals that cannot be accounted for in dendroecologically-based chronosequences. Stands older than 200-300 years, for which only a minimum age can be determined, are indeed often pooled in an open age class (e.g. Bouchard, Pothier and Gauthier, 2008 ; Christensen and Peet, 1984 ; De Grandpré, Morissette and Gauthier, 2000). Our results show that the slow replacement of *P. mariana* with *A. balsamea* on suitable sites may take much longer than that amount of time (200-300 years) because of the combined effects of the longevity of *P. mariana* and the non-monotonous aspect of the replacement process (Gauthier *et al.*, 2010 ; Pham *et al.*, 2004). This type of canopy succession would be truncated more often in high fire frequency areas. Therefore, this mechanism is not an effect of landscape-level heterogeneity in fire frequency *per se* as the local fire history remains the main determinant of canopy composition. However, landscape-level heterogeneity in fire frequency can be consider as an indirect determinant of stand-scale canopy composition, as it determines where in the landscape such a long successional process is more likely to be uninterrupted by a fire event.

Moreover, the landscape-level heterogeneity in fire frequency is an important driver of landscape structure as it contributes to an aggregation of young and old stands across the landscape. Such an aggregation may have important repercussions on other species such as the spruce budworm (*Choristoneura fumiferana*) whose epidemic dynamics is intimately related to its preferred host *A. balsamea* and its relative importance at the landscape level (Bergeron and Leduc, 1998 ; Campbell, MacLean and Bergeron, 2008 ; Morin, 1994). The ecological and socio-economical importance of this defoliator (MacLean *et al.*, 2002) alone could thus justify the incorporation the landscape-level heterogeneity in fire frequency in future models of this landscape's natural dynamics as a potential source of feedback at the landscape level. Other species associated with either stand types could also be affected, notably understorey species whose dispersion potential is often limited.

Secondly, our results suggest that there may also be an influence of fire frequency areas on the variability in species composition in early succession. The smaller variability in stand composition that was observed in young stands located in high fire frequency areas could indeed be explained in part by the stronger prevalence of *P. mariana* in old stands, which would favour the reestablishment of the same species to the detriment of other early successional species.

Finally, our main predictions that early- and late-successional specialists would be favoured by fire frequency areas in which their preferred conditions (young vs. old stands) are found more often were shown to be partly right. As predicted, late-successional *A. balsamea* is favoured by low fire frequency areas, but the relative abundance of early-successional specialists *P. banksiana, P. tremuloides* and *B. papyrifera* does not show the opposite trend. The bottom line is that local environmental factors, including local fire history, remain the predominant determinants of stand composition. However, the aggregation of young and old stands within the landscape may play an important role in the population dynamics of many floral and faunal populations that are associated with either one of these two distinctive states of boreal stand development. Within a metapopulation framework, heterogeneity in fire frequency in such large patches of landscape reflects on habitat turnover and may be an important parameter to incorporate into future studies.

3.7 References

Baker, W.L. 1995. «Longterm response of disturbance landscapes to human intervention and global change». *Landscape Ecology*, vol. 10, no 3, p. 143-159.

Bakusis, E.V., and H.S. Hansen. 1965. *Balsam fir: a monographic review.* Minneapolis, US.: The University of Minnesota Press.

Bergeron, Y., S. Gauthier, M. Flannigan and V. Kafka. 2004. «Fire regimes at the transition between mixedwood and coniferous boreal forest in northwestern Quebec». *Ecology*, vol. 85, no 7, p. 1916-1932.

Bergeron, Yves. 2000. «Species and stand dynamics in the mixed woods of Quebec's southern boreal forest.». *Ecology*, vol. 81, no 6, p. 1500-1516.

Bergeron, Yves, and Alain Leduc. 1998. «Relationships between change in fire frequency and mortality due to spruce budworm outbreak in the southeastern Canadian boreal forest.». *Journal of Vegetation Science*, vol. 9, no 4, p. 493-500.

Bouchard, M., D. Pothier and S. Gauthier. 2008. «Fire return intervals and tree species succession in the North Shore region of eastern Quebec». *Canadian Journal of Forest Research*, vol. 38, no 6, p. 1621-1633.

Brassard, B. W., H. Y. H. Chen, J. R. Wang and P. N. Duinker. 2008. «Effects of time since stand-replacing fire and overstory composition on live-tree structural diversity in the boreal forest of central Canada». *Canadian Journal of Forest Research*, vol. 38, no 1, p. 52-62.

Bridge, S.R.J. (2001). Spatial and temporal variations in the fire cycle across Ontario. Ontario Ministry of Natural Resources - Northeast Science & Technology

Burton, P. J., M. A. Parisien, J. A. Hicke, R. J. Hall and J. T. Freeburn. 2008. «Large fires as agents of ecological diversity in the North American boreal forest». *International Journal of Wildland Fire*, vol. 17, no 6, p. 754-767.

Campbell, E. M., D. A. MacLean and Y. Bergeron. 2008. «The severity of budworm-caused growth reductions in balsam fir/spruce stands varies with the hardwood content of surrounding forest landscapes». *Forest Science*, vol. 54, no 2, p. 195-205.

Christensen, N. L., and R. K. Peet. 1984. «Convergence during secondary forest succession». *Journal of Ecology*, vol. 72, no 1, p. 25-36.

Cyr, D. 2011. «Cycle des feux, vieilles forêts et aménagement en forêt boréale de l'est du Canada - PhD Thesis». Montreal, Université du Québec à Montréal.

Cyr, D., Y. Bergeron, S. Gauthier and A. Larouche. 2005. «Are the Old-Growth Forests of the Clay Belt Part of a Fire-Regulated Mosaic?». *Canadian Journal of Forest Research*, vol. 35, no 1, p. 65-73.

Cyr, D., S. Gauthier and Y. Bergeron. 2007. «Scale-dependent determinants of heterogeneity in fire frequency in a coniferous boreal forest of eastern Canada». *Landscape Ecology*, vol. 22, no 9, p. 1325-1339.

De Grandpré, L., S. Gauthier, C. Allain, D. Cyr, S. Périgon, A.T. Pham, D. Boucher, J. Morisette, G. Reyes, T. Aakala and T. Kuuluvainen. 2009. «Towards an ecosystem approach to managing the boreal forest in the North Shore region». In *Ecosystem management in the boreal forest*, Les Presses de l'Université du Québec, S. Gauthier, M.-A. Vaillancourt, A. Leduc, L. De Grandpré, D. Kneeshaw, H. Morin, P. Drapeau et Y. Bergeron, p. 229-255. Quebec: Les Presses de l'Université du Québec.

De Grandpré, Louis, Jacques Morissette and Sylvie Gauthier. 2000. «Long-term post-fire changes in the northeastern boreal forest of Quebec.». *Journal of Vegetation Science*, vol. 11, no 6, p. 791-800.

DesRochers, A., and R. Gagnon. 1997. «Is ring count at ground level a good estimation of black spruce age?». *Canadian Journal of Forest Research*, vol. 27, no 8, p. 1263-1267.

Eberhart, K.E., and P.M. Woodard. 1987. «Distribution of residual vegetation associated with large fires in Alberta». *Canadian Journal of Forest Research*, vol. 17, no 10, p. 1207-1212.

Environment Canada. 1996. *Canadian climate normals 1947-1996*: Canadian Climate Program. Environment Canada. Atmospheric Environment Service.

Foster, D. R., D. H. Knight and J. F. Franklin. 1998. «Landscape Patterns and Legacies Resulting From Large, Infrequent Forest Disturbances». *Ecosystems*, vol. 1, no 6, p. 497-510.

Galipeau, C., D. Kneeshaw and Y. Bergeron. 1997. «White spruce and balsam fir colonization of a site in the southeastern boreal forest as observed 68 years after fire». *Canadian Journal of Forest Research*, vol. 27, no 2, p. 139-147.

Gauthier, S., Y. Bergeron and J.P. Simon. 1993. «Cone serotiny in jack pine: ontogenetic, positional, and environmental effects.». *Canadian Journal of Forest Research*, vol. 23, no 3, p. 394-401.

Gauthier, S., D. Boucher, J. Morissette and L. De Grandpré. 2010. «Fifty-seven years of composition change in the eastern boreal forest of Canada». *Journal of Vegetation Science*, vol. 21, no 4, p. 772-785.

Gavin, D.G., L.B. Brubaker and K. Lertzman. 2003. «Holocene fire history of a coastal temperate rain forest based on soil charcoal radiocarbon dates». *Ecology*, vol. 84, no 1, p. 186-201.

Girardin, M. P., A. A. Ali, C. Carcaillet, M. Mundelsee, I. Drobyshev, C. Hély and Y. Bergeron. 2009. «Heterogeneous response of circumboreal wildfire risk to climate change since the early 1900s». *Global Change Biology*, vol. 15, no 11, p. 2751-2769.

Greene, D F, J C Zasada, L Sirois, D Kneeshaw, H Morin, I Charron and M J Simard. 1999. «A review of the regeneration dynamics of North American boreal forest tree species.». *Canadian Journal of Forest Research*, vol. 29, no 6, p. 824-839.

Harper, K.A., Y. Bergeron, P. Drapeau, S. Gauthier and L. De Grandpré. 2005. «Structural development following fire in black spruce boreal forest». *Forest Ecology and Management*, vol. 206, no 1-3, p. 293-306.

Hellberg, E., M. Niklasson and A. Granström. 2004. «Influence of landscape structure on patterns of forest fires in boreal forest landscapes in Sweden». *Canadian Journal of Forest Research*, vol. 34, p. 332-338.

Holm, S. 1979. «A Simple Sequentially Rejective Multiple Test Procedure». *Scandinavian Journal of Statistics* vol. 6, p. 65-70.

Humbert, L., D. Gagnon, D. Kneeshaw and C. Messier. 2007. «A shade tolerance index for common understory species of northeastern North America». *Ecological Indicators*, vol. 7, no 1, p. 195-207.

Johnson, E.A. (1992). Fire and vegetation dynamics: Studies from the North American boreal forest. New York, Cambridge University Press

Johnstone, J. F., and F. S. Chapin Iii. 2006. «Fire interval effects on successional trajectory in boreal forests of northwest Canada». *Ecosystems*, vol. 9, no 2, p. 268-277.

Kafka, V., S. Gauthier and Y. Bergeron. 2001. «Fire Impacts and Crowning in the Boreal Forest: Study of a Large Wildfire in Western Quebec». *International Journal of Wildland Fire*, vol. 10, no 2, p. 119-127.

Keeton, W.S., and J.F. Franklin. 2005. «Do remnant old-growth trees accelerate rates of succession in mature Douglas-fir forests?». vol. 75, no 1, p. 103-118.

Kruskal, J.B. 1964. «Multidimensional scaling by optimizing goodness of fit to a nonmetric hypothesis». *Psychometrika*, vol. 29, no 1, p. 1-27.

Larsen, C P S. 1997. «Spatial and temporal variations in boreal forest fire frequency in northern Alberta.». *Journal of Biogeography*, vol. 24, no 5, p. 663-673.

Lefort, Patrick, Sylvie Gauthier and Yves Bergeron. 2003. «The influence of fire weather and land use on the fire activity of the lake Abitibi Area, Eastern Canada.». *Forest Science.*, vol. 49, no 4, p. 509-521.

Legendre, Pierre, and Louis Legendre. 1998. *Numerical Ecology*, 2nd English. New York: Elsevier.

Li, C., I. G. W. Corns and R. C. Yang. 1999. «Fire frequency and size distribution under natural conditions: A new hypothesis». *Landscape Ecology*, vol. 14, no 6, p. 533-542.

MacLean, D.A., K.P. Beaton, K.B. Porter, W.E. MacKinnon and M.G. Budd. 2002. «Potential wood supply losses to spruce budworm in New Brunswick estimated using the spruce budworm decision support system». *The Forestry Chronicle*, vol. 78, no 5, p. 739-750.

Madoui, A., A. Leduc, S. Gauthier and Y. Bergeron. 2010. «Spatial pattern analyses of post-fire residual stands in the black spruce boreal forest of western Quebec». *International Journal of Wildland Fire*, vol. 19, no 8, p. 1110-1126.

Mansuy, N., S. Gauthier, A. Robitaille and Y. Bergeron. 2010. «The effects of surficial deposit-drainage combinations on spatial variations of fire cycles in the boreal forest of eastern Canada». *International Journal of Wildland Fire*, vol. 19, no 8, p. 1083-1098.

McCune, B., and T.F.H. Allen. 1985. «Will similar forests develop on similar sites?». *Canadian Journal of Botany*, vol. 63, no 3, p. 367-376.

Morin, Hubert. 1994. «Dynamics of balsam fir forests in relation to spruce budworm outbreaks in the Boreal Zone of Quebec». *Canadian Journal of Forest Research*, vol. 24, no 4, p. 730-741.

Motzkin, G., P. Wilson, D. R. Foster and A. Allen. 1999. «Vegetation patterns in heterogeneous landscapes: The importance of history and environment». *Journal of Vegetation Science*, vol. 10, no 6, p. 903-920.

Oksanen, Jari, Roeland Kindt, Pierre Legendre, Bob O'Hara, Gavin L Simpson, Peter M Solymos, Henry H. Stevens and Helene Wagner (2009). Vegan: Community Ecology Package, R package version 1.15-2 En ligne. <http://CRAN.R-project.org/package=vegan>.

Parent, Sylvain, Hubert Morin and Christian Messier. 2000. «Effects of adventitious roots on age determination in balsam fir (Abies balsamea) regeneration.». *Canadian Journal of Forest Research*, vol. 30, no 3, p. 513-518.

Payette, S. 1992. «Fire as a controling process in the North American boreal forest». In *A system analysis of the global boreal forest,* H.H. Shugart, R. Leemans et G.B. Bonan, p. 144-169. New York: Cambridge University Press.

Perala, D.A. 1990. «*Populus tremuloides* Michx. Quaking aspen». In *Silvics of North America - Vol. 2 Hardwoods,* R.H. Burns et B.H. Honkala, p. 555-569: US Department of Agriculture.

Peters, V. S., S. E. Macdonald and M. R. T. Dale. 2005. «The interaction between masting and fire is key to white spruce regeneration». *Ecology,* vol. 86, no 7, p. 1744-1750.

Pham, A. T., L. De Grandpré, S. Gauthier and Y. Bergeron. 2004. «Gap dynamics and replacement patterns in gaps of the northeastern boreal forest of Quebec». *Canadian Journal of Forest Research,* vol. 34, no 2, p. 353-364.

Robitaille, A, and J.P. Saucier (1998). Paysages régionaux du Québec méridional. Québec, Les Publications du Québec

Rudolph, T.D., and P.R. Laidly. 1990. «*Pinus banksiana* Lamb. Jack pine». In *Silvics of North America - Vol. 1 Conifers,* R.H. Burns et B.H. Honkala, p. 280-293: US Department of Agriculture.

Safford, L.O., J.C. Bjorkbom and J.C. Zasada. 1990. «*Betula papyrifera* Marsh. Paper birch». In *Silvics of North America - Vol. 2 Hardwoods,* R.H. Burns et B.H. Honkala, p. 158-171: US Department of Agriculture.

Smirnova, E., Y. Bergeron and S. Brais. 2008. «Influence of fire intensity on structure and composition of jack pine stands in the boreal forest of Quebec: Live trees, understory vegetation and dead wood dynamics». *Forest Ecology and Management,* vol. 255, no 7, p. 2916-2927.

Turner, M.G., W.W. Hargrove, R.H. Gardner and W.H. Romme. 1994. «Effects of fire on landscape heterogeneity in Yellowstone National Park, Wyoming». *Journal of Vegetation Science,* vol. 5, no 5, p. 731-742.

Viereck, J.S., and W.F. Johnson. 1990. «*Picea mariana* (Mill.) B.S.P. Black spruce». In *Silvics of North America - Vol. 1 Conifers,* R.H. Burns et B.H. Honkala, p. 227-237: US Department of Agriculture.

Wein, R.W., and D.A. MacLean (1983). The role of fire in northern circumpolar ecosystems. Toronto, Canada, John Wiley & Sons Ltd.

Weir, J M H, E A Johnson and K Miyanishi. 2000. «Fire frequency and the spatial age mosaic of the mixed-wood boreal forest in western Canada.». *Ecological Applications*, vol. 10, no 4, p. 1162-1177.

Wimberly, M. C., and T. A. Spies. 2002. «Landscape- Vs Gap-Level Controls on the Abundance of a Fire-Sensitive, Late-Successional Tree Species». *Ecosystems*, vol. 5, no 3, p. 232-243.

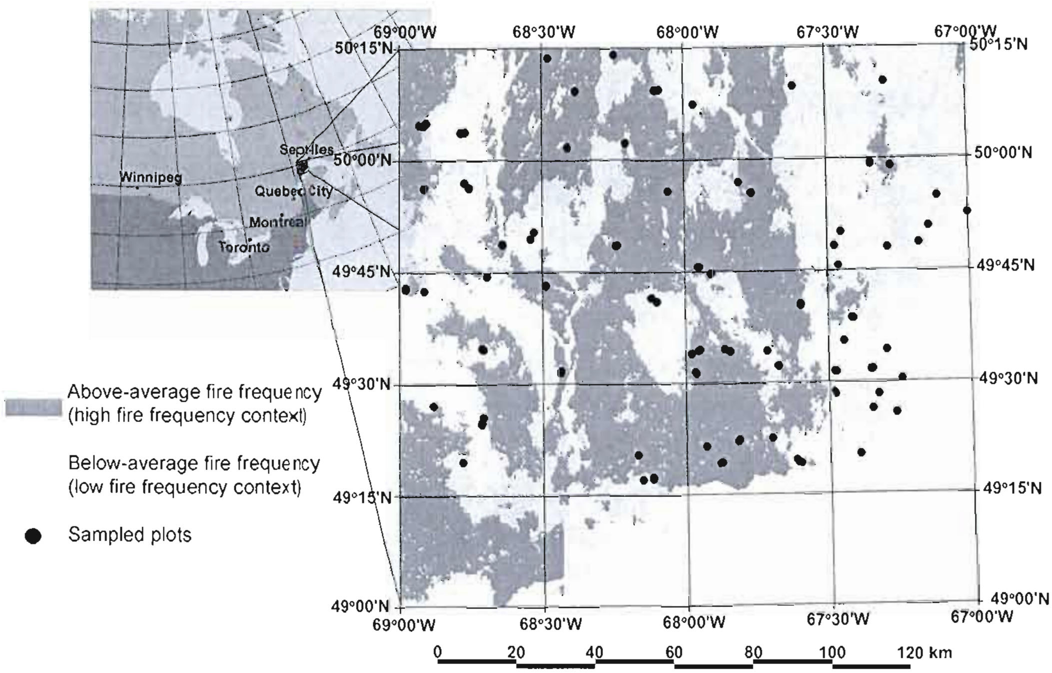


Figure 3.1 Study area and spatial distribution of sampled plots. Note that some sampled plots are clustered. These clusters are made up of 2-4 plots, with each pair within these clusters being separated by 100 to 425 m.

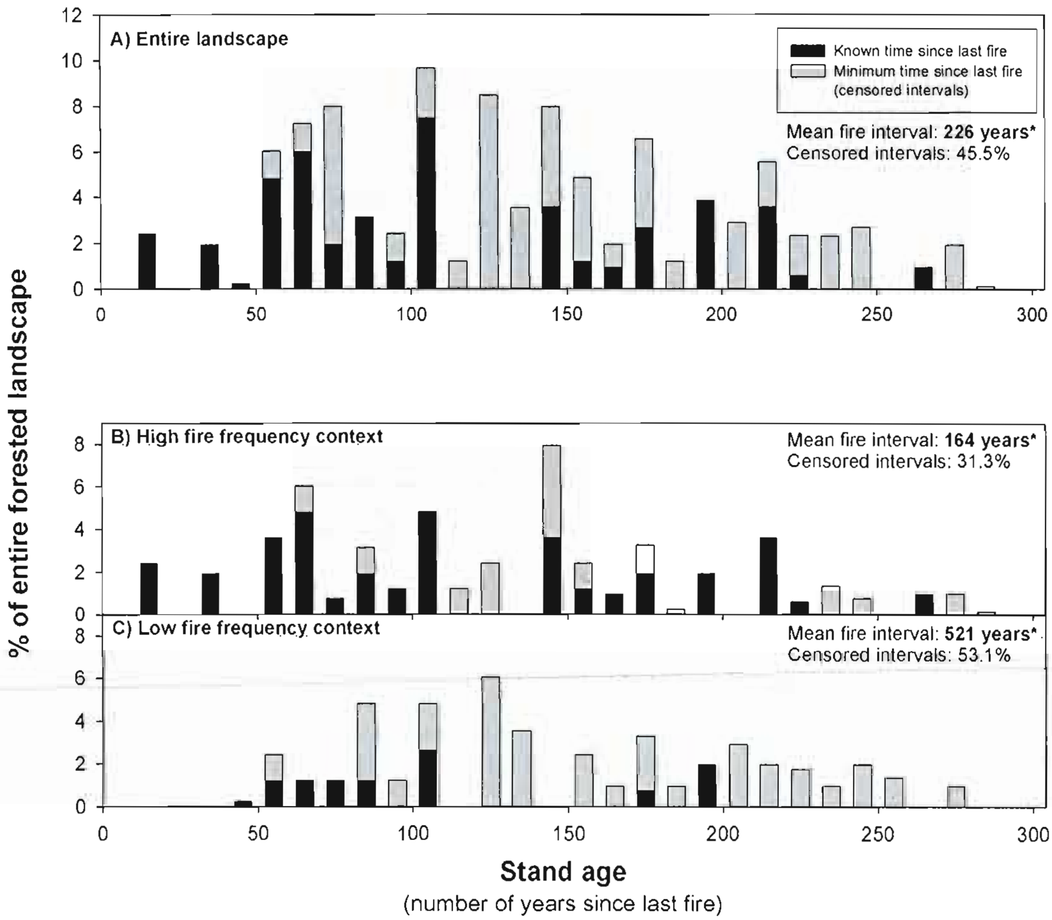
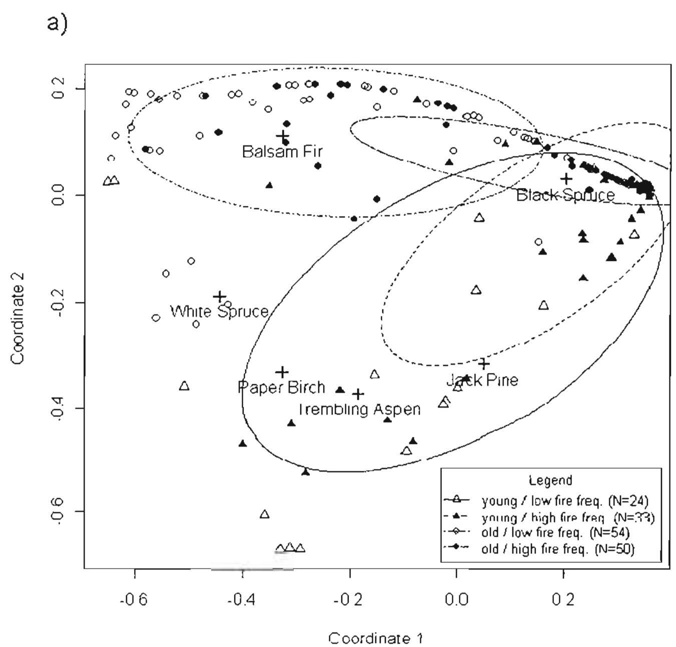


Figure 3.2 Age-class distribution at the landscape level for a) the entire landscape, b) high fire frequency areas (above average fire frequency), and c) low fire frequency areas (below average fire frequency). The proportions shown here are representative of the forested landscape (adapted from Cyr et al. 2007), but some of the younger stands where the canopy was not closed were not sampled for vegetation and are thus not included in this study.



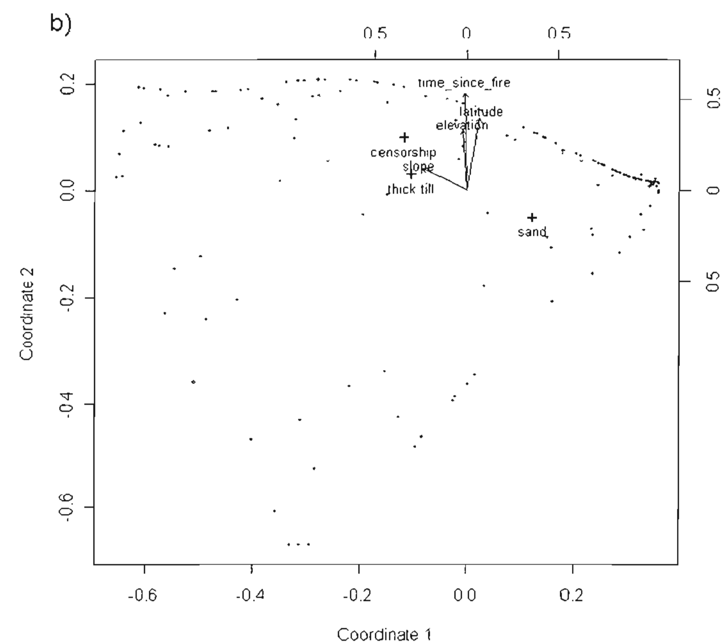


Figure 3.3 NMDS ordinations showing sampled plots on the basis of the relative basal area of each species. The final stress was 5.5309 after 20 iterations. a) 50% confidence ellipses for each group and species centroids are shown. Groups significantly (P<0.0001) differ based on 10 000 permutations within the same age-class. b) Environmental covariate fitting is represented as vectors for continuous covariates and centroids for categorical covariates. Upper right axis indicates correlations between continuous covariates and ordination axis.

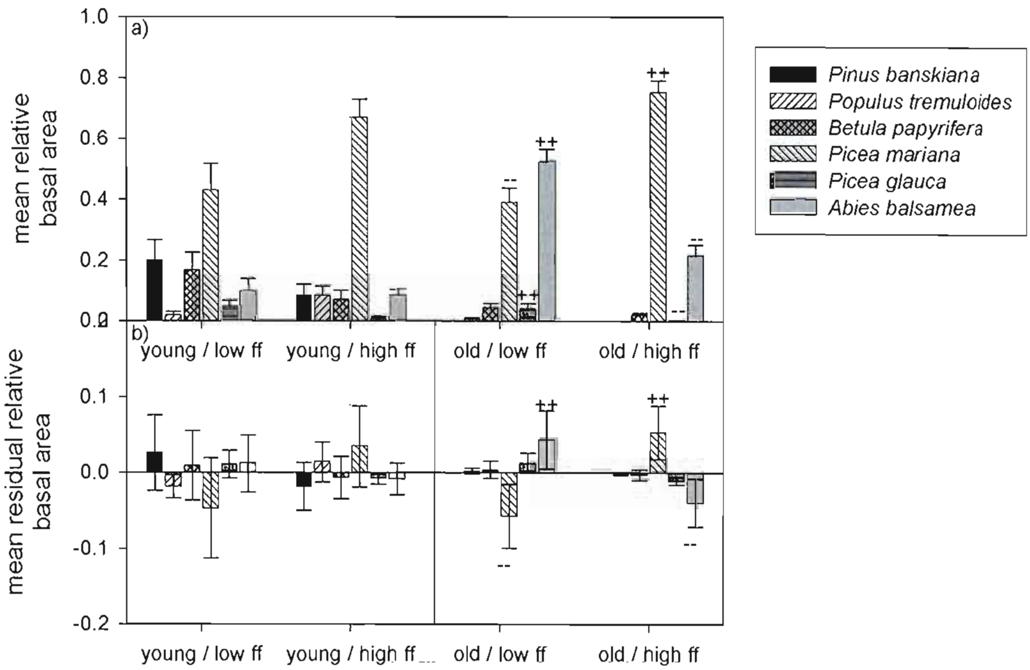


Figure 3.4 **a)** Mean relative abundance of the six most common tree species for each fire frequency and age-class (<150 years and ≥150 years), and **b)** residual values after removing the variance explained by local environmental covariates. Error bars indicate standard error. Significant differences in mean relative basal area (and residuals) between fire frequency areas within the same age-class are indicated by plus (+) and minus (-) signs. $P < 0.05$ (- or +), $P < 0.01$ (-- or ++) and $P < 0.001$ (--- or +++), after Holm's (1979) correction for multiple comparisons. Detailed results for all pair-wise comparisons can be found in Appendix 3.2.

Table 3.1 Local environmental covariates and correlations with NMDS axis. *P-values are based on 10 000 permutations.

	Spearman's *Rho* (non-parametric correlation coefficient)			*P-value**
	NMDS1	***NMDS2***	***NMDS3***	
Latitude (decimal degrees)	0.0113	0.3608	0.0509	**<0.0001**
Longitude (decimal degrees)	-0.2367	0.0844	0.0867	0.0624
Elevation (meters)	-0.0322	0.3229	0.0657	**0.0017**
Rocky outcrop (binary)	0.0803	0.0190	-0.0046	0.6651
Shallow till (binary)	-0.1094	0.0346	-0.1160	0.0663
Deep till (binary)	-0.2044	0.1988	-0.0023	**0.0199**
Glacio-fluvial (binary)	0.1572	-0.1320	0.0859	**0.0023**
North aspect (binary)	0.0284	-0.0006	-0.0450	0.8073
South aspect (binary)	0.0583	0.1473	0.0833	0.3805
Slope (percent)	-0.2703	0.0941	-0.1278	**0.0003**
Drainage (ordinal, seven classes)	-0.0001	0.1094	-0.0735	0.5144
Time since fire (years)	0.0028	0.5017	-0.1014	**<0.0001**
Censorship (binary)	-0.2790	0.5319	0.12998	**<0.0001**
NMDS 1st axis	1	0.3454	-0.2373	
NMDS 2nd axis	0.3454	1	-0.2730	
NMDS 3rd axis	-0.2373	-0.2730	1	

Appendix 3.1 Parameter estimates for multiple linear regressions conducted for removing the variance explained by local environmental covariates on each species' relative basal area for young stands (tsf < 150 years). Parameter estimates ± standard deviations are indicated.

	Abies balsamea		*Betula papyrifera*		*Picea glauca*		*Picea mariana*		*Pinus banksiana*		*Populus tremuloides*	
Intercept	10.5818	±7.5107	26.1157	±8.9830	9.9607	±3.1899	-55.486	±16.1243	3.2251	±10.4332	1.3029	±6.1693
Latitude (decimal degrees)	-0.1607	±0.1400	-0.4347	±0.1674	-0.1779	±0.0594	1.0960	±0.3006	-0.2987	±0.1945	0.0339	±0.1150
Longitude (decimal degrees)	0.0398	±0.0663	0.0695	±0.0793	0.0180	±0.0281	-0.0265	±0.1423	-0.1776	±0.0921	0.0417	±0.0544
Elevation (meters)	0.0004	±0.0003	-0.0001	±0.0003	0.0001	±0.0001	-0.0005	±0.0006	-0.0002	±0.0004	0.0005	±0.0002
Rocky outcrop (binary)	-0.0506	±0.0861	0.1166	±0.1030	0.0480	±0.0365	0.0134	±0.1849	-0.0019	±0.1196	-0.1094	±0.0707
Shallow till (binary)	0.0056	±0.0886	0.2900	±0.1059	0.0516	±0.0376	-0.0446	±0.1902	-0.1118	±0.1230	-0.1262	±0.0727
Deep till (binary)	0.0634	±0.0765	0.2911	±0.0915	0.1033	±0.0324	-0.2977	±0.1642	-0.0074	±0.1062	-0.1105	±0.0628
Glacio-fluvial (binary)	-0.0090	±0.0817	0.1666	±0.0977	0.0788	±0.0347	-0.3568	±0.1754	0.2908	±0.1135	-0.1134	±0.0671
North aspect (binary)	0.0103	±0.0744	-0.1127	±0.0889	0.0064	±0.0316	0.1636	±0.1597	-0.1009	±0.1033	0.0798	±0.0611
South aspect (binary)	-0.0382	±0.0845	-0.1580	±0.1011	-0.0311	±0.0359	0.1609	±0.1815	0.0495	±0.1174	0.0537	±0.0694
Slope (percent)	0.0024	±0.0016	0.0027	±0.0019	0.0002	±0.0006	-0.0047	±0.0034	-0.0036	±0.0022	0.0027	±0.0013
Drainage (ordinal)	-0.0111	±0.0301	0.0573	±0.0360	0.0001	±0.0128	-0.0365	±0.0647	-0.0523	±0.0418	0.0004	±0.0247
Time since fire (years)	0.0010	±0.0009	0.0003	±0.0011	0.0007	±0.0003	0.0026	±0.0019	-0.0013	±0.0012	-0.0024	±0.0007
Censorship (binary)	0.0000	±0.0000	0.0000	±0.0000	0.0000	±0.0000	0.0000	±0.0000	0.0000	±0.0000	0.0000	±0.0000

Appendix 3.1b Parameter estimates for multiple linear regressions conducted for removing the variance explained by local environmental covariates on each species' relative basal area for old stands (tsf $\geq$ 150 years). Parameter estimates ± standard deviations are indicated.

	Abies balsamea		*Betula papyrifera*		*Picea glauca*		*Picea mariana*		*Pinus banksiana*		*Populus tremuloides*	
Intercept	2.9900	±11.0131	5.7153	±2.8801	1.9455	±3.2284	-10.6846	±12.1921	-	-	-0.0429	±0.8228
Latitude (decimal degrees)	0.1885	±0.1820	-0.1103	±0.0476	-0.0440	±0.0533	-0.0045	±0.2015	-	-	-0.0109	±0.0136
Longitude (decimal degrees)	0.1729	±0.0608	0.0042	±0.0159	-0.0052	±0.0178	-0.1656	±0.0673	-	-	-0.0084	±0.0045
Elevation (meters)	0.0002	±0.0003	0.0001	±0.0001	-0.0001	±0.0001	-0.0001	±0.0003	-	-	0.0001	±0.0001
Rocky outcrop (binary)	-0.0005	±0.1545	-0.0291	±0.0404	-0.0657	±0.0453	0.0841	±0.1711	-	-	-0.0009	±0.0115
Shallow till (binary)	0.0761	±0.1393	-0.0017	±0.0364	-0.0387	±0.0408	-0.0589	±0.1542	-	-	0.0123	±0.0104
Deep till (binary)	0.2163	±0.1460	0.0186	±0.0382	-0.0417	±0.0428	-0.2152	±0.1617	-	-	0.0035	±0.0109
Glacio-fluvial (binary)	0.1192	±0.1583	-0.0138	±0.0414	-0.0435	±0.0464	-0.0723	±0.1753	-	-	0.0048	±0.0118
North aspect (binary)	-0.0991	±0.0754	0.0203	±0.0197	-0.0218	±0.0221	0.0983	±0.0835	-	-	0.0025	±0.0056
South aspect (binary)	-0.1750	±0.0778	-0.0157	±0.0203	-0.0218	±0.0228	0.2102	±0.0861	-	-	0.0011	±0.0058
Slope (percent)	0.0036	±0.0020	0.0021	±0.0005	0.0008	±0.0006	-0.0063	±0.0022	-	-	0.0001	±0.0001
Drainage (ordinal)	-0.0183	±0.0312	0.0029	±0.0081	-0.0036	±0.0091	0.0179	±0.0345	-	-	0.0050	±0.0023
Time since fire (years)	-0.0023	±0.0010	0.0002	±0.0002	-0.0001	±0.0003	0.0021	±0.0011	-	-	-0.0001	±0.0001
Censorship (binary)	0.2155	±0.0634	-0.0174	±0.0165	0.0131	±0.0185	-0.2228	±0.0701	-	-	0.0057	±0.0047

Appendix 3.2 Details of permutational comparisons of mean relative species' abundance between fire frequency areas for each age-class. a) Before and b) after removal of the variance explained by local environmental covariates. *P-value estimated based on 10 000 permutations. ** P-values are adjusted using Holm's (1979) procedure. See also Figure 4.

a)

	Young stands (tsf < 150 years)		Old stands (tsf > 150 years)	
	P-value*	*Adjusted P-values***	P-value*	*Adjusted P-values***
Abies balsamea	0.7353	0.7353	**<0.0001**	**0.0060**
Betula papyrifera	0.1488	0.5045	0.1628	0.4885
Picea glauca	0.1038	0.5045	**0.0030**	**0.0120**
Picea mariana	**0.0140**	0.0839	**<0.0001**	**0.0060**
Pinus banksiana	0.1109	0.5045	-	-
Populus tremuloides	0.1009	0.5045	0.1998	0.4885

b)

	Young stands (tsf < 150 years)		Old stands (tsf > 150 years)	
	P-value*	*Adjusted P-values***	P-value*	*Adjusted P-values***
Abies balsamea	0.8811	1	**<0.0001**	**0.0060**
Betula papyrifera	0.8092	1	0.4076	1.0000
Picea glauca	0.7842	1	0.1309	0.5235
Picea mariana	0.3626	1	**<0.0001**	**0.0060**
Pinus banksiana	0.3007	1	-	-
Populus tremuloides	0.6653	1	0.6014	1.0000

CHAPITRE IV

FOREST MANAGEMENT IS DRIVING THE EASTERN NORTH AMERICAN BOREAL FOREST OUTSIDE OF ITS NATURAL RANGE OF VARIABILITY

4.1 Résumé

Le rôle des feux dans la dynamique naturelle de la forêt boréale nord-américaine est crucial. Voilà pourquoi il est souvent suggéré que les impacts des perturbations anthropiques (e.g. coupes) sur les paysages aménagés seront atténués si celles-ci émulent le mieux possible les patrons et processus normalement générés par les perturbations naturelles (e.g. feux de forêt). Afin d'établir des cibles d'aménagement, nous avons reconstitué la variabilité naturelle des intervalles moyens entre les feux au cours des 6800 dernières années à l'aide du charbon enfoui dans des sédiments stratifiés de lacs d'Abitibi. Nous avons ensuite utilisé un modèle simple permettant de transposer cette variabilité naturelle des intervalles entre deux feux en un éventail de structures d'âge des peuplements à l'échelle du paysage. Ces nouvelles cibles d'aménagement offrent une flexibilité accrue pour l'aménagement forestier comparativement aux cibles précédentes basées sur une valeur unique quantifiant l'activité des feux et considère le caractère changeant des paysages forestiers boréaux au cours des époques, mais demeurent suffisamment conservatrices afin de maintenir une marge de manœuvre qui pourrait s'avérer nécessaire dans l'éventualité d'événement imprévisibles. Malgré cela, l'état actuel du paysage à l'étude indique que les coupes forestières ont déjà altéré considérablement la structure d'âge des peuplements à l'échelle du paysage au point de l'éloigner de sa plage de variabilité naturelle. Par conséquent, des changements substantiels dans nos aménagements sont nécessaires si, collectivement, nous décidons d'opter pour un aménagement basé sur la dynamique des perturbations naturelles.

4.2 Abstract

Fire is fundamental to the natural dynamics of the North American boreal forest. It is therefore often suggested that the impact of anthropogenic disturbances (e.g. logging) on a managed landscape are attenuated if the patterns and processes created by them resemble those of natural disturbances (e.g. fire). To provide forest management guidelines, we investigate the long-term variability in the mean fire interval (MFI) of a boreal landscape in eastern North America, as reconstructed from lacustrine sedimentary charcoal. We translate the natural variability in MFI into a range of landscape age structures using a simple modeling approach. Using the array of possible forest age structures confers flexibility for managers while being conservative enough to keep some room to maneuver in case of unpredictable natural disturbances. However, an assessment of the current state of the landscape suggests that logging has caused a shift in the age-class distribution towards a stronger representation of young stands with a concurrent decrease in old-growth stands. Logging is indeed quickly bringing the studied landscape outside of its long-term natural range of variability, implying that substantial changes in management practices are required, if we collectively decide to maintain these fundamental attributes of the boreal forest.

4.3 Introduction

Natural ecosystems have developed within ranges of conditions that can serve as references for setting conservation targets or assessing the current ecological integrity of managed ecosystems [Ecol. Appl. 1999, special issue Vol. 9 (4)]. Disturbance regimes are key processes in many types of ecosystems and contribute to a large extent to creating the variety of ecological conditions that exist through both space and time (Reynolds, 2002). Disturbance regimes characteristics, including frequency, spatial extent, and severity, are particularly important in generating this natural variability at various spatial and temporal scales.

In the boreal forest, fire is the primary disturbance that creates a complex mosaic of stands varying in age, composition, and structure, within which other disturbances and processes interact. It is for this reason that many suggest that timber management strategies be based on our knowledge of the main characteristics of regional fire regimes (Hunter, 1993). Hence, managers would apply what conservationists call a *coarse filter* that maintains key habitat attributes required by most of the ecosystem's species. In this paper we focus on disturbance frequency, which can be expressed as the mean fire interval (MFI). The MFI, defined as the mean number of years between two fires, averaged over a reference time period, is responsible for the creation of a landscape mosaic consisting of stands of different ages (Fig. 4.1). While some organisms simply need long continuity to colonize and exploit a suitable habitat patch (Norden and Appelqvist, 2001), others are dependent on attributes associated with specific points along the age-class distribution of a natural fire regime. Many forest attributes are indeed related to the time elapsed since the last fire including tree species composition, structure, dead woody debris abundance, and amount of organic matter. In contrast to the natural disturbance regime, current management practices are usually characterized by clearcuts with intervals systematically shorter than the MFI. Furthermore, while wildfires can affect stands of virtually any age, harvesting specifically targets older stands. These practices result in an extensive transformation of forested landscapes (Fig. 4.1) with a great number of known and unknown consequences. The still poorly understood role of old-growth stands in natural landscapes is of particular concern (Kneeshaw and Gauthier, 2003).

In this paper, we used the case study of a large and well-documented area of the eastern part of the North American boreal forest (Fig. 4.2). The fire history of the region for the last 300 years along with the resulting age-class distribution at the landscape scale is well documented (Bergeron *et al.*, 2004b). The MFI varied between 92 and 360 years, when partitioned into three periods delineated by significant changes in climate and human occupation history (Bergeron *et al.*, 2004b). This high variability highlights the fact that no single MFI value can be used as a unique reference. This is partly why we suggest applying a coarse filter in light of the *natural variability approach.*

In a review of the natural variability concepts, Landres and coauthors (1999) discuss the imprecision surrounding the words "natural" and "variability". To clarify this concept, they define natural variability *as the ecological conditions, and the spatial and temporal variation in these conditions, that are relatively unaffected by people, within a period of time and geographical area appropriate to an expressed goal.* In this study, we use pre-European settlement conditions as a natural reference point and the age-class distribution at the landscape scale as a key-attribute of primary concern in the boreal forest (Hunter, 1993). However, incorporating "variability" into a management approach can be complex, as it is necessary, as Landres and coauthors' definition states, to choose the proper spatio-temporal scales.

For example, any given age-class distribution in the natural landscape is far less regular than the hypothetical ones depicted in figure 1. This is because the fire activity in a given landscape fluctuates considerably on an interannual and interdecadal basis. It doesn't seem reasonable, necessary, or precautious, however, to reproduce such short-term variations through harvesting because: (1) human communities require a relatively constant timber allocation for obvious socio-economic reasons, (2) unpredictable fire events will continue to occur, as fire suppression has not proven effective in the North American coniferous boreal forest, and (3) as harvesting is now systematic throughout the entire boreal forest, it is therefore unreasonable to include the same extreme scenarios everywhere at the same time, as this would compromise the ability of adjacent landscapes to serve as migration pools (e.g. metapopulation dynamics) should these extreme scenarios be detrimental to the needs of some species. Furthermore, the age-class distribution of large landscapes (>1,000,000 ha) has a strong inertia, especially when the burn rates are relatively low, as is generally the case in the eastern part of the North American boreal forest. In light of modeling studies (Baker, 1995), it is reasonable to suggest that the extreme MFI values of 92 and 360 years that were observed in the study area should not be used as boundaries in the context of the natural variability approach, as they applied only to several decades (Bergeron *et al.*, 2004b) and, therefore, did not considerably transform the long-term age-class distribution at the landscape scale. We therefore suggest that only long-term variability in the MFI estimated from a relatively large landscape should be considered for setting management targets under the natural variability approach.

The main objective of our paper is to translate the long-term variability in MFI, reconstructed using charcoal found in lacustrine sediments into a range of ecological conditions, i.e. the landscape scale age-class distributions that formerly prevailed for a period of sufficient time to be used as sound and scientifically well-supported guidelines for management targets. In addition, we also endeavor to determine whether or not the landscape has been driven away from its natural trajectory by forest management practices by comparing the current state of the study area with its historical variability range.

4.4 Methods

A long-term fire history was reconstructed using sedimentary charcoal from three lakes and dated using ^{14}C and ^{210}PB isotopes (Carcaillet *et al.*, 2001). Only charcoal fragments larger than 150 μm were considered, as particles of this size generally do not travel more than a few hundreds of meters from a fire (Higuera *et al.*, 2007). Charcoal accumulation peaks were then isolated to build fire event chronologies beginning as far back as 7600 BP for one of the lakes, although only results spanning the last 6800 years were available for all three lakes (Carcaillet *et al.*, 2001).

These three lakes (Fig. 4.2) were considered as a representative sample of the surroundings and the fire intervals from all three lakes were pooled in order to estimate the MFI across the landscape. Two averaging methods based on the two-parameter Weibull probability density distribution were used. The Weibull-modeled MFI is

$$= b\Gamma(1/c + 1)$$

where Γ is the gamma function, b and c are respectively the scale and the shape parameters of the Weibull distribution (Johnson and Gutsell, 1994). In the first approach, the Weibull-modeled MFI of relatively constant fire regimes was calculated by detecting regime shifts by means of sequential t-tests (Rodionov, 2004).

To perform these sequential t-tests, fire intervals were transformed in number of fires per century, as Rodionov's algorithm was originally intended for discrete, annually resolved datasets. A 1000-yr-equivalent cut-off length, which determines the minimum length of the regimes, and a 5% significance threshold were used for regime shift detection. For relatively constant regimes, 95% confidence intervals were also reported (Fig. 4.5). The second approach was a smoothing method by which we fitted the Weibull distribution within a moving window of 13 observations and reported the estimated MFI along our time series. This moving window roughly corresponded to a little more than 1000 years during periods with low fire frequency and about 300 years during periods with high fire frequency. The Weibull distribution parameters and 95% confidence intervals were estimated using the LIFEREG procedure in SAS 9.1 (SAS Institute Inc. 2003) by means of maximum likelihood.

The fire intervals distributions and 95% confidence intervals within relatively constant regimes are used for establishing management targets based on long-term natural variability in MFI. The smoothing method, which is more influenced by extreme values, is only reported for comparison purposes.

To translate the range of MFI variability into corresponding ranges of age-class representation, we used the cumulative form of the Weibull distribution, which derives from Johnson and Gutsell (1994), such as:

$$A(t) = e^{-\left(t/b\right)^{c}}$$

To estimate the proportion of the landscape comprised within a given age class, we calculated

$$A(t_2) - A(t_1)$$

where t_1 and t_2 are number of years corresponding to the boundaries of the age-class of interest. We choose to use the negative exponential distribution, the simpler case of the Weibull distribution where $c = 1$, because this parameter was not significantly different from 1 in either one of the periods of relatively constant regimes (Fig. 4.5). In more concrete terms, this means that the probability of fire is considered as spatially and temporally constant in the following steps of our procedure.

To assist in distinguishing between stages of silvicultural and conservation relevance (Oliver and Larson, 1996), we used large age classes, i.e. regenerating (0-40 yr old), young closed-canopy (41-80 yr old), mature stands (80-100 yr old) and, over-mature and old-growth stands (≥101 yr old). The definition of the age classes was also constrained by the information available in the most recent provincial data (Bureau du Forestier en chef, 2007) used to estimate the current age-class distribution. This information from 3 different management units was compiled and weighted accordingly to the proportion of the area they respectively occupy.

Situations where the current landscape conditions are within the range covered by periods of relatively constant regimes were considered as an *acceptable* management target. This range is referred to as a **conservative range of variability**. Situations where the age-class representation was outside this range of variability but inside the 95% confidence intervals were considered as *of concern,* as although these situations likely occurred during the postglacial history of this landscape, they were probably uncommon and did not last for long periods. They are therefore considered as extremes, which are not appropriate as targets for a coarse-filter approach. Finally, situations where the age-class representations were outside this **extended range of variability** were considered as ecologically *unacceptable,* since these situations are not representative of natural landscape states that persisted for a significant amount of time. In the last two cases, it is advisable that management actions be undertaken in order to bring the age-class representations back within the conservative range of variability. To be cautious, we suggest the conservative range as the one to favor for setting age-class distribution management targets, with the extended range of variability being kept as "maneuvering room" in the eventuality of unpredictable events, such as natural disturbances.

4.5 Results and Discussion

4.5.1 Long-term variability in fire activity and age-class distribution at the landscape level

Sedimentary charcoal records show a strong variability in the MFI during the last 6800 years (Fig. 4.3). The period between 6800 and 3200 BP was characterized by a relatively long MFI while the period after 3200 BP shows a shorter MFI with slightly longer intervals during the last millennium (Fig. 4.3). Climatic drivers are currently the most plausible explanation for these changes, as pollen records show no clear relationships between vegetation flammability, based on species assemblages and fire activity during this period (Carcaillet *et al.*, 2001).

Consequently, the age-class distribution at the landscape level also varied considerably (Fig. 4.4), especially the proportions of over-mature and old-growth stands (≥101 yr old, Fig. 4b) as well as the young forests (0-40 yr old). This first appears to be a good result from a management perspective, as it allows for some flexibility.

Using the most recent provincial data (Bureau du Forestier en chef, 2007), we estimate that none of the current age-class representations fall within the suggested targets, as they are all outside the extended range. There is a very high over-representation of younger age classes compared to our estimated ranges of natural variability. In fact, under the natural fire regime, regenerating stands rarely comprised more than 30-38% of the landscape whereas it currently covers about 47%. This change is strong empirical evidence of how fast extensive harvesting with modern methods can modify the age-class distribution at the landscape scale as mechanized harvesting only started during the 1970's. The relatively low fire frequency that was observed during this period (Bergeron *et al.*, 2004b) further supports this assertion. The selective nature of harvesting that specifically targets older successional stages, as opposed to fire which generally affects all successional stages, explains why the transformation of the landscape is happening much faster than what would result from a comparable natural disturbance rate. The concurrent decline in over-mature and old-growth stage representation, may have strong effects on biodiversity.

4.5.2 Management implications and conclusions

Our knowledge of the biodiversity associated with over-mature and old-growth stages is rather limited in the North American boreal forest when compared to the Fennoscandian boreal or temperate forests. The consequences of the ongoing reduction of these late-successional stages are therefore difficult to predict. Birds and mammals rarely seem completely restricted to late-successional stages, although some species reach their peak abundance in such stands (Drapeau *et al.*, 2003 ; Fisher and Wilkinson, 2005). Poorly known taxa such as lichens, mosses, and soil-dwelling arthropods, which make up a very large part of the boreal biodiversity, are likely the most affected. Furthermore, despite clear differences in their respective anthropic histories, the eastern North American boreal forest and the Fennoscandian boreal forest are more similar than previously thought (Imbeau, Mönkkönen and Desrochers, 2001), as the long MFI that characterizes their respective natural fire regimes (Carcaillet *et al.*, 2007) allows for a substantial portion of the landscape to exceed the age limit for the typical harvesting rotation. European foresters have almost completely eliminated old forests from their landscapes due to their longer logging history (World Wildlife Fund, 2003). It is estimated that around 50% of Fennoscandian red-listed species are threatened due to forestry practices that have greatly reduced the range of ecological conditions (Berg *et al.*, 1994), mainly by decreasing the amount of old-growth stands in the landscapes and their related attributes. The example of Fennoscandian forestry, which is undoubtedly a model of performance in terms of timber production in a boreal system, should perhaps also be seen as a source of mistakes not to repeat for wildlife management.

The almost ubiquitous influence of fire throughout the boreal forest has fostered a false perception of unlimited resilience vis-à-vis these dramatic disturbances. However, this quality has been abused to justify the systematic use of clearcuts with relatively short rotations. Historically, MFIs have not been so short as to considerably limit the presence of over-mature and old-growth stands, at least in the eastern part of the North American boreal forest. Indeed, late-successional stands are naturally quite abundant in this part of the continent, having consistently made up more than 40% of the landscape throughout most of the postglacial history (Fig. 4.4). Furthermore, western Quebec's forested landscape has always been more diverse in terms of age-class distribution than what is currently aimed for by current forest management; this pattern is likely similar throughout most boreal regions. Clearcuts performed with rotations systematically shorter than the MFIs are unquestionably creating younger landscapes and are consequently diminishing the proportion of over-mature and old-growth stands well below their historical abundance. This trend subsequently threatens the biodiversity associated with these stands. Considerable changes in our management are needed. Practically speaking, at least 40% of the landscape should be subject to either longer rotations (Burton, Kneeshaw and Coates, 1999), silvicultural treatments closer to smaller scale disturbance dynamics such as partial cutting (Bergeron, 2004), or plain conservation. The chosen approach and proportion of the landscape subject to each treatment would vary as a function of the regional forest's dynamics and fire regime characteristics.

Finally, we suggest that the long-term variability in MFI obtained from paleoecological reconstructions (e.g. Fig. 4.3) is the most relevant data source for providing boreal forest management guidelines based on the natural variability approach. It is particularly pertinent as it encompasses a long history of varying ecological conditions and acknowledges the resilience of the boreal forest when faced with disturbance regime changes. The deviation from the natural conditions that was caused by extensive harvesting however, has the potential to harm biodiversity. When long-term data are not available, a potential compromise appears to be the use of the average time since fire observed in a landscape, as it has been shown to encapsulate in one single value the variation in fire frequency over a 300-400 year period. This approach can be used in the eastern boreal forest where the current fire frequency is lower than the historical one (Bergeron *et al.*, 2004a).

4.6 Acknowledgements

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4.7 References

Baker, W.L. 1995. «Longterm response of disturbance landscapes to human intervention and global change». *Landscape Ecology*, vol. 10, no 3, p. 143-159.

Berg, A., B. Ehnstrom, L. Gustafsson, T. Hallingback, M. Jonsell et J. Weslien. 1994. «Threatened plant, animal, and fungus species in Swedish forests: Distribution and habitat associations». *Conservation Biology*, vol. 8, no 3, p. 718-731.

Bergeron, Y. 2004. «Is regulated even-aged management the right strategy for the Canadian boreal forest?». *Forestry Chronicle*, vol. 80, no 4, p. 458-462.

Bergeron, Y., M. Flannigan, S. Gauthier, A. Leduc et P. Lefort. 2004a. «Past, current and future fire frequency in the Canadian boreal forest: implications for sustainable forest management». *Ambio*, vol. 33, no 6, p. 356-360.

Bergeron, Y., S. Gauthier, M. Flannigan et V. Kafka. 2004b. «Fire regimes at the transition between mixedwood and coniferous boreal forest in northwestern Quebec». *Ecology*, vol. 85, no 7, p. 1916-1932.

Bureau du Forestier en chef. 2007. «Possibilité forestière 2008-2013 - Résultats régionaux - Unités d'aménagement forestier 082-51, 085-51, 086-51.». En ligne. <www.forestierenchef.gouv.qc.ca/>. Consulté le 15 août 2007.

Burton, P.J., D.D. Kneeshaw et K.D. Coates. 1999. «Managing forest harvesting to maintain old growth in boreal and sub-boreal forests». *The Forestry Chronicle*, vol. 75, no 4, p. 623-631.

Carcaillet, C., I. Bergman, S. Delorme, G. Hornberg et O. Zackrisson. 2007. «Long-term fire frequency not linked to prehistoric occupations in northern Swedish boreal forest». *Ecology*, vol. 88, no 2, p. 465-477.

Carcaillet, Christopher, Yves Bergeron, Pierre J H Richard, Bianca Frechette, Sylvie Gauthier et Yves T Prairie. 2001. «Change of fire frequency in the eastern Canadian boreal forests during the Holocene: Does vegetation composition or climate trigger the fire regime?». *Journal of Ecology*, vol. 89, no 6, p. 930-946.

Drapeau, P., A. Leduc, Y. Bergeron, S. Gauthier et J. P. Savard. 2003. «Bird communities of old spruce-moss forests in the Clay Belt region: Problems and solutions in forest management, Les communautés d'oiseaux des vieilles forêts de la pessière à mousses de la ceinture d'argile: Problèmes et solutions face à l'aménagement forestier». *Forestry Chronicle*, vol. 79, no 3, p. 531-540.

Fisher, J.T., et L. Wilkinson. 2005. «The response of mammals to forest fire and timber harvest in the North American boreal forest». *Mammal Review*, vol. 35, no 1, p. 51-81.

Higuera, P. E., M. E. Peters, L. B. Brubaker et D. G. Gavin. 2007. «Understanding the origin and analysis of sediment-charcoal records with a simulation model». *Quaternary Science Reviews*, vol. 26, no 13-14, p. 1790-1809.

Hunter, M.L. Jr. 1993. «Natural fire regimes as spatial models for managing boreal forests». *Biological Conservation.*, vol. 65, no 2, p. 115-120.

Imbeau, L., M. Mönkkönen et A. Desrochers. 2001. «Long-term effects of forestry on birds of the eastern Canadian boreal forests: A comparison with Fennoscandia». *Conservation Biology*, vol. 15, no 4, p. 1151-1162.

Johnson, E.A., et S.L. Gutsell. 1994. «Fire frequency models, methods and interpretations.». *Advances in Ecological Research*, vol. 25, p. 239-287.

Kneeshaw, D., et S. Gauthier. 2003. «Old-growth in the boreal forest: A dynamic perspective at the stand and landscape level». *Environmental Reviews*, vol. 11, p. S99-S114.

Landres, P. B., P. Morgan et F. J. Swanson. 1999. «Overview of the use of natural variability concepts in managing ecological systems». *Ecological Applications*, vol. 9, no 4, p. 1179-1188.

Norden, B., et T. Appelqvist. 2001. «Conceptual Problems of Ecological Continuity and Its Bioindicators». *Biodiversity and Conservation*, vol. 10, no 5, p. 779-791.

Oliver, C.D, et B.C. Larson. 1996. *Forest stand dynamics*. New York: John Wiley and Sons p.

Reynolds, C.S. 2002. «Ecological pattern and ecosystem theory». *Ecological Modelling*, vol. 158, no 3, p. 181-200.

Rodionov, S.N. 2004. «A sequential algorithm for testing climate regime shifts». *Geophysical Research Letters*, vol. 31, no 9, p. L09204 09201-09204.

World Wildlife Fund. 2003. *State of Europe's forest protection*. Vienna: World Wildlife Fund p.

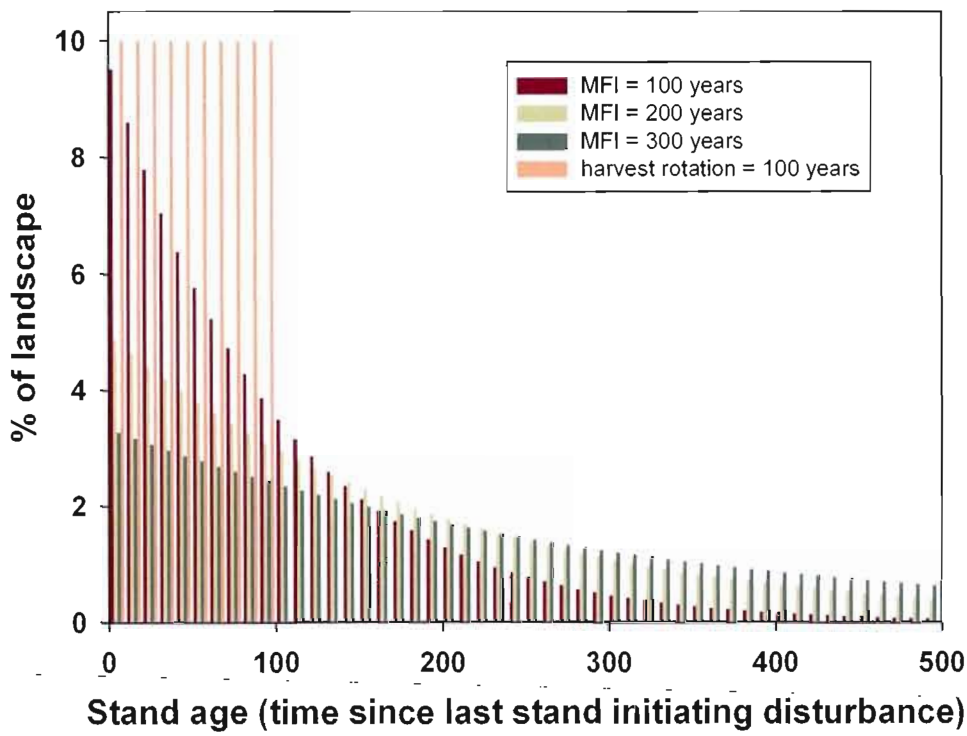


Figure 4.1 Landscape-scale age-class distributions under spatially and temporally constant fire regimes of varying mean fire intervals (MFIs) and under a "perfect" silvicultural system with a harvest rotation typical of the study area (100 years).

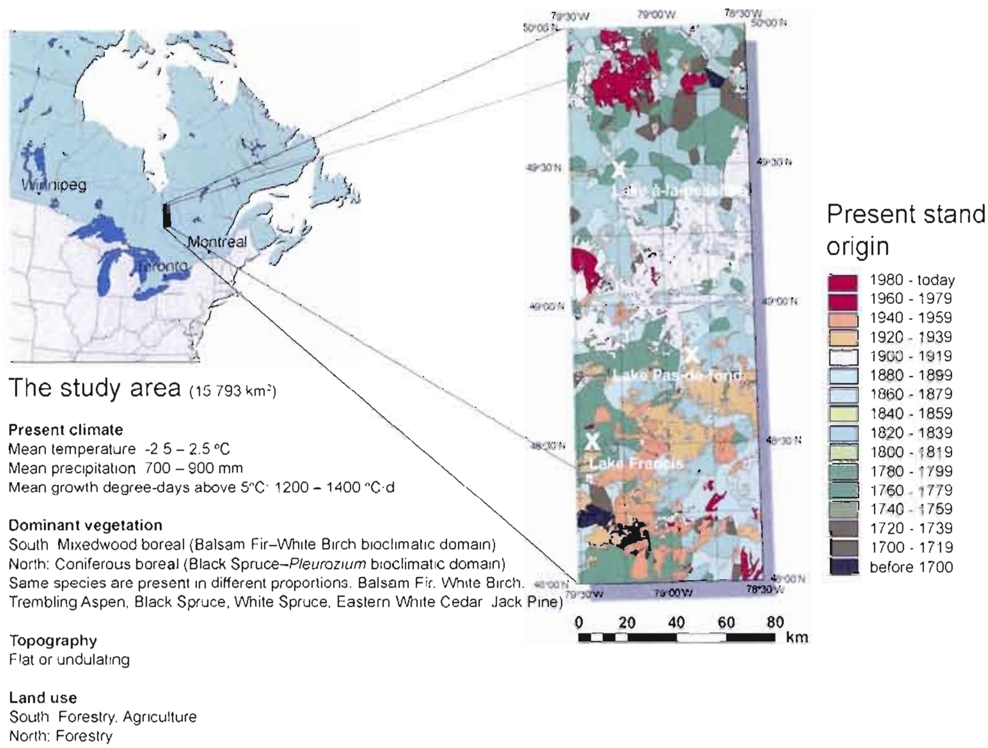


Figure 4.2 General description of the study area.

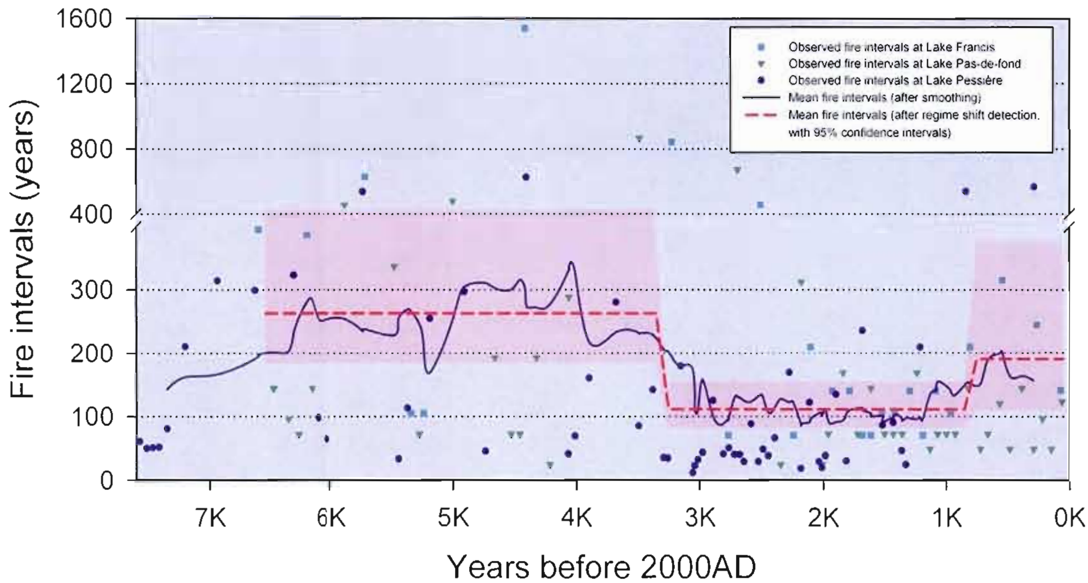


Figure 4.3 Fire intervals observed during the last 7600 years reconstructed from charcoal obtained from stratified lake sediments. The conservative range (from constant regimes, red dashed-line) covers from 111 years to 267 years and the extended range (from 95% confidence intervals, light red area) covers from 82 to 419 years.

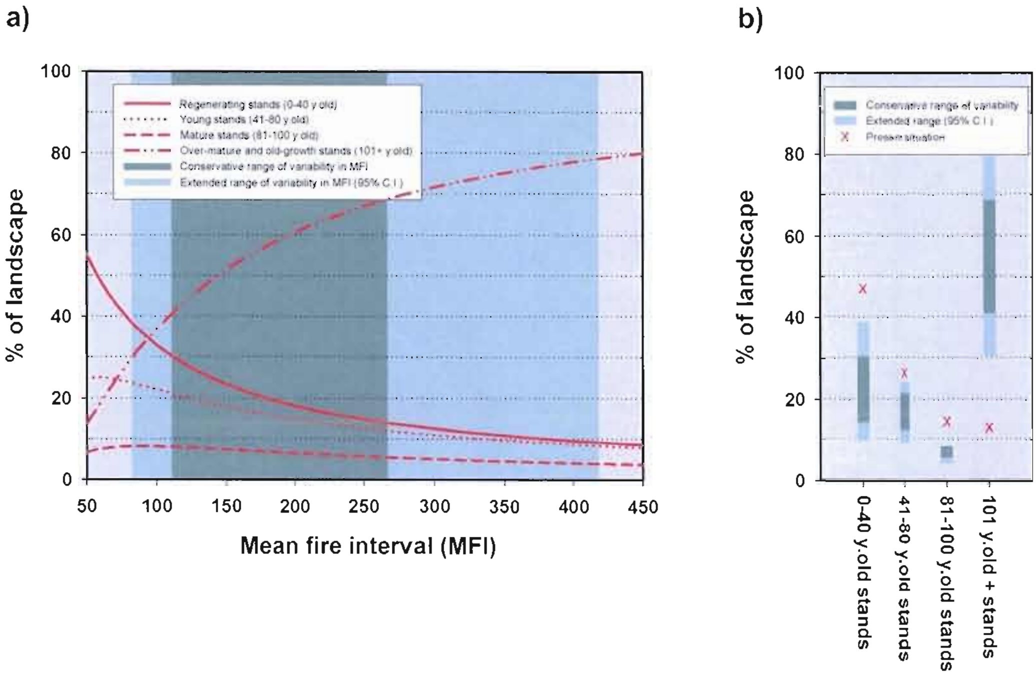
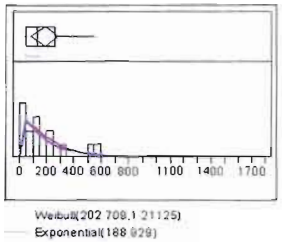


Figure 4.4 **a)** Proportions occupied by each age class modeled under varying MFI. **b)** Management targets for age-class representation following the natural variability approach. An estimate of the current representation of each age class within the landscape is provided for comparison purposes. Note that the relative abundance of age classes is also influenced by the time frame they cover, as some age classes are wider than others.

Distributions period=1. 838BP and after

Intervals



Empirical Quantiles

100 0%	maximum	568 00
99 5%		568 00
97 5%		568 00
90 0%		553 50
75 0%	quartile	262 50
50 0%	median	132 00
25 0%	quartile	48 00
10 0%		48 00
2 5%		48 00
0 5%		48 00
0 0%	minimum	48 00

Moments

Mean	188 92857
Std Dev	174 59116
Std Err Mean	46 661449
upper 95% Mean	289 7345
lower 95% Mean	88 12264
N	14

Fitted 2 parameter Weibull

Parameter Estimates

Type	Parameter	Estimate	Lower 95%	Upper 95%
Scale	b	202 70947	122 10464	325.96675
Shape	c	1 2112468	0 7806024	1 7367686

Modeled median

Percentile	Quantile
0 5000000	149 7822

Fitted Exponential

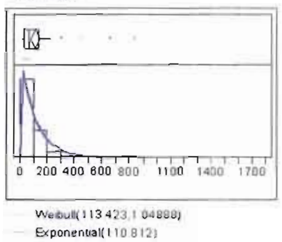
Parameter Estimates

Type	Parameter	Estimate	Lower 95%
Scale	b	188 92857	118 60418

Adequacy likelihood ratio test
H0: Shape parameter c equals 1
ChiSquare = 0.82648
p-value = 0.3633

Distributions period=2. 3292BP to 927BP

Intervals



Empirical Quantiles

100 0%	maximum	840 00
99 5%		840 00
97 5%		735 00
90 0%		210 00
75 0%	quartile	138 75
50 0%	median	72 00
25 0%	quartile	38 00
10 0%		24 00
2 5%		15 38
0 5%		11 00
0 0%	minimum	11 00

Moments

Mean	110 8125
Std Dev	140 31675
Std Err Mean	17 539593
upper 95% Mean	145 86258
lower 95% Mean	75 762419
N	64

Fitted 2 parameter Weibull

Parameter Estimates

Type	Parameter	Estimate	Lower 95%	Upper 95%
Scale	b	113 42272	87 898933	145 28952
Shape	c	1 0488771	0 8769914	1 2303506

Modeled Median

Percentile	Quantile
0 5000000	78 97292

Fitted Exponential

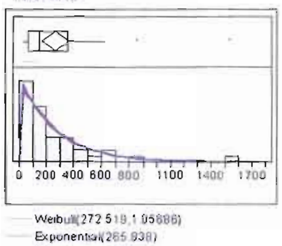
Parameter Estimates

Type	Parameter	Estimate	Lower 95%
Scale	b	110 8125	87 571231

Adequacy likelihood ratio test
H0: Shape parameter c equals 1
ChiSquare = 0.29794
p-value = 0.5853

Distributions period=3. 7347BP to 3380BP

Intervals



Empirical Quantiles

100 0%	maximum	1540 0
99 5%		1540 0
97 5%		1540 0
90 0%		628 4
75 0%	quartile	360 5
50 0%	median	144 0
25 0%	quartile	72 0
10 0%		44 2
2 5%		24 0
0 5%		24 0
0 0%	minimum	24 0

Moments

Mean	265 83784
Std Dev	294 18631
Std Err Mean	48 363931
upper 95% Mean	363 92444
lower 95% Mean	167 75124
N	37

Fitted 2 parameter Weibull

Parameter Estimates

Type	Parameter	Estimate	Lower 95%	Upper 95%
Scale	b	272 51949	194 29338	376 76144
Shape	c	1 0568611	0 8205925	1 3179868

Modeled Median

Percentile	Quantile
0 5000000	192 6579

Fitted Exponential

Parameter Estimates

Type	Parameter	Estimate	Lower 95%
Scale	b	265 83784	195 7981

Adequacy likelihood ratio test
H0: Shape parameter c equals 1
ChiSquare = 0.20509
p-value = 0.6506

Figure 4.5 Empirical moments and estimated parameters of fitted distributions for the three periods of constant regimes.

CONCLUSION GÉNÉRALE

Au cours des deux dernières décennies environ, l'intérêt voué à l'étude des feux en forêt boréale de l'est du Canada a été en grande partie motivé par les appréhensions relatives aux effets de l'aménagement forestier extensif, particulièrement à l'échelle du paysage. Les cycles des feux relativement longs documentés depuis dans cette région de la forêt boréale nord-américaine ont en effet invalidé le mythe selon lequel les feux limitent la présence de vieilles forêts dans plusieurs régions (Bergeron *et al.*, 2006 ; Bergeron *et al.*, 2001). Il n'y a maintenant plus de doute sur le fait que les forêts dépassant en âge les rotations forestières prévues (60-100 ans) sont grandement négligées par ce type d'aménagement. En un premier temps, les résultats de cette thèse confirment cet état de fait pour le territoire étudié sur la Côte-Nord sur la base de l'historique des feux des 300 dernières années reconstituée à l'aide de méthodes dendroécologiques. C'est autour de 60% du territoire qui est occupé par des vieilles forêts (chapitre 1 et 2), en faisant abstraction de l'impact récent des coupes forestières. De plus, l'analyse approfondie des données paléoécologiques couvrant les 6800 dernières années en Abitibi indiquent que la proportion du territoire forestier productif n'a vraisemblablement jamais diminué en deçà de 30% à 40% de façon persistante (chapitre 4) en dépit de la variabilité naturelle observée tout au long de cette période. Ces proportions sont importantes et négligées dans un système d'aménagement forestier extensif caractérisé par une utilisation presque exclusive des coupes à faible rétention de tiges matures, avec le risque que cela comporte pour la diversité biologique.

L'estimation du cycle des feux et son incertitude

C'est dans le premier chapitre que nous avons quantifié le cycle des feux pour le territoire à l'étude sur la Côte-Nord. Deux évaluations du cycle des feux étaient déjà disponibles pour un territoire englobant celui de la présente thèse et se chiffrent à 270 ans à l'ouest du 68^e parallèle et 675 ans à l'est (Bouchard, Pothier and Gauthier, 2008). En utilisant une méthode comparable, c'est-à-dire une analyse de survie basée sur la distribution exponentielle négative, le cycle des feux du territoire à l'étude dans la présente thèse est estimé à 295 ans, ce qui est similaire à l'estimation obtenue par Bouchard et coll. (2008) pour la portion est de leur grand territoire. Toutefois, les simulations effectuées dans le cadre de ce premier chapitre suggèrent que cette méthode, basée sur la distribution exponentielle négative, puisse mener à une surestimation substantielle du cycle des feux dans certaines conditions et que celle-ci ne soit pas la plus appropriée. En effet, cette méthode semble être la plus sensible aux variations de l'activité des feux observées au cours des 100-300 dernières années. Lorsque que l'activité des feux diminue à l'intérieur d'une telle période, ce qui semble avoir été le cas pour l'ensemble de la forêt boréale de l'est du Canada (Bergeron *et al.*, 2006 ; Bergeron *et al.*, 2001), les estimations du cycle des feux obtenues sur la base de la distribution exponentielle négative sont plus grandes que la valeur réelle. Parmi les autres types d'analyses de survie évalués dans le cadre de ce chapitre, les régressions de Cox se sont avérées les plus robustes face à cette source d'erreur. L'erreur sur l'estimation peut être particulièrement importante lorsque l'échantillon du paysage contient un fort pourcentage d'observations censurées (temps depuis le dernier feu minimum), ce qui est le cas lorsque le cycle est long par rapport à la longévité des espèces utilisées, tel que sur la Côte-Nord. Par conséquent, le cycle des feux sur le territoire à l'étude dans le cadre de cette thèse serait plutôt de l'ordre de 226 ans, soit la valeur obtenue à l'aide de la régression de Cox après avoir été ajustée pour un léger biais indépendant des variations temporelles. Fait à noter, malgré cet écart notable dans l'estimation du cycle, le pourcentage de forêts n'ayant pas subi de feu depuis plus de 100 ans demeure important quelle que soit la méthode utilisée. En effet, dans un système en équilibre caractérisé par de tels cycles, soit 226 et 295 ans, c'est en moyenne 64% et 71% de forêts de plus de 100 ans qui composeraient le paysage, respectivement.

La deuxième conclusion de ce premier chapitre est que toute estimation du cycle des feux obtenue à l'aide d'une analyse de survie basée sur un échantillonnage transversal du paysage (*snapshot image*) est associée à un intervalle de confiance relativement grand. Dans le cas du territoire de 1,5 Mha à l'étude sur la Côte-Nord, où le cycle des feux est d'environ 226 ans et où le pourcentage d'observations censurées est 53.2%, l'intervalle de confiance à 95% englobe environ ±60-70 ans lorsque calculé par *bootstrapping*, une technique basée sur le rééchantillonnage du jeu de données original, ce qui correspond assez bien aux résultats obtenus par modélisation lors de simulations de conditions similaires. De tels intervalles de confiance étendent d'autant plus le champ du possible quant à la représentativité des vieilles forêts, mais encore une fois tout indique qu'elles sont dominantes dans le paysage puisqu'elles occupent entre 53% et 71%.

L'approche par modélisation utilisée afin d'évaluer la justesse et la précision des trois types d'analyse de survie a permis de considérer plusieurs sources d'incertitudes dans l'estimation du cycle des feux, ce qui n'est pas le cas si on ne fait que rapporter l'intervalle de confiance produit de manière analytique par les logiciels statistiques, et qui ne sont principalement influencés que par l'effort d'échantillonnage et la proportion de données censurées. Pour une estimation du cycle des feux comme celles couramment effectuées à partir d'échantillons ou de cartes de temps depuis le dernier feu, il y a une autre source d'incertitude reliée à la perte graduelle d'information due au rebrûlage. En effet, n'importe quel paysage actuel n'est en fait qu'une seule réalisation d'un phénomène stochastique (Armstrong, 1999). Le caractère fortement aléatoire des feux de forêts fait en sorte qu'une activité des feux équivalente peut donner différentes configurations de paysage caractérisées par des distributions de classes d'âge à l'échelle du paysage différentes; les forêts affectées n'étant pas les même d'une fois à l'autre. L'incertitude associée à ce caractère aléatoire ne peut pas être diminuée en augmentant l'effort d'échantillonnage puisqu'elle est plutôt reliée à la disparition graduelle des traces d'anciens feux. Une approche par modélisation permet de tenir compte de cette source d'incertitude spécifique au phénomène des feux de forêt qui s'ajoute à l'effort d'échantillonnage et à la présence d'observations censurées. Il est ainsi possible d'en évaluer l'impact sur la précision des estimations. Cette approche a aussi l'avantage d'être transparente au niveau des sources d'incertitude qui sont considérées et celles qui ne le sont pas. Dans le cas de la présente étude, par exemple, l'effet de l'autocorrélation spatiale et temporelle n'est pas considéré et pourrait éventuellement constituer un niveau de sophistication supplémentaire intéressant à ajouter dans une version ultérieure du modèle, le cas échéant le paysage modélisé devrait être simulé en deux dimensions avec un modèle de feux plus réaliste sur le plan spatial.

La longueur du cycle des feux peut être particulièrement instable lorsqu'observée sur un petit territoire ou sur une période de temps trop courte (Bridge, 2001 ; Bridge, Miyanishi and Johnson, 2005). Dans de tels cas, il devient délicat ou même mal avisé de proposer de telles estimations en tant que cibles pour l'aménagement forestier. L'importante variabilité temporelle associée à l'activité des feux, particulièrement dans les régions où le cycle est relativement long comme c'est le cas sur la Côte-Nord et dans l'est du Canada en général, rend donc nécessaire le recourt à de longues périodes de référence pour l'obtention d'une estimation régionalement spécifique valable. Même en prenant toutes les précautions possibles, l'estimation du cycle reste associée à une marge d'erreur considérable dont les répercussions varient en fonction de l'utilisation souhaitée de l'information. Dans le contexte d'un aménagement forestier écosystémique basé sur la dynamique des perturbations naturelles où on cherche à reproduire une mosaïque contenant des proportions de jeunes et de vieilles forêts relativement représentatives de ce que produit le régime des perturbations naturelles, l'intervalle de confiance associé à l'estimation du cycle des feux sur la Côte-Nord a peu d'impact sur l'importance relative des vieilles forêts sur le territoire.

Par contre, certaines applications de cette information sont davantage compromises, ou du moins complexifiées, par l'imprécision entourant les estimations du cycle des feux. D'une part, il y a la contribution des feux de forêt au bilan de carbone sous un régime de perturbations naturelles, contribution qui doit être considérée afin de mesurer les impacts réels des pays et secteurs industriels reliés à la forêt boréale (Kurz *et al.*, 2008). Il s'agit là d'un enjeu considérable dans le contexte d'un virage graduel vers une économie du carbone où une marge d'erreur aussi importante que celle mise en évidence dans ce premier chapitre peut correspondre à un écart monétaire important entre les cas de figures les plus optimistes et les plus pessimistes. En deuxième lieu, les attributions de volumes de bois dans un régime de rendement soutenu sont aussi fortement influencées par le régime des feux futur (Armstrong, 2004 ; Leduc *et al.*, in prep.), l'activité des feux dans l'avenir étant généralement prédite sur la base de l'activité passée modulée par les modèles climatiques (e.g. Amiro *et al.*, 2009 ; Balshi *et al.*, 2009 ; Bergeron *et al.*, in press ; Wotton, Nock and Flannigan, 2010). L'incertitude associées à l'activité des feux dans le passé doit donc être aussi incorporée dans la fourchette de scénarios à simuler, et contribue par conséquent à augmenter l'incertitude associée à l'évaluation des allocations de volume de bois.

Hétérogénéité spatiale de la fréquence des feux et répercussions sur la composition forestière à l'échelle du paysage

Dans le deuxième chapitre, j'évalue les sources potentielles d'hétérogénéité spatiale associées à la fréquence des feux. J'utilise ici le terme fréquence plutôt que cycle, l'un étant l'inverse de l'autre (cycle = 1/fréquence moyenne). La principale contribution de ce chapitre est, en un premier temps, d'avoir identifié les facteurs environnementaux associés à une hétérogénéité de la fréquence des feux, mais surtout, d'avoir pu identifier les échelles spatiales où l'association est effective. La longitude et la position sur la pente sont deux facteurs reliés à la fréquence des feux ayant pu être identifiés sans transformation dans le territoire de la Côte-Nord. Par contre, l'exposition de la pente, un facteur topographique couramment identifié comme déterminant de la fréquence des feux n'a pu l'être qu'en considérant une échelle spatiale relativement grande. En effet, un voisinage de 4 000 m à 10 000 m doit être considéré pour détecter statistiquement une association entre la fréquence des feux et l'exposition dominante des versants. Cette influence de l'exposition dominante crée un important gradient de fréquence des feux indépendant des autres déterminants, dont la présence n'aurait pas été détectée si un continuum d'échelles spatiales n'avait pas été balayé.

L'hétérogénéité de la fréquence des feux ainsi générée est donc principalement observable à des échelles spatiales intermédiaires à celles plus couramment étudiées. Il semble donc y avoir une hétérogénéité spatiale de la fréquence des feux intra-régionale aussi importante, voire davantage, que celle habituellement observée d'une région à l'autre. Les conséquences potentielles d'une telle hétérogénéité sont à la fois d'ordre socio-économique, dans une perspective d'aménagement, et d'ordre plus écologique, dans une perspective d'organisation du paysage. Un tel patron de fréquence des feux généré par le contexte topographique peut éventuellement être mis à profit dans une analyse de risque bio-économique, notamment, où le risque de feu peut être non seulement évalué pour l'ensemble du paysage, mais pondéré à une échelle spatiale plus fine. Cette information pourrait donc être mise à profit dans le contexte d'un zonage fonctionnel comme la TRIADE, par exemple, en fonction des objectifs visés. Il est à prévoir que certaines valeurs compétionneront entre elles puisque les investissements importants alloués à un éventuel aménagement intensif, d'un point de vue financier par exemple, auraient avantage à être concentrés dans les zones à faible fréquence des feux, D'autre part, les efforts de conservation pourrait aussi avoir avantage à y être concentrés si un des objectifs visés est de préserver des vieilles forêts. Quoi qu'il en soit, une telle information, permettra de mieux évaluer les risques de feux futurs à une échelle spatiale plus fine que ce qui est pour l'instant possible en considérant les cycles de feux pour des régions entières. Toutefois, il est fortement probable que de tels déterminants soient régionalement spécifiques et ne s'appliquent donc pas uniformément sur l'ensemble de la forêt boréale.

D'un point de vue écologique, l'hétérogénéité de la fréquence des feux contribue à structurer le paysage en agglomérant les jeunes et les vieilles forêts, qui se concentrent respectivement dans les zones à haute et faible fréquence des feux. Ces zones sont fort probablement persistantes puisque déterminées par des caractéristiques permanentes du paysage. Par conséquent, et bien que les feux de forêt demeurent un phénomène largement stochastique, cette agglomération est vraisemblablement permanentes considérant les échelles spatiales impliquées. Cela influence donc potentiellement la dynamique des populations d'organismes associées aux jeunes et vieilles forêts, notamment les principales espèces d'arbres qui influencent à leur tour les attributs d'habitats d'autres espèces. Cela implique que les taux de renouvellement des parcelles d'habitat potentiel (*patch turnover*) de telles espèces, un paramètre important en modélisation des habitats, varient considérablement d'un endroit à l'autre.

L'impact potentiel de cette hétérogénéité spatiale sur la dynamique des principales espèces d'arbres est le sujet du troisième chapitre, où était évaluée l'hypothèse selon laquelle les espèces spécialistes de début ou de fin de succession seraient favorisées par un contexte de forte ou de faible fréquence des feux. Il était attendu qu'en termes absolus, il y aurait davantage de spécialistes de début de succession dans les jeunes forêts, comme le pin gris, le bouleau blanc et le peuplier faux-tremble, et inversement pour le principal spécialiste de fin de succession dans les vieilles forêts, le sapin baumier. Toutefois, nous cherchions à déterminer si, en termes relatifs, ces espèces occuperaient plus souvent les sites qui leurs sont propices considérant les facteurs environnementaux locaux et le temps écoulé depuis le dernier feu, lorsque situé dans un contexte relatif de faible ou de forte fréquence des feux. Bien que le sapin baumier se soit avérée plus abondant que l'épinette noire dans les contextes de faible fréquence des feux, toutes autres choses étant égales, l'hypothèse n'a pas pu être supportée en ce qui concerne les espèces de début de succession. Il n'a pas été possible d'attribuer directement ces différences à l'appartenance à un contexte de plus forte ou de plus faible fréquence des feux. Par contre, des intervalles plus longs entre les feux semblent favoriser une succession de l'épinette noire vers le sapin, une succession qui peut vraisemblablement se réaliser sur une période plus longue que celle normalement couverte par les reconstitutions dendroécologiques. L'hétérogénéité spatiale de la fréquence des feux telle que décrite ici entraîne toutefois une agrégation des vieux et des jeunes peuplements, et influence par le fait même la répartition spatiales de toutes les espèces et non seulement celle du sapin baumier et de l'épinette noire. Ainsi, cette hétérogénéité pourrait très bien avoir une influence sur la dynamique des métapopulations d'autres espèces associées à l'un ou l'autre des types de couvert présents sur le territoire.

Variabilité temporelle à long terme reliée aux feux de forêt

Dans le quatrième et dernier chapitre principal de cette thèse, un autre niveau de variabilité environnementale reliée aux feux de forêts a été étudié : la variabilité temporelle à long terme. Cette étude a été effectuée sur un autre territoire où le cycle des feux récent est un peu plus court que sur la Côte-Nord, soit environ 139 ans (Bergeron *et al.*, 2001). La principale contribution de cette étude est d'abord et avant tout de proposer une méthode permettant de définir une plage de variabilité naturelle de la fréquence des feux, qui est ensuite traduite en plage de variabilité naturelle de proportions de classes d'âge à l'échelle du paysage. Un tel exercice demande à ce que certains choix soient faits compte tenu du flou entourant la notion de variabilité naturelle. Sans revenir sur les détails du raisonnement ayant motivé nos choix, détails qui sont exposés en introduction du chapitre en question, nous y proposons principalement de se baser sur la variabilité à long terme telle que représentée par les reconstitutions paléoécologiques et de faire abstraction des variations à court terme. Cette variabilité à long terme constitue un domaine de conditions environnementales à l'intérieur duquel les organismes associés à différents stade de développement de la forêt ont évolué au cours de la majeure partie de l'Holocène. Dans le contexte de l'application du filtre brut, il devient ainsi possible de reconnaître la variabilité naturelle et d'étendre le domaine des conditions acceptables selon les principes d'un aménagement écosystémique, offrant par le fait même plus de flexibilité à notre planification stratégique et plus de robustesse dans les cibles désignées.

Ainsi délimité, le spectre des conditions environnementales passé ne justifie toujours pas l'utilisation presque exclusive de coupes à faible rétention de couvert émulant plus ou moins fidèlement l'impact des feux de forêt. En effet, nous avons évalué qu'en un peu plus de trois décennies d'aménagement extensif à peine, dans un contexte de très faible activité des feux, l'application de ce type de coupes a considérablement modifié la proportion des classes d'âge à l'échelle du paysage à un point tel que la proportion de vieilles forêts se situe déjà en deçà de ce qui est suggéré comme limite inférieure de la plage de variabilité à long terme. Les variations à court terme de l'activité des feux ont fort probablement créé de telles conditions pendant de courts laps de temps, et à une échelle spatiale relativement restreinte, mais les données paléoécologiques ne permettent d'identifier aucune période au cours de laquelle d'aussi faibles proportions de vieilles forêts auraient été présentes de façon persistante au cours de toute son histoire postglaciaire.

Vers une hiérarchisation explicite de l'aménagement forestier

Au cours de cette thèse, j'ai exploré et décrit quelques aspects de la variabilité associée aux feux de forêt (chapitres 1, 2, 4) ainsi que certaines de leur répercussions sur la dynamique successionelle des principales espèces d'arbre en forêt boréale de l'Est du Canada (chapitre 3). Comme il en a été mention en introduction générale, une grande partie de ce qui a motivé ce projet de recherche est la démonstration de plus en plus étayée que cette variabilité contribue à générer la diversité écosystémique (Burton *et al.*, 2008 ; Gauthier, Leduc and Bergeron, 1996 ; Romme, 1982), spécifique (Foster and King, 1986) et génétique (Gauthier, Bergeron and Simon, 1996), des valeurs qui sont mises à risque par un aménagement extensif visant une normalisation de la forêt pour des fins de productivité en matière ligneuse. Maintenir ou restaurer cette variabilité à travers notre aménagement est un défi considérable. Une façon de compartimenter cette variabilité et, en quelque sorte la réduire à un niveau de complexité gérable, est de la hiérarchiser (Wu and David, 2002). De plus, bien que la diversité biologique demeure une valeur préoccupante dans le contexte d'une exploitation à grande échelle de la forêt boréale pour des raisons éthiques, légales et parfois utilitaristes, c'est de plus en plus la résilience des écosystèmes boréaux face aux changements environnementaux à venir qui suscite inquiétude. Encore une fois, une hiérarchisation explicite de nos aménagements constitue une avenue prometteuse.

Définie dans son sens le plus large, la résilience est la capacité d'un système de récupérer d'une perturbation sans qu'il ne bascule dans un état alternatif qualitativement différent contrôlé par un ensemble de processus distincts (Holling, 1992 ; Holling and Meffe, 1996). Jusqu'à tout récemment, en aménagement forestier, la seule préoccupation directement liée à la résilience consistait à s'assurer que le site était remis en production après la coupe en préservant la régénération pré-établie et, au besoin, en reboisant. Au cours de ce doctorat, je me suis principalement attardé à un niveau hiérarchique supérieur à l'échelle du site, le paysage. L'échelle du paysage est un niveau d'organisation de la forêt boréale qui, historiquement, a été négligé et considérablement altéré par l'aménagement extensif encore aujourd'hui prédominant. De grandes améliorations sont en cours, notamment par l'augmentation des superficies d'aires protégées, mais aussi par la mise en œuvre de stratégies d'aménagement davantage inspirées de la dynamique naturelle des perturbations. En effet, les pressions populaires et les pressions des marchés du bois, notamment par l'entremise de processus de certification environnementale, ont motivé l'intégration de ces nouvelles préoccupations reliées au maintien des processus et patrons observables à l'échelle du paysage. La certification FSC, par exemple, exige explicitement le maintien et/ou la restauration d'un grand nombre d'attributs du paysage sur la base du portrait de la forêt préindustrielle, du régime des perturbations naturelles qui la caractérisait, et des attributs qui en ont découlé, par exemple la représentativité des types de peuplements et des classes d'âge, ou de la taille et la connectivité des massifs de forêt non perturbée (Forest Stewardship Council - Canada Working Group, 2004), pour n'en nommer que quelques-uns.

L'ajout d'un tel niveau hiérarchique dans notre conceptualisation de la forêt boréale et dans notre planification stratégique en aménagement était essentielle pour en maintenir la résilience. En effet, la théorie des hiérarchies et l'étude des systèmes complexes suggèrent qu'à mesure que le nombre de niveaux hiérarchiques d'un système augmente, son comportement devient plus prévisible en dépit d'une complexité accrue (Pattee, 1972). Ceci s'explique par les contraintes que chaque niveau exerce sur les autres, restreignant ainsi les degrés de liberté associés qui leurs sont associés. Une plus grande profondeur hiérarchique conférerait donc plus de stabilité à un système pourtant d'autant plus complexe. En pratiquant des coupes totales à un rythme plus élevé que ce qui est produit par les feux et en les répartissant mal, nous avons non seulement raréfié certains éléments des paysages comme les vieilles forêts en deçà des valeurs observées sur l'ensemble de l'Holocène (chapitre 4), nous avons aussi en quelque sorte « aplati » la structure hiérarchique de la forêt boréale en appliquant des prescriptions sylvicoles sur la seule base des facteurs édaphiques locaux en négligeant presque totalement l'organisation spatiale des paysages soumis à un régime de perturbations naturelles.

Beaucoup de travail reste à faire afin d'assurer la résilience du système dans son ensemble puisque les processus en cause à l'échelle du paysage tels que la dynamique des perturbations naturelles et ses interactions avec le milieu physique (chapitre 2), la dynamique successionelle des principales espèces d'arbre (chapitre 3) et des métapopulations dépendantes de différents stades successionels, ainsi que leurs propres interactions avec d'autres niveaux hiérarchiques (climat, économie humaine, etc...) sont beaucoup moins connues ou, du moins, très imprévisibles. De plus, comme les processus effectifs aux niveaux supérieurs affectent par définition des superficies plus grandes et sont généralement plus lents (O'Neill *et al.*, 1986), les suivis sont plus complexes, et les délais (*lag*) considérables. Voilà pourquoi je suggère que l'application du principe de précaution est d'autant plus important en ce qui concerne les niveaux hiérarchiques supérieurs.

Une des pistes de solution graduellement mise en œuvre et permettant de concilier le maintien et/ou la restauration de la structure hiérarchique des paysages boréaux avec l'atteinte d'objectifs de développement socio-économiques est de partitionner la récolte en l'assimilant à des processus naturels ayant cours à plus d'un niveau hiérarchique à la fois, soit à l'échelle du paysage et à l'échelle du peuplement. L'intégration de coupes partielles, affectant seulement une fraction du couvert végétal à l'échelle du peuplement semble une option valable permettant de prélever un volume de bois similaire tout en préservant une structure de paysage plus représentative de la dynamique naturelle des feux. Alors que les coupes totales s'apparentent aux feux en tant que perturbation sévère effective à de grandes échelles spatiotemporelles, les coupes partielles peuvent quant à elles être assimilées à des perturbations souvent qualifiées de « secondaires » comme les épidémies d'insectes et le vent, puisque davantage sélectives et effectives à des échelles spatiotemporelles inférieures. Cette stratégie n'est pas nouvelle et connaît présentement un essor encourageant, mais semble aussi se justifier par certains des développements théoriques récents évoqués ci-haut.

Enfin, le plus grand défi associé à l'aménagement forestier est possiblement reliée à la lenteur des processus opérant en forêt et, parallèlement, aux grandes échelles spatiotemporelles impliquées. Ceci, conjugué à une culture politique et sociale valorisant le court terme et basé sur l'illusion de stabilité environnementale à l'échelle de nos courtes vies, porte entrave à des décisions éclairées et tend à favoriser les positions extrêmes et simplistes en matière de gestion des ressources naturelles (industrialisation à outrance vs conservationisme radical). La mise en commun des valeurs et des expertises est donc primordiale à une gestion durable des forêts dans un contexte de changements environnementaux accentués par l'humain. C'est en bonne partie à travers des exercices de modélisation informatique que nous pourrons mettre en commun et structurer les éléments d'un système complexe et aménagé tel que la forêt boréale. Un nombre croissant d'outils de modélisation sont disponibles et dépasse largement les capacités des modèles de croissance et de productivité traditionnels qui étaient généralement entièrement déterministes et non-spatiaux (Daniels and Burkhart, 1975). Ces modèles sont plus ou moins spécialisés et peuvent simuler les perturbations (e.g. FLAP-EX [feux] Boychuk *et al.*, 1997), la régénération et la croissance (e.g. SORTIE-ND Coates *et al.*, 2003), la qualité de l'habitat d'espèces focales (e.g. Réseaux bayésiens d'appréciation Marcot *et al.*, 2001 ; Smith *et al.*, 2007 ; Uusitalo, 2007) ou encore forment des plateformes de modélisation, des méta-modèles (e.g. SELES, LANDIS-II Fall and Fall, 2001 ; Scheller *et al.*, 2007), qui peuvent faire interagir différents modèles en les organisant de manière hiérarchique, tout en étant contraints par les projections de simulations climatiques (GCM, RCM, etc...). Leur utilisation est relativement récente et les études de cas d'une portée géographique restreinte. De plus, l'expertise est très souvent limitante et devra être comblée dans les prochaines années afin de faire le pont entre l'ensemble des connaissances disciplinaires et la prise de décision en matière d'aménagement. De plus, et sans négliger l'apport futur d'études de terrain et d'observations empiriques, il faudra davantage tirer profit de l'abondance d'information numérisée actuellement disponible à travers les inventaires forestiers et la télédétection. Ici je ne veux pas négliger l'apport de futures études de terrain et d'observations empiriques puisque c'est souvent conjuguées à celles-ci par l'entremise d'algorithmes d'apprentissage-machine que les données numérisées expriment leur plein potentiel (e.g. chapitre annexe ; Cyr *et al.*, 2010). Enfin, quels que soient les progrès techniques et cybernétiques qui nous permettront de mieux simuler le futur de la forêt boréale et d'intégrer nos valeurs ainsi que nos scénarios d'aménagement, on ne peut pas s'attendre à pouvoir prédire avec certitude ce qu'il en adviendra. Nous savons (avec certitude) que plusieurs phénomènes tels que les feux de forêts sont associés à une grande incertitude du fait de leur nature stochastique ou chaotique. L'objectif est donc pour l'instant de chercher les attracteurs potentiels, pour employer un terme des théories des systèmes complexes, à mieux intégrer la notion de risque et à établir une carte des écueils à éviter dans nos prises de décisions, bref, à gérer tant notre ignorance que l'incertitude. Les connaissances empiriques recueillies jusqu'à présent sur les feux de forêts telles que celles présentées dans le cadre de ce doctorat seront centrales à cet exercice.

RÉFÉRENCES CITÉES DANS L'INTRODUCTION ET LA CONCLUSION GÉNÉRALES

Allen, T.F.H., and T.B. Starr. 1982. *Hierarchy: perspectives for ecological complexity*. Chicago: University of Chicago Press p.

Amiro, B. D., A. Cantin, M. D. Flannigan and W. J. De Groot. 2009. «Future emissions from Canadian boreal forest fires». *Canadian Journal of Forest Research*, vol. 39, no 2, p. 383-395.

Armstrong, G. W. 1999. «A stochastic characterisation of the natural disturbance regime of the boreal mixedwood forest with implications for sustainable forest management». *Canadian Journal of Forest Research*, vol. 29, no 4, p. 424-433.

--------. 2004. «Sustainability of timber supply considering the risk of wildfire». *Forest Science*, vol. 50, no 5, p. 626-639.

Attiwill, Peter M. 1994. «The disturbance of forest ecosystems: The ecological basis for conservative management.». *Forest Ecology and Management*, vol. 63, no 2-3, p. 247-300.

Balshi, M. S., A. D. McGuire, P. Duffy, M. Flannigan, J. Walsh and J. Melillo. 2009. «Assessing the response of area burned to changing climate in western boreal North America using a Multivariate Adaptive Regression Splines (MARS) approach». *Global Change Biology*, vol. 15, no 3, p. 578-600.

Bergeron, P.Y., B. Harvey, A. Leduc and S. Gauthier. 1999a. «Strategies for forest management based on the dynamics of natural disturbances: Stand- and forest-level considerations». *Forestry Chronicle*, vol. 75, no 1, p. 49-54.

Bergeron, Y, D. Cyr, M. P. Girardin and C. Carcaillet. in press. «Will climate change drive 21st century burn rates in Canadian boreal forest outside of its natural variability: Collating global climate model experiments with sedimentary charcoal data». *International Journal of Wildland Fire.*

Bergeron, Y., D. Cyr, C.R. Drever, M. Flannigan, S. Gauthier, D. Kneeshaw, E. Lauzon, A. Leduc, H. Le Goff, D. Lesieur and K. Logan. 2006. «Past, current, and future fire frequencies in Quebec's commercial forests: Implications for the cumulative effects of harvesting and fire on age-class structure and natural disturbance-based management». *Canadian Journal of Forest Research,* vol. 36, no 11, p. 2737-2744.

Bergeron, Yves, Sylvie Gauthier, Victor Kafka, Patrick Lefort and Daniel Lesieur. 2001. «Natural fire frequency for the eastern Canadian boreal forest: Consequences for sustainable forestry.». *Canadian Journal of Forest Research,* vol. 31, no 3, p. 384-391.

Bergeron, Yves, Brian Harvey, Alain Leduc and Sylvie Gauthier. 1999b. «Stratégie d'aménagement forestier qui s'inspire de la dynamique des perturbations naturelles: considérations à l'échelle du peuplement et de la forêt». *The Forestry Chronicle,* vol. 75, no 1, p. 55-61.

Bouchard, M., D. Pothier and S. Gauthier. 2008. «Fire return intervals and tree species succession in the North Shore region of eastern Quebec». *Canadian Journal of Forest Research,* vol. 38, no 6, p. 1621-1633.

Boychuk, Dennis, Ajith H Perera, Michael T Ter-Mikaelian, David L Martell and Chao Li. 1997. «Modelling the effect of spatial scale and correlated fire disturbances on forest age distribution.». *Ecological Modelling,* vol. 95, no 2-3, p. 145-164.

Bridge, S.R.J. (2001). Spatial and temporal variations in the fire cycle across Ontario. Ontario Ministry of Natural Resources - Northeast Science & Technology

Bridge, S.R.J., K. Miyanishi and E.A. Johnson. 2005. «A critical evaluation of fire suppression effects in the boreal forest of Ontario». *Forest Science,* vol. 51, no 1, p. 41-50.

Brundtland, G.H (1987). Our common future: The World Commission on Environment and Development. Oxford University Press. Oxford

Burton, P. J., M. A. Parisien, J. A. Hicke, R. J. Hall and J. T. Freeburn. 2008. «Large fires as agents of ecological diversity in the North American boreal forest». *International Journal of Wildland Fire*, vol. 17, no 6, p. 754-767.

Carcaillet, C, H Almquist, H Asnong, R H W Bradshaw, J S Carrion, M J Gaillard, K Gajewski, J N Haas, S G Haberle, P Hadorn, S D Muller, P J H Richard, I Richoz, M Rosch, M F Sanchez Goni, Stedingk H von, A C Stevenson, B Talon, C Tardy, W Tinner, E Tryterud, L Wick and K J Willis. 2002. «Holocene biomass burning and global dynamics of the carbon cycle.». *Chemosphere*, vol. 49, no 8, p. 845-863.

Coates, K. D., C. D. Canham, M. Beaudet, D. L. Sachs and C. Messier. 2003. «Use of a spatially explicit individual-tree model (SORTIE/BC) to explore the implications of patchiness in structurally complex forests». *Forest Ecology and Management*, vol. 186, no 1-3, p. 297-310.

Coulombe, G., J. Huot, J. Arsenault, E. Bauce, J.-T. Bernard, A. Bouchard, M.A. Liboiron and G. Szaraz (2004). Commission d'étude sur la gestion de la forêt publique québécoise. Québec En ligne. <http://www.commission-foret.qc.ca/rapportfinal.htm>. Consulté le 25 août 2010.

Courtois, R., A. Gingras, D. Fortin, A. Sebbane, B. Rochette and L. Breton. 2008. «Demographic and behavioural response of woodland caribou to forest harvesting». *Canadian Journal of Forest Research*, vol. 38, no 11, p. 2837-2849.

Cyr, D., S. Gauthier, D. A. Etheridge, G. J. Kayahara and Y. Bergeron. 2010. «A simple Bayesian Belief Network for estimating the proportion of old-forest stands in the Clay Belt of Ontario using the provincial forest inventory». *Canadian Journal of Forest Research*, vol. 40, no 3, p. 573-584.

Daniels, T.W., and H.E. Burkhart. 1975. *Simulations of individual tree growth and stand development in managed loblolly pine plantations*. Blacksburg, VA: Polytechnical Institute and State University Publications: FWS-5-75 p.

Fall, A., and J. Fall. 2001. «A domain-specific language for models of landscape dynamics». *Ecological Modelling*, vol. 141, no 1-3, p. 1-18.

Forest Stewardship Council - Canada Working Group. 2004. «National boreal standard». En ligne.
<http://www.fsccanada.org/docs/39146450F65AB88C.pdf>.

Foster, D R, and G A King. 1986. «Vegetation pattern and diversity in southeast Labrador, Canada: Betula papyrifera forest development in relation to fire history and physiography.». *Journal of Ecology*, vol. 74, no 2, p. 465-484.

Foster, D. R., D. H. Knight and J. F. Franklin. 1998. «Landscape Patterns and Legacies Resulting From Large, Infrequent Forest Disturbances». *Ecosystems*, vol. 1, no 6, p. 497-510.

Franklin, J. F., T. A. Spies, R. V. Pelt, A. B. Carey, D. A. Thornburgh, D. R. Berg, D. B. Lindenmayer, M. E. Harmon, W. S. Keeton, D. C. Shaw, K. Bible and J. Chen. 2002. «Disturbances and structural development of natural forest ecosystems with silvicultural implications, using Douglas-fir forests as an example». *Forest Ecology and Management*, vol. 155, no 1-3, p. 399-423.

Franklin, Jerry F., David Lindenmayer, James A. MacMahon, Arthur McKee, John Magnuson, David A. Perry, Robert Waide and David Foster. 2000. «Threads of Continuity. There are immense differences between even-aged silvicultural disturbances (especially clearcutting) and natural disturbances, such as windthrow, wildfire, and even volcanic eruptions.». *Conservation in Practice: Conservation in Practice*, vol. 1, no 1, p. 8-17.

Gauthier, S., Y. Bergeron and J.-P. Simon. 1996. «Effects of fire regime on the serotiny level of jack pine». *Journal of Ecology*, vol. 84, p. 539-548.

Gauthier, S., A. Leduc, B. Harvey, Y. Bergeron and P. Drapeau. 2001. «Les perturbations naturelles et la diversité écosystémique». *Le Naturaliste Canadien*, vol. 125, p. 10-17.

Gauthier, S., M.-A. Vaillancourt, A. Leduc, L. De Grandpré, D. Kneeshaw, H. Morin, P. Drapeau and Y. Bergeron. 2008. *Aménagement écosystémique en forêt boréale*. Québec: Les Presses de l'Université du Québec p.

Gauthier, Sylvie, Alain Leduc and Yves Bergeron. 1996. «Forest dynamics modelling under natural fire cycles: A tool to define natural mosaic diversity for forest management.». *Environmental Monitoring and Assessment*, vol. 39, no 1-3, p. 417-434.

Greene, D F, J C Zasada, L Sirois, D Kneeshaw, H Morin, I Charron and M J Simard. 1999. «A review of the regeneration dynamics of North American boreal forest tree species.». *Canadian Journal of Forest Research*, vol. 29, no 6, p. 824-839.

Haeussler, S., and D. Kneeshaw. 2003. «Comparing forest management to natural processes». In *Towards a sustainable management of the boreal forest,* P.J. Burton, C. Messier, D.W. Smith et W.L. Adamovicz, p. 307-368. Ottawa, Canada: NRC Research Press.

Hanski, I. 2001. «Spatially realistic theory of metapopulation ecology». *Naturwissenschaften*, vol. 88, no 9, p. 372-381.

Hanski, I., and O. Ovaskainen. 2003. «Metapopulation theory for fragmented landscapes». *Theoretical Population Biology*, vol. 64, no 1, p. 119-127.

Harvey, B, A. Leduc, S. Gauthier and Y. Bergeron. 2002. «Stand-landscape integration in natural disturbance-based management of the southern boreal forest». *Forest Ecology and Management*, vol. 155, p. 369-385.

Holling, C S, and Gary K Meffe. 1996. «Command and control and the pathology of natural resource management». *Conservation Biology.*, vol. 10, no 2, p. 328-337.

Holling, C.S. 1992. «Cross-scale morphology, geometry, and dynamics of ecosystems». *Ecological Monographs*, vol. 62, p. 447-502.

Hubbell, S.P. 2001. *The Unified Neutral Theory of Biodiversity and Biogeography.* Princeton, NJ: Princeton University Press p.

Hunter, M.L. Jr. 1993. «Natural fire regimes as spatial models for managing boreal forests». *Biological Conservation.*, vol. 65, no 2, p. 115-120.

Hunter, M.L. Jr. (1990). Wildlife, forests and forestry: Principles of managing forests fore biological diversity. Englewoods Cliffs, New Jersey, Prentice-Hall Inc.

--------. 1999. *Maintaining biodiversity in forest ecosystems.* Cambridge, UK.: Cambridge University Press p.

Jayen, K., A. Leduc and Y. Bergeron. 2006. «Effect of Fire Severity on Regeneration Success in the Boreal Forest of Northwest Quebec, Canada». *Ecoscience*, vol. 13, no 2, p. 143-151.

Johnson, E.A. (1992). Fire and vegetation dynamics: Studies from the North American boreal forest. New York, Cambridge University Press

Kafka, V., S. Gauthier and Y. Bergeron. 2001. «Fire Impacts and Crowning in the Boreal Forest: Study of a Large Wildfire in Western Quebec». *International Journal of Wildland Fire*, vol. 10, no 2, p. 119-127.

Kneeshaw, D., and S. Gauthier. 2003. «Old-growth in the boreal forest: A dynamic perspective at the stand and landscape level». *Environmental Reviews*, vol. 11, p. S99-S114.

Kohm, K.A, and J.F. Franklin. 1997. *Creating a forestry for the twenty-first century: the science of ecosystem management.* Washington, DC: Island Press p.

Kurz, W. A., G. Stinson, G. J. Rampley, C. C. Dymond and E. T. Neilson. 2008. «Risk of natural disturbances makes future contribution of Canada's forests to the global carbon cycle highly uncertain». *Proceedings of the National Academy of Sciences of the United States of America*, vol. 105, no 5, p. 1551-1555.

Kurz, Werner A, and Michael J Apps. 1994. «The carbon budget of Canadian forest: A sensitivity analysis of changes in disturbance regimes, growth rates, and decomposition rates.». *Environmental Pollution*, vol. 83, no 1-2, p. 55-61.

Kuuluvainen, T. 2002. «Natural variability of forests as a reference for restoring and managing biological diversity in boreal Fennoscandia». *Silva Fennica*, vol. 36, no 1, p. 97-125.

Leduc, A., F. Raulier, S. Gauthier, P. Y. Bernier and Y. Bergeron. in prep. «Wildfire as a hidden harvester in the assessment of annual allowable cut for North American boreal forests».

Levins, R. 1969. «Some demographic and genetic consequences of environmental heterogeneity for biological control». *Bulletin of the Entomological Society of America*, vol. 15, p. 237-240.

MacArthur, R. H., and E. O. Wilson. 1967. *The Theory of Island Biogeography.* Princeton, N.J.: Princeton University Press p.

Marcot, B.G., R.S. Holthausen, M.G. Raphael, M.M. Rowland and M.J. Wisdom. 2001. «Using Bayesian belief networks to evaluate fish and wildlife population viability under land management alternatives from an environmental impact statement». *Forest Ecology and Management*, vol. 153, no 1-3, p. 29-42.

McCune, B., and T.F.H. Allen. 1985. «Will similar forests develop on similar sites?». *Canadian Journal of Botany*, vol. 63, no 3, p. 367-376.

McRae, D. J., L. C. Duchesne, B. Freedman, T. J. Lynham and S. Woodley. 2001. «Comparisons between wildfire and forest harvesting and their implications in forest management». *Environmental Reviews*, vol. 9, no 4, p. 223-260.

Ministère des Resources Naturelles et de la Faune du Québec. 2010. «Loi sur l'aménagement durable du territoire forestier». Les Publications du Québec. En ligne. <http://www2.publicationsduquebec.gouv.qc.ca/dynamicSearch/telecharge.php?type=2&file=/A_18_1/A18_1.html>. Consulté le 26 août 2010.

Motzkin, G., P. Wilson, D. R. Foster and A. Allen. 1999. «Vegetation patterns in heterogeneous landscapes: The importance of history and environment». *Journal of Vegetation Science*, vol. 10, no 6, p. 903-920.

Nguyen, Xuan Thuy, Yves Bergeron, Dan Simard, Jim W Fyles and David Pare. 2000. «The importance of forest floor disturbance in the early regeneration patterns of the boreal forest of western and central Quebec: A wildfire versus logging comparison.». *Canadian Journal of Forest Research*, vol. 30, no 9, p. 1353-1364.

Noss, R.F. 1987. «From plant communities to landscape in conservation inventories: a look at the nature conservancy». *Biological Conservation*, vol. 41, p. 11-37.

--------. 1990. «Indicators for monitoring biodiversity: a hierarchical approach». *Conservation Biology*, vol. 4, no 4, p. 355-364.

O'Neill, R.V. 2001. «Is it time to bury the ecosystem concept? (with full military honors, of course!)». *Ecology*, vol. 82, no 12, p. 3275-3284.

O'Neill, R.V., D.L. DeAngelis, J.B. Waide and T.F.H. Allen. 1986. *A hierarchical concept of ecosystems*, no Monographs in population biology. Princeton: Princeton University Press p.

Pattee, H.H. 1972. «The evolution of self-simplifying systems.». In *The relevance of general system theory,* E. Laszlo, p. 33-41. New York: Braziller.

Payette, S. 1992. «Fire as a controling process in the North American boreal forest». In *A system analysis of the global boreal forest,* H.H. Shugart, R. Leemans et G.B. Bonan, p. 144-169. New York: Cambridge University Press.

Perera, A.H., and L.J. Buse. 2004. «Emulating natural disturbance in forest management: An overview». In *Emulating natural forest landscape disturbances: Concepts and applications,* A.H. Perera, L.J. Buse et M.G. Weber, p. 3-7. New York: Columbia University Press.

Romme, W.H. 1982. «Fire and landscape diversity in subalpine forests of Yellowstone National Park». *Ecological Monographs,* vol. 52, p. 199-221.

Romme, William H, Edwin H Everham, Lee E Frelich, Max A Moritz and Richard E Sparks. 1998. «Are large, infrequent disturbances qualitatively different from small, frequent disturbances?». *Ecosystems,* vol. 1, no 6, p. 524-534.

Sanderson, J., and L.D. Harris. 2000. *Landscape ecology: A top-down approach.* Boca Raton, Fl.: Lewis Publishers p.

Scheller, R. M., J. B. Domingo, B. R. Sturtevant, J. S. Williams, A. Rudy, E. J. Gustafson and D. J. Mladenoff. 2007. «Design, development, and application of LANDIS-II, a spatial landscape simulation model with flexible temporal and spatial resolution». *Ecological Modelling,* vol. 201, no 3-4, p. 409-419.

Senici, D., H.Y.H Chen, Y Bergeron and D. Cyr. 2010. «Spatiotemporal variations of fire frequency in central boreal forest». *Ecosystems,* vol. 13, p. 1227-1238.

Smith, C. S., A. L. Howes, B. Price and C. A. McAlpine. 2007. «Using a Bayesian belief network to predict suitable habitat of an endangered mammal - The Julia Creek dunnart (Sminthopsis douglasi)». *Biological Conservation,* vol. 139, no 3-4, p. 333-347.

Thiffault, E., N. Bélanger, D. Paré and A. D. Munson. 2007. «How do forest harvesting methods compare with wildfire? A case study of soil chemistry and tree nutrition in the boreal forest». *Canadian Journal of Forest Research,* vol. 37, no 9, p. 1658-1668.

Turner, Monica G, and Virginia H Dale. 1998. «Comparing large, infrequent disturbances: What have we learned?». *Ecosystems*, vol. 1, no 6, p. 493-496.

Uusitalo, L. 2007. «Advantages and challenges of Bayesian networks in environmental modelling». *Ecological Modelling*, vol. 203, no 3-4, p. 312-318.

Wardle, D. A., M. C. Nilsson and O. Zackrisson. 2008. «Fire-derived charcoal causes loss of forest humus». *Science*, vol. 320, no 5876, p. 629.

Wein, R.W., and D.A. MacLean (1983). The role of fire in northern circumpolar ecosystems. Toronto, Canada, John Wiley & Sons Ltd.

Wotton, B. M., C. A. Nock and M. D. Flannigan. 2010. «Forest fire occurrence and climate change in Canada». *International Journal of Wildland Fire*, vol. 19, no 3, p. 253-271.

Wu, J., and J. L. David. 2002. «A spatially explicit hierarchical approach to modeling complex ecological systems: Theory and applications». *Ecological Modelling*, vol. 153, no 1-2, p. 7-26.

ANNEXE 1

A SIMPLE BAYESIAN BELIEF NETWORK FOR ESTIMATING THE PROPORTION OF OLD FOREST STANDS IN THE CLAY BELT OF ONTARIO USING THE PROVINCIAL FOREST INVENTORY

A1.1 Résumé

La différence entre les paysages forestiers boréaux produits par les régimes de perturbations naturelles et ceux produits par l'aménagement extensif est importante et de mieux en mieux documentée. Afin de concilier la récolte avec le maintien de la biodiversité et des autres services rendus par l'écosystème, les politiques gouvernementales et les processus de certification prônent de plus en plus la mise en œuvre de stratégies d'aménagement permettant de maintenir les principales caractéristiques du paysages à l'intérieur de leur plage de variabilité naturelle. Une des entraves à l'atteinte d'un tel objectif est le manque d'information complète, tant sur le plan spatial que temporel, au sujet de ces grandes caractéristiques paysagères, notamment la proportion du paysage occupée par les vieilles forêts. L'objectif de cette étude consistait à quantifier la proportion de vieilles forêts dans un très vaste paysage en combinant deux sources d'information incomplètes mais complémentaires, i.e. un inventaire forestier provincial et une reconstitution dendroécologique de l'historique des feux à l'aide d'un réseau bayésien d'appréciation. Cette étude a été réalisée dans un paysage de 6.5 Mha correspondant à la portion de la ceinture d'argile située en Ontario. Les résultats indiquent que 72.4% de ce territoire est occupé par des peuplements qui n'ont subi aucun feu au cours des 150 dernières années. Nous discutons des implications de ces résultats en aménagement forestier ainsi que du potentiel d'application de la méthode utilisée dans de futurs travaux.

A1.2 Abstract

The differences between boreal forest landscapes produced by natural disturbance regimes and landscapes produced by harvesting is important and increasingly well-documented. In order to continue harvesting operations while maintaining biodiversity and other ecosystem services, government policies and certification processes are pushing for practices that preserve landscape features within their range of natural variability. One major shortcoming in the implementation of such a strategy is the lack of complete spatial or temporal information about these landscape features, such as the proportion of old stands, which are believed to act as a coarse-filter for conservation if they remain representative enough of natural conditions. The objective of this study was to quantify the proportion of old stands in a very large landscape by combining fragmentary knowledge from two different sources, i.e. a provincial forest inventory and existing fire history reconstructions using a Bayesian Belief Network (BBN). This study was conducted over a 6.5 M-ha-landscape located within the Clay Belt of the province of Ontario, Canada, and suggests that more than 72.4% of this area is occupied by stands where no fire occurred during the last 150 years. Implications for management and potential for future research are discussed.

A1.3 Introduction

A forest management approach that works within the limits established by natural disturbance regimes (i.e. prior to extensive industrial alteration of the landscape) represents a coarse-filter ecological forest management approach (Attiwill, 1994 ; Hunter, 1999 ; Kohm and Franklin, 1997) which may achieve a balance between maintaining biodiversity and ecosystem function while serving human commodity needs (Bergeron *et al.*, 1999 ; Franklin, 1993 ; Galindo-Leal and Bunnel, 1995 ; Seymour and Hunter, 1999). Under this approach, at the landscape level, forest management targets the maintenance of a variety of stand age-classes whose respective abundances fall within their natural range of variability.

Targeting a natural age class distribution is particularly challenging in the eastern part of the Canadian boreal forest where the natural fire cycle is relatively long and more than half of the landscape can be occupied by stands older than 100 years (Bergeron *et al.*, 2006 ; Bergeron *et al.*, 2004). Such long fire cycles result in the presence of extensive areas of uneven-aged forest stands in mid- and late-seral stages of succession with associated stand attributes which include different combinations of vertical and horizontal diversity, the presence of large cavity trees, and large inputs of coarse woody debris (Harper *et al.*, 2002 ; 2003 ; 2005 ; Kneeshaw and Gauthier, 2003 ; McCarthy, Small and Rubino, 2001). Current forest management practices aim to decrease the proportion of old forests (Etheridge *et al.*, 2005), sometimes down to levels that were never reached during the entire post-glacial history of the boreal forest (Cyr *et al.*, 2009). If the management goal is maintaining a natural disturbance pattern associated with long fire cycles, then the predominant use of short rotation, even-aged silviculture is ecologically inappropriate.

In order to determine the natural historical proportion of old forest on the landscape we can use provincial fire records augmented with dendroecological research. The extent of recent fires are usually documented in provincial fire records although the completeness of these records varies considerably from one region to another, especially in remote areas of Quebec, Ontario, Manitoba, Saskatchewan and the Northwest Territories (Stocks *et al.*, 2003). In the boreal forest, the timeframe covered by these records rarely exceeds 60-80 years making the information temporally limited. This length of time is less than the time needed for the first post-disturbance cohort to be succeeded to the next cohort via gap phase dynamics and does not account for the important variability of fire activity caused by climate and land use changes over the last 200-300 years. Consequently, provincial fire records are limited in determining the amount of old forest and need to be augmented by dendroecological studies specifically designed to reconstruct long-term fire history. Although these studies usually encompass the necessary longer timeframe (200-300 years), they are also more costly and sparsely distributed throughout the boreal forest making them spatially limited rather than temporally restricted. The general objective of this study was to develop a model that could relate dendroecologically reconstructed fire history to other sources of available information that are available for the entire landbase and to extrapolate fire history to the larger regional landscape. There is an increasing demand from both provincial policies and market pressure through certification programs such as the FSC (Forest Stewardship Council - Canada Working Group, 2004) for regionally specific information about natural disturbance regimes and resulting boreal landscapes .

The province of Ontario is an example where forest management is directed to follow the emulation of the natural disturbance pattern through the Crown Forest Sustainability Act (Ontario Ministry of Natural Resources, 1994). In boreal Ontario, forest management aims to approximate natural landscape patterns created by stand replacing fire regimes. However, only short-term provincial fire records (Ontario Ministry of Natural Resources, 2007) and one spatially limited long-term dendroecological study (Bergeron *et al.*, 2001) are available to guide forest management. We use these two fire history sources in combination with Ontario's operational Forest Resources Inventory (FRI) map to infer time since last fire on a larger area, which in turn allows an assessment of the proportion of old forests. The FRI map was not designed for reconstructing fire histories; however it contains basic mensuration attributes such as species composition, stand age, stocking, and height which are useful in an extrapolation exercise. We present an inductive method that was developed in the field of machine learning, a subfield of artificial intelligence. Among the variety of learning algorithms that currently exist, we chose to use Bayesian networks, also known as Bayesian Belief Networks (BBN), to relate information about disturbance history, vegetation composition and structure as well as the physical environment, to achieve our extrapolation exercise. Ultimately, it is believed that this model will also take advantage of the spatial resolution of the provincial forest inventory and will allow for a to improved description of spatial patterns produced by fire.

A1.4 Methods

A1.4.1 Bayesian Belief Networks (BBNs)

Formally, BBNs are directed acyclic graphs whose nodes represent variables (or correlates) and whose arcs encode conditional dependencies between the variables (Marcot *et al.*, 2001 ; Pearl, 1991). Both the conditional dependencies, which are expressed through conditional probability tables (CPT), and the structure of the model, can be "learned" using many algorithms that are implemented within a large selection of existing software packages or toolboxes.

There are several reasons why BBNs present a promising machine learning approach for natural resource management (Marcot *et al.*, 2006). Like most machine learning approaches, BBNs have the ability to deal with the uncertainty associated with operational FRI which has a certain level of imprecision and inaccuracy (Pinto *et al.*, 2007 ; Thompson *et al.*, 2007). While some machine learning methods can be described as abstract mathematical black boxes, BBNs are graphical probabilistic models that retain most of our intuitive understanding of the modeled system during the entire course of the model's development right up to the end product (Naïm *et al.*, 2004). This transparency is advantageous in the multidisciplinary context of natural resources management for both the development and the communication of the model results to decision-makers and other non-modeler stakeholder groups because previous experience in modeling is not necessary to contribute or to understand how the model works (Marcot *et al.*, 2006). Finally, BBNs can incorporate different kinds of information including empirical data, theoretical relationships and expert knowledge and can also operate relatively well with incomplete information as they will always yield the most likely inference given the best information available. Therefore, BBNs work very similarly to human judgment as they share a comparable flexibility and, like human experts, the ability to predict improves with more "experience" and better information for learning. Further details about BBNs in general are found in Pearl (1991, 2000), and specific applications to natural resources management are illustrated in several other publications (cf. special issue in Can J. For Res [36] ; Marcot *et al.*, 2001 ; Smith *et al.*, 2007 ; Uusitalo, Kuikka and Romakkaniemi, 2005).

A1.4.2 Study area

The study area was an approximately 6.5 million ha portion of the 125 000 km^2 Clay Belt located in northeastern Ontario adjacent to Quebec (Fig. A1.1) (Lefort *et al.*, 2002). The Clay Belt physiographic unit is the result of glacial Lake Barlow-Ojibway, which left a lacustrine clay deposit that largely leveled the topography (Boissonneau, 1966). Consequently, a vast proportion of the area is made up of poorly drained soils that often develop into a thick layer of organic matter through the process of paludification (Simard *et al.*, 2007). Better drained sites, such as glacio-fluvial deposits and tills, are found on eskers and hills, respectively, but make up a smaller proportion of the area. This predominance of poorly drained soils is indeed particular to this region and greatly influences forest dynamics.

The study area is located within the Boreal Shield Ecozone (Ecological Stratification Working Group, 1995) and characterized as the Humid Mid-Boreal Ecoclimatic Region (Ecoregions Working Group, 1989). The mean annual precipitation varies from 652-1029 mm with summer mean rainfall ranging from 220-291 mm (Lefort *et al.*, 2002). The mean annual temperature ranges from -0.5 to 2.5 ^{o}C and the mean length of growing season ranges between 167 and 185 days (Mackey *et al.*, 1996a, 1996b).

On clay sites, mature stands primarily consist of black spruce (*Picea mariana (*Mill.*) BSP)* and balsam fir (*Abies balsamea* (L.) Mill.), while trembling aspen (*Populus tremuloides* Michx.) is usually present on recently disturbed sites. Jack pine (*Pinus* banksiana Lamb.) can make up almost pure stands on recently burned well-drained sites while eastern white cedar (*Thuja occidentalis* (L.)) and white spruce (*Picea glauca* (Moench) Voss) usually occur in late successional stands (Gauthier, De Grandpré and Bergeron, 2000). White birch (*Betula* papyrifera Marsh.) is also found scattered throughout every successional stage except for some recently disturbed well drained sites where it can be more common (Gauthier, De Grandpré and Bergeron, 2000).

A1.4.3 Construction of the BBN

The BBN was developed following the guidelines presented by Marcot *et al.* (2006) using the modeling shell Netica™ (version 3.25 Norsys Systems Corporation, Vancouver, BC). The development of the model commenced with a simple influence diagram that represented our general understanding of fire dynamics in the boreal forest (Fig. A1.2). The more detailed model was developed through a trial and error process trying to optimize the accuracy and precision of the model's inference of fire history by means of a cross-validation using independent random samples from the training area. All polygons of productive stands were assigned a time since fire value and the harvesting history described. During this process, expert judgment was used to: 1) adjust the detailed structure of the model, 2) evaluate which environmental correlates to include; and 3) define the discretization of these correlates. In this study, only the parameterization of the model, i.e. the learning of the CPT, was completely automated and initiated from uniform distributions, which was an adequate procedure considering the massive amount of empirical data that was available. The structure of the model followed generally accepted knowledge of disturbance-vegetation dynamics in the boreal forest, where disturbance history and physical environment influence vegetation and structural composition (Fig. A1.2).

The Lake Abitibi Model Forest (LAMF), which resides on the Clay Belt (Fig. A1.1), was used as the "training area" for the development of the model as a full set of the necessary environmental correlates including fire and harvesting history was available. All of the environmental correlates considered in the model were either taken directly from the literature, e.g. from a time since fire map (Gauthier *et al.*, 2002), from the operating company's record (harvesting history), or from the FRI, and incorporated into the BBN without any transformation. The list of environmental correlates considered depended on the availability of information and known vegetation-disturbance dynamics in the Clay Belt and the boreal forest in general (cf Fig. A1.3 for final list).

The fire history for the LAMF was reconstructed for the last 300 years (Gauthier *et al.*, 2002) and showed a gradual increase in the fire cycle, from 78 years (<1850), to 196 (1850-1920), to 422 years (>1920), which corresponds well to the start of the settlement period for this region. A similar pattern was described in the adjacent Abitibi region of Quebec (Bergeron *et al.* ; Bergeron *et al.*). The FRI was developed from large-scale aerial photo (1:20 000) interpretation that allowed for general characterization of the forest in terms of forest structure (i.e. species compostion, stocking and developmental stage). Forest stands were delineated using photographs and stand attributes were assessed using field calibration plots. Tree species composition was described as the percentage of crown occupancy at the nearest 10% for all species contributing at least 10% to the canopy of the stand. The stand age and height were estimated for dominant species or co-dominant species and the stocking was defined as the stand basal area relative to the normal basal area predicted from normal yield tables (Ontario Ministry of Natural Resources, 2007). The productivity index (site class), used as a general proxy for edaphic conditions, was defined from the age to height relationship in the same normal yield tables. From the initial list of considered environmental correlates the only one not incorporated was the relative abundance of white birch, which decreased the performance of the model in inferring the time since last fire. The LAMF FRI consisted of 901 275 ha (45 123 polygons) of productive area for which a time since fire and the harvesting history was assigned. Although the proportion of old forests within the Clay Belt may vary at finer scales, post-fire dynamics are believed to be consistent throughout the entire area.

It is necessary for the functioning of a BBN, which is based on conditional probabilities, that all continuous variables included in the model be expressed as discrete variables. It is usually recommended to keep the number of possible states relatively low (i.e. two or three) as it makes it easier to populate the CPT because the data is spread across fewer states (Marcot *et al.*, 2006). Given the massive amount of cases from which our BBN could learn from, populating the CPT was not an issue, but the number of states was kept relatively low as a way to temper the relative imprecision of the FRI (Pinto *et al.*, 2007 ; Thompson *et al.*, 2007).We tested various sets comprising two to four different states for all continuous variables. Particular attention was given to the number of states of the focal node of the BBN, time since fire, as that number would influence the design of the BBN itself. We chose to work with only two classes (≤150 and >150 years) for three main reasons. Firstly, the age of old forests (TSF > 150 years) is often known only to limited extent (i.e. only a minimum estimation of TSF could be obtained from dendroecological fire history reconstruction as TSF may exceed the age of the oldest trees). Splitting that upper class into several other classes would therefore be very difficult as the information provided for the learning of the BBN become increasingly uncertain around 150 years after fire. Secondly, the exact age of younger forests is known directly from recent fire provincial archives. Inferring more precisely the TSF in stands younger than 80 years was therefore judged unnecessary. And lastly, important changes in stand structure and sometimes species composition usually occur around 150 years after fire (Harper *et al.*, 2002). The dynamics through which these changes occur are what forester management aims to emulate through uneven-aged management. Ultimately, the goal is to assess the proportion of these stands and we have designed the BBN accordingly.

For continuous variables, such as those describing vegetation composition and structure, we initiated a trial and error process using discrimination thresholds that could best discriminate between old and young stands on the basis of our knowledge of local successional pathways and scientific literature (Gauthier, De Grandpré and Bergeron, 2000 ; Gauthier *et al.*, 2002 ; Vasiliauskas *et al.*, 2004). Several combinations of possible states and discretization thresholds were attempted. With no preconceived idea of how a given correlate would be related to TSF we initiated the trial and error process with discretization thresholds that resulted in relatively uniform global frequency distributions (e.g. latitude and stocking). For species relative abundance three possible states were used (i.e. absent, present and abundant) considering that these would provide an intuitive yet accurate portrait of each stand that would also acknowledge the relative imprecision of the FRI.

Special attention was given to the boundary delineation of fires, which was considered unevenly reliable depending on the time since fire. Indeed, recent burns were delineated with more precision than older burns. Moreover, the reliability of the information generally decreased in close proximity to boundaries as fire severity is generally more variable near the edges of burned areas (Perera *et al.*, 2009). We chose to exclude this source of ambiguity by not considering the information provided by the fire map when stands were located near the edges of burned areas. Therefore, the model had fewer cases to learn from, but it was felt that this should allow the model to better discriminate between young and old stands. The affected stands were located within a 2000m buffer inside the boundaries of older burns (≥150 years) and within a 1000m buffer inside more recent burns for which the time since fire was arbitrarily considered ambiguous. These stands (40.2%) were still incorporated into the training data set after the removal all prior knowledge of fire history as conditional dependencies between other correlates could contribute in populating CPTs that were not directly linked to TSF.

A1.4.4 Model assessment

Cross-validation of model performance was an integral part of the model development. Each iteration of the model was trained by randomly selecting 36 098 cases from the training area (80% of total) while the testing was made using the remaining 20% for which a trust-worthy time since fire could be assigned (N=5 393). Model training and testing were therefore performed using independent portions of the training data set.

The adjustments to the model that were done during the trial and error process were aimed at optimizing the accuracy of the inference of TSF. The accuracy can be assessed in many ways depending on the purpose of the model. Since our objectives are to discriminate between young and old stands, and to assess their proportions on a larger landscape, we attempted to find a balance between the overall accuracy, which is the proportion of all cases whose age-class are correctly classified, and minimizing the absolute difference between type I (false negative) and type II (false positive) errors, which relates to the bias that the model may have towards one age-class or the other. Here, type I and II errors can be inverted depending on what is considered to be positive and negative. All these values can be obtained from a "confusion matrix" that presents all combinations of "actual" states against "predicted" states (Table A1.1). This confusion matrix can be used to adjust the estimated proportions of old and young forest stands if there is a bias toward either one of them:

$$W^T = V^T U$$

where U is the *user probability matrix* (cf. Table A1.1) and W and V are adjusted and predicted case counts, respectively, represented in the form of column vectors (Hess and Bay, 1997).

A sensitivity analysis was performed of the expected time since fire to each environmental correlate calculated in Netica™ using the standard Bayesian learning algorithm, which allowed a ranking of the relative influence of each correlate. Variance reduction was used as a measure of sensitivity (Pearl, 1991), which also allowed for the determination of whether the model behaved in agreement with our current understanding of the system. The predictions of the model were also integrated into a Geographic Information System (GIS) (ArcMap 9.2, ESRI 2006) to visually assess whether the spatial patterns corresponded to those of the fire map of the training area.

For the final model the cross-validation was repeated using 100 random and independent pairs of training/testing sets in order to obtain bootstrap 95% percentile confidence intervals of accuracy.

A1.5 Results

A1.5.1 Model's behavior and performance

The final structure of the model (Fig. A1.3) was a close extension of the simplified model (Fig. A1.2). Almost every attempt to deviate from this starting structure resulted in inferior performance, with the exception of the relative abundance of black spruce (discussed below). The cross-validation indicated an overall accuracy of 80.8% with a bootstrap 95% percentile confidence interval contained within 79.9% and 81.8%. However, the error was unevenly partitioned between old and recently burned stands. The model predicted time since fire better when it was higher than 150 yrs (Table A1.1). Therefore, the unadjusted estimations overestimated the proportion of old forest by 9.1%, according to the fire map from which the model was trained.

Among all environmental correlates, the relative abundance of early (jack pine and poplar) and late (balsam fir) successional tree species were the best indicators of time since last fire according to the sensitivity analysis (Table A1.2). These correlates were followed by vegetation structure variables (photointerpreted age, stocking, height) and edaphic conditions (productivity index), while larch (*Larix laricina* (Du Roi) K. Koch) and white spruce contributed, but to a lesser extent. Knowledge of harvesting history and latitude contribute little to the inference of time since last fire while black spruce did not have any influence on the inference.

A1.5.2 Extrapolation

In general, the prediction patterns appeared to be confirmed by a visual comparison with the spatial distribution of known recent fires, especially in the south-west portion of the Clay Belt study area where there was an aggregation of recent burns that correspond with the model predictions of younger forest (Fig. 5). A large track of predicted young forest in the north central part of the study area, however, did not appear to be validated.

Since the cross-validation in the training area indicated a bias toward old forest stands, the estimated proportion of old forest was adjusted using the confusion matrix. The unadjusted and adjusted estimates are lower on the entire Clay Belt compared to the LAMF (unadjusted: 76.4%; adjusted: 72.5%, Fig. 6) but clearly indicated that stands older than 150 years-old are present on the majority of the study area.

A1.6 Discussion

A1.6.1 Model behavior and predictions

No single correlate considered alone was a strong predictor of time since fire (TSF) according to the variance reduction percentages. For instance, only when jack pine was abundant did it lead to an inference of TSF being less than 150 years, which only applied to 2.86% of all the stands (Table A1.2.). The 3.91% variance reduction provided by the relative abundance of jack pine would appear quite weak in the frequentist framework of multiple linear or nonlinear regressions. However, the ranked relative influences of correlates is in agreement with current knowledge of the post-fire dynamics of the Clay Belt area and their combined contribution provided a useful tool for inferring TSF from the FRI, as suggested by the 81% classification success.

The contribution of the relative abundance of species such as jack pine, poplars and balsam fir followed the successional pathways typical of the region. These three species are closely related to either early (jack pine and poplars) or late (balsam fir) successional stages (Gauthier, De Grandpré and Bergeron, 2000). The sensitivity analysis indicated that black spruce, which is present or abundant on more than 90% of the study and training areas, had no influence on the inference due to the absence of a direct link between black spruce and TSF in the BBN. The abundance of black spruce was relatively constant throughout all successional stages at the landscape scale (Gauthier, De Grandpré and Bergeron, 2000), which restrained its potential contribution to the inference of TSF. However, the structure of black spruce stands may change considerably as TSF increases. After a typical severe burn, a first cohort of black spruce often establishes and develops into a tall, fully stocked stand until it starts to break apart around 150 years post-fire (Harper *et al.*, 2003) (i.e. tall fully stocked stands are more common when TSF < 150 years). Such a change in stand structure seems to be accounted for by the model as indicated by the sensitivity analysis (Table A1.2).

Recently disturbed (< 30 years TSF) and oldest forest stands (> 200 years TSF) can be similar in height and stocking and that may explain the weaker contribution of these correlates to the inference. Site productivity, which was a proxy for edaphic conditions, contributed more than the basic structural attributes, possibly related to the paludification process on the Clay Belt where lower site productivity from paludification is associated with longer TSF (Fenton *et al.*, 2005). Thus the link between black spruce and TSF was only indirect as black spruce polygons were separated from fire history in the BBN by structural attributes and the productivity index.

The photointerpreted age also contributed although its influence seems counterintuitive since stands of young photointerpreted age are encountered more often where TSF is more than 150 years. These stands may consist of trees that did not originate from the last fire but are part of a second or subsequent cohort. This finding suggests that using photointerpreted age as a proxy for time since last fire was not appropriate in such a system where fire-free intervals often exceeds the age of the older trees unless it is combined with some indicator of structure. Several correlates contributed relatively poorly to the inference, such as larch and white spruce, whose presence are usually more related to edaphic conditions than to TSF on the Clay Belt (Gauthier, De Grandpré and Bergeron, 2000).

Latitude also did not greatly contribute to the inference of time since last fire which is an agreement with Bergeron *et al.* (2001) who found that there was no difference in the fire cycle between the southern and the northern part of an adjacent study area. Harvesting history also did not contribute to the inference since it is likely that historically stands chosen for harvesting are not based upon stand age (e.g., harvest oldest stands first) but upon high volume.

For the Clay Belt of Ontario, the knowledge of the prevalence of old forest stands (TSF >150 years) that was already documented for the LAMF (Gauthier *et al.*, 2002) was extended to the entire area. Our results show a slightly lower proportion of old forest stands in the entire Clay Belt that supports the general belief of a west-east gradient of decreasing fire activity. However, this gradient was not very strong, especially considering that most of the large fires that affected the south-western portion of the Clay Belt apparently started outside of the region (Fig. 5). This suggests that the wet lowland physiographic characteristics of the Clay Belt may have an influence on the overall fire regime of a comparable magnitude to the regional climate. Thus the Clay Belt has considerably lower fire activity relative to the rest of the area associated with the Humid Mid-Boreal Ecoclimatic Region, and that it is made up of a matrix of old forest stands where younger patches can be found.

The cross-validation suggested an overestimation of the proportion of old forest by the model. A blind run of the model in the training area, where all prior knowledge of fire history was removed, yielded an estimate of 85% which is 9% higher than the actual value. Our interpretation of this overestimation mainly resides in the fact that unburned patches within the perimeter of burned areas are usually not reported. These old stands for which a short TSF was assigned potentially provided "poor examples" for the BBN to learn from and to use in the testing phase. Both steps certainly contributed in generating the observed bias. The proportions of unburned stands within the perimeter of burned areas are reported are often quite substantial. For example, 44% of the area affected by the 1988 Yellowstone fires was left unburned or only lightly burned (Turner *et al.*, 1994). Similarly, 32.2% of the area contained by the outmost boundaries of a 1995 in the Abitibi region of Quebec were either completely unburned (2.6%) or had mixed patches with green trees in greater proportion than the scorched ones (27.6%) (Kafka, Gauthier and Bergeron, 2001). The overall proportion of old forest stands can be adjusted for this bias but this does not necessarily mean that the unadjusted estimation is erroneous. We suggest that some proportion of this error was not, in fact, a classification error but an error introduced by the limited resolution of the fire map itself. A field survey or a close examination of aerial or satellite images would be necessary to confirm and quantify the extent of such an error. The typical proportions of unburned patches that are reported in the literature, however, are very similar to the 36% classification error of allegedly young stands (Table A1.2), according to the fire map. Our opinion is that the actual overall proportion of old forest is much likely somewhere between our adjusted and unadjusted estimates. The adjusted estimate is probably more representative of large continuous tracks of old forests while the unadjusted estimates is probably more representative of the sum of all old forests, including the "residual" old forest stands within recent burns.

A1.6.2 Critical assessment of the model

Uusitalo (2007) reviewed the inherent advantages and challenges to the use of BBN in environmental and management modeling. Among the possible pitfalls of working with BBN are the lack of support for feedback loops, the difficulties of collecting and structuring expert knowledge, and the obligation of discretizing continuous variables (Uusitalo, 2007).

BBN complexity and completeness can be limited by the lack of support for feedback loops of BBNs because they are by definition acyclic. Incorporating feedback loops would have been essential if the purpose of our model was to simulate fire regimes in a dynamic landscape with heterogeneous probability of burning. Then we need to account for possible feedback from vegetation composition towards disturbance regimes and edaphic conditions through the process of paludification, for example (Cyr *et al.*, 2005 ; Fenton *et al.*, 2005). However, our goal was to obtain a snapshot image of the fire history for a large landscape, therefore the lack of support for feedback loops was not considered a major inconvenience in the present study.

Our use of expert knowledge during the development of the model was relatively limited when compared to other studies because the learning of conditional dependencies between variables relied completely on empirical observations. Expert knowledge was used only during the development of the model's structure as well as during the discretization of continuous variables. In some studies of very complex systems, it may be difficult to establish which variables are the causes and which are the effects. In our study, however, we purposely limited ourselves to the use of environmental correlates for which data are widely available from provincial inventory. Moreover, the direction of causal relationships revealed to be rather uncontroversial, judging by the comments received after presenting preliminary versions of the model at a workshop and a conference.

Discretizing continuous variables may cause some loss of predictive power because it leads to focusing on rough characteristics of conditional dependencies between environmental correlates. However, this loss of predictive power is generally observed when the relationship between correlates are linear while the non-linear relationship in our model may have actually been better captured with variables that are discretized (Myllymäki *et al.*, 2001). Furthermore, increasing the number of possible states of each correlate was not beneficial to the model's inferences despite the fact that the number of cases available to train the model was sufficient to adequately populate the CPTs. This result can be partly explained by the relative imprecision and inaccuracy that characterize the FRI (Pinto *et al.*, 2007 ; Thompson *et al.*, 2007), which were likely moderated by discretizing continuous variables into broad categories.

Our 81% classification success remains hard to objectively assess due to the lack of a comparable study. However, we believe our model to be robust as forest resource inventories have not been considered accurate enough to be useful for fire history reconstruction since they were mainly developed from photo interpretation. We also consider our attempt to produce an unbiased and robust estimation of the proportion of old forest stands to be a success. The possibility to adjust for any potential bias using the confusion matrix through the cross-validation was clearly a valuable feature of this method.

A1.6.3 Consequences for management

Forest management planning directed by emulation of the natural disturbance pattern policy require regionally specific targets for the proportion of old forest in an unevenaged condition. In the absence of a formal fire history reconstruction based on field surveys, the method described in this paper provides an unbiased and objective method to derive old forest targets. The method is inexpensive compared to constructing a formal TSF map and is flexible in accepting various types of input information thus can be easily applied to an entire managed landbase where only a broad level inventory and one or a few representative fire history reconstructions are available.

A1.6.4 Potential Future Research

We believe that the method presented here has the potential to better describe spatial patterns generated by natural fire regimes. It could also be used to obtain an objective method of distinguishing between "residual" old stands and large tracks of old forest in regions where fire history reconstructions are sparsely distributed. The eastern boreal forest is characterized by fire-free intervals that are usually longer than the longevity of the first post-fire cohort, hence creating a matrix of old forest stands within which more recently burned areas are sparsely distributed (Bergeron *et al.*, 2006). Whereas in the western boreal forest shorter fire-free intervals create a matrix of first-cohort stands within which old stands are more or less sparsely dispersed (Boychuk and Perera, 1997 ; Johnson, Miyanishi and Weir, 1995). The method presented here allows for the assessment of regional patterns within the broad eastern and western areas.

This model was aspatial and, thus, considers each stand separately. The results were incorporated into a GIS *a posteriori*. Incorporating spatial information would be an improvement of the model that could be addressed in further developments. Forest fire is indeed a very contagious process (Li and Apps, 1996 ; Peterson, 2002) where stands with similar TSF are usually often found close to one another. Considering such spatial information would most certainly improve the classification success and, possibly, the resolution at which TSF can be inferred.

A1.7 References

Attiwill, Peter M. 1994. «The disturbance of forest ecosystems: The ecological basis for conservative management.». *Forest Ecology and Management*, vol. 63, no 2-3, p. 247-300.

Bergeron, P.Y., B. Harvey, A. Leduc and S. Gauthier. 1999. «Strategies for forest management based on the dynamics of natural disturbances: Stand- and forest-level considerations». *Forestry Chronicle*, vol. 75, no 1, p. 49-54.

Bergeron, Y., D. Cyr, C.R. Drever, M. Flannigan, S. Gauthier, D. Kneeshaw, E. Lauzon, A. Leduc, H. Le Goff, D. Lesieur and K. Logan. 2006. «Past, current, and future fire frequencies in Quebec's commercial forests: Implications for the cumulative effects of harvesting and fire on age-class structure and natural disturbance-based management». *Canadian Journal of Forest Research*, vol. 36, no 11, p. 2737-2744.

Bergeron, Y., S. Gauthier, M. Flannigan and V. Kafka. 2004. «Fire regimes at the transition between mixedwood and coniferous boreal forest in northwestern Quebec». *Ecology*, vol. 85, no 7, p. 1916-1932.

Bergeron, Yves, Sylvie Gauthier, Victor Kafka, Patrick Lefort and Daniel Lesieur. 2001. «Natural fire frequency for the eastern Canadian boreal forest: Consequences for sustainable forestry.». *Canadian Journal of Forest Research*, vol. 31, no 3, p. 384-391.

Boissonneau, A.N. 1966. «Glacial history of northeastern Ontario». *Canadian Journal of Earth Science*, vol. 3, p. 559-578.

Boychuk, D., and A.H. Perera. 1997. «Modeling temporal variability of boreal landscape age-classes under different fire disturbance regimes and spatial scales». *Canadian Journal of Forest Research*, vol. 27, no 7, p. 1083-1094.

Cyr, D., Y. Bergeron, S. Gauthier and A. Larouche. 2005. «Are the Old-Growth Forests of the Clay Belt Part of a Fire-Regulated Mosaic?». *Canadian Journal of Forest Research*, vol. 35, no 1, p. 65-73.

Cyr, D., S. Gauthier, Y. Bergeron and C. Carcaillet. 2009. «Forest management is driving the eastern North American boreal forest outside its natural range of variability». *Frontiers in Ecology and the Environment*, vol. 7, no 10, p. 519-524.

Ecological Stratification Working Group (1995). A national ecological framework for Canada. Ottawa, On., Agriculture and Agri-Food Canada, Research Branch, Centre for Land Biological Resources Research and Environment Canada, State of the Environment Derectorate, Eco

Ecoregions Working Group (1989). Ecoclimatic regions of Canada, First Approximation. Ecoregions. Ecological Land Classification Series No. 23. Ottawa, On., Ecoregions Working Group of the Canada Committee on Ecological Land Classification. Sutainable Development Branch, Canadian Wildlife Service, Conservation and Protection, Environment Canada

Etheridge, D. A., D. A. MacLean, R. G. Wagner and J. S. Wilson. 2005. «Changes in landscape composition and stand structure from 1945-2002 on an industrial forest in New Brunswick, Canada». *Canadian Journal of Forest Research*, vol. 35, no 8, p. 1965-1977.

Fenton, N., N. Lecomte, S. Legare and Y. Bergeron. 2005. «Paludification in Black Spruce (Picea Mariana) Forests of Eastern Canada: Potential Factors and Management Implications». *Forest Ecology and Management*, vol. 213, no 1-3, p. 151-159.

Forest Stewardship Council - Canada Working Group. 2004. «National boreal standard». En ligne. <http://www.fsccanada.org/docs/39146450F65AB88C.pdf>.

Franklin, J.F. 1993. «Preserving biodiversity: species, ecosystems, or landscapes». *Ecological Applications*, vol. 3, p. 202-205.

Galindo-Leal, C., and F.L. Bunnel. 1995. «Ecosystem management: implications and opportunities of a new paradigm». *The Forestry Chronicle*, vol. 71, no 5, p. 601-606.

Gauthier, S., L. De Grandpré and Y. Bergeron. 2000. «Differences in forest composition in two boreal forest ecoregions of Québec». *Journal of Vegetation Science*, vol. 11, p. 781-790.

Gauthier, S., P. Lefort, Y. Bergeron and P. Drapeau (2002). Time since fire map, age-class distribution and forest dynamics in the Lake Abitibi Model Forest. Saint-Foy, Qc., Natural Resources Canada, Canadian Forest Service, Laurentian Forestry Centre, Information Report LAU-X-125E

Harper, K., Y. Bergeron, S. Gauthier and P. Drapeau. 2002. «Post-fire development of canopy structure and composition in black spruce forests of Abitibi, Québec: a landscape scale study». *Silva Fennica*, vol. 36, no 1, p. 249-263.

Harper, K., C. Boudreault, L. DeGrandpré, P. Drapeau, S. Gauthier and Y. Bergeron. 2003. «Structure, composition, and diversity of old-growth black spruce boreal forest of the Clay Belt region in Quebec and Ontario». *Environmental Reviews*, vol. 11, p. S79-S98.

Harper, K.A., Y. Bergeron, P. Drapeau, S. Gauthier and L. De Grandpré. 2005. «Structural development following fire in black spruce boreal forest». *Forest Ecology and Management*, vol. 206, no 1-3, p. 293-306.

Hess, G.R., and J.M. Bay. 1997. «Generating confidence intervals for composition-based landscape indexes». *Landscape Ecology*, vol. 12, no 5, p. 309-320.

Hunter, M.L. Jr. 1999. *Maintaining biodiversity in forest ecosystems*. Cambridge, UK.: Cambridge University Press.

Johnson, E A, K Miyanishi and J M H Weir. 1995. «Old-growth, disturbance, and ecosystem management.». *Canadian Journal of Botany*, vol. 73, no 6, p. 918-926.

Kafka, V., S. Gauthier and Y. Bergeron. 2001. «Fire Impacts and Crowning in the Boreal Forest: Study of a Large Wildfire in Western Quebec». *International Journal of Wildland Fire*, vol. 10, no 2, p. 119-127.

Kneeshaw, D., and S. Gauthier. 2003. «Old-growth in the boreal forest: A dynamic perspective at the stand and landscape level». *Environmental Reviews*, vol. 11, p. S99-S114.

Kohm, K.A, and J.F. Franklin. 1997. *Creating a forestry for the twenty-first century: the science of ecosystem management*. Washington, DC: Island Press.

Lefort, P., B. Harvey, J. Parton and G.K.M. Smith. 2002. «Synthesizing knowledge of the Claybelt to promote sustainable forest management». *The Forestry Chronicle*, vol. 78, no 5, p. 665-671.

Li, Chao, and Michael J Apps. 1996. «Effects of contagious disturbance on forest temporal dynamics.». *Ecological Modelling*, vol. 87, no 1-3, p. 143-151.

Mackey, B. G., D. W. McKenney, Y. Q. Yang, J. P. McMahon and M. F. Hutchinson. 1996a. «Erratum: Site regions revisited: A climatic analysis of Hill's site regions for the province of Ontario using a parametric method (Canadian Journal of Forest Research (1996) 26 (333-354))». *Canadian Journal of Forest Research*, vol. 26, p. 1112.

--------. 1996b. «Site regions revisited: A climatic analysis of Hill's site regions for the province of Ontario using a parametric method». *Canadian Journal of Forest Research*, vol. 26, p. 333-354.

Marcot, B.G., R.S. Holthausen, M.G. Raphael, M.M. Rowland and M.J. Wisdom. 2001. «Using Bayesian belief networks to evaluate fish and wildlife population viability under land management alternatives from an environmental impact statement». *Forest Ecology and Management*, vol. 153, no 1-3, p. 29-42.

Marcot, B.G., J.D. Steventon, G.D. Sutherland and R.K. McCann. 2006. «Guidelines for developing and updating Bayesian belief networks applied to ecological modeling and conservation». *Canadian Journal of Forest Research*, vol. 36, no 12, p. 3063-3074.

McCarthy, Brian C, Christine J Small and Darrin L Rubino. 2001. «Composition, structure and dynamics of Dysart Woods, an old-growth mixed mesophytic forest of southeastern Ohio.». *Forest Ecology and Management*, vol. 140, no 2-3, p. 193-213.

Myllymäki, P., T. Silander, H. Tirri and P. Uronen. 2001. *B-course: A web service for Bayesian data analysis*: *Proceedings of the International Conference on Tools with Artificial Intelligence*. 247-256 p.

Naïm, P., P.-H. Wuillemin, P. Leray, O. Pourret and A. Becker (2004). Réseaux bayésiens. Paris, Groupe Eyrolles

Ontario Ministry of Natural Resources. 1994. «Crown Forest Sustainability Act». En ligne. <http://www.e-laws.gov.on.ca/html/statutes/english/elaws_statutes_94c25_e.htm>.

-------- (2007). Forest information manual: Forest management planning technical specifications. Technical Series, Government of Ontario En ligne. <http://www.mnr.gov.on.ca/en/Business/Forests/Publication/MNR_E000214P.html>.

Pearl, J. (1991). Probabilistic reasoning in intelligent systems: Networks of plausible inference. San Mateo, California, Morgan Kaufmann Publishers, Inc.

--------. 2000. *Causality: models, reasoning, and inference.* Cambridge, UK: Cambridge University Press.

Perera, A. H., B. D. Dalziel, L. J. Buse and R. G. Routledge. 2009. «Spatial variability of stand-scale residuals in Ontario's boreal forest fires». *Canadian Journal of Forest Research*, vol. 39, no 5, p. 945-961.

Peterson, G.D. 2002. «Contagious disturbance, ecological memory, and the emergence of landscape pattern». *Ecosystems*, vol. 5, no 4, p. 329-338.

Pinto, F., M. Ter-Mikaelian, J.-M. Sobze and D. Rouillard (2007). A method to validate stand attributes in a forest resource inventory: Case study in Nipissing Forest, Ontario. Sault Ste.Marie, Ontario, Applied Research and Development, Ontario Ministry of Natural Resources

Seymour, R. S., and M.L. Jr Hunter. 1999. «Principles of ecological forestry». In *Maintaining biodiversity in forest ecosystems,* M.L. Hunter, p. 22-61. Cambridge: Cambridge University Press.

Smith, C. S., A. L. Howes, B. Price and C. A. McAlpine. 2007. «Using a Bayesian belief network to predict suitable habitat of an endangered mammal - The Julia Creek dunnart (Sminthopsis douglasi)». *Biological Conservation*, vol. 139, no 3-4, p. 333-347.

Stocks, B.J., J.A. Mason, J.B. Todd, E.M. Bosch, B.M. Wotton, B.D. Amiro, M.D. Flannigan, K.G. Hirsch, K.A. Logan, D.L. Martell and W.R. Skinner. 2003. «Large forest fires in Canada, 1959-1997». *Journal of Geophysical Research*, vol. 108, p. doi:10.1029/2001JD000484.

Thompson, I.D., S.C. Maher, D.P. Rouillard, J.M. Fryxell and J.A. Baker. 2007. «Accuracy of forest inventory mapping: Some implications for boreal forest management». *Forest Ecology and Management*, vol. 252, no 1-3, p. 208-221.

Turner, M.G., W.W. Hargrove, R.H. Gardner and W.H. Romme. 1994. «Effects of fire on landscape heterogeneity in Yellowstone National Park, Wyoming». *Journal of Vegetation Science*, vol. 5, no 5, p. 731-742.

Uusitalo, L. 2007. «Advantages and challenges of Bayesian networks in environmental modelling». *Ecological Modelling*, vol. 203, no 3-4, p. 312-318.

Uusitalo, L., S. Kuikka and A. Romakkaniemi. 2005. «Estimation of Atlantic salmon smolt carrying capacity of rivers using expert knowledge». *ICES Journal of Marine Science*, vol. 62, no 4, p. 708-722.

Vasiliauskas, S., H.Y.H. Chen, J. Parton, P. Henry, G. Lucking, M. Brienesse, S. Osawa and R. Arnup (2004). Successional pathways - proposed SFMN rules for notheastern regional standard forest units. Version 2. Ontario Ministry of Natural Resources. South Porcupine, On.: 12 pp. p

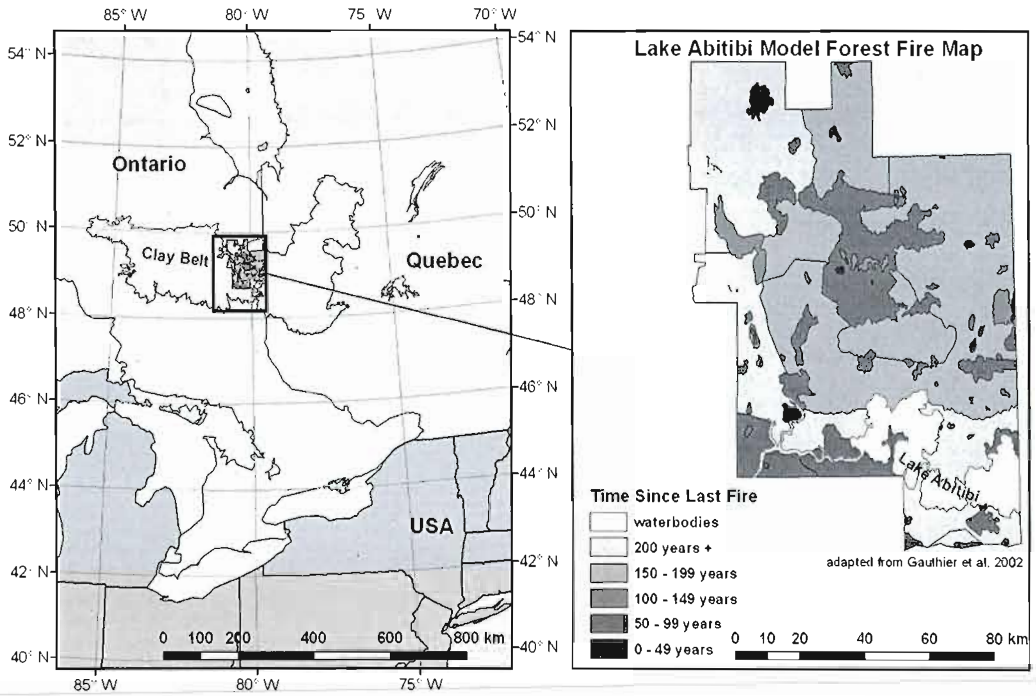


Figure A1.1 The study area is an approximately 6.5 million ha portion of Clay Belt located in northeastern Ontario (a). The training area for the Bayesian Belief Network model is located on the Lake Abitibi Model Forest (b) where detailed disturbance history and a forest inventory is available.

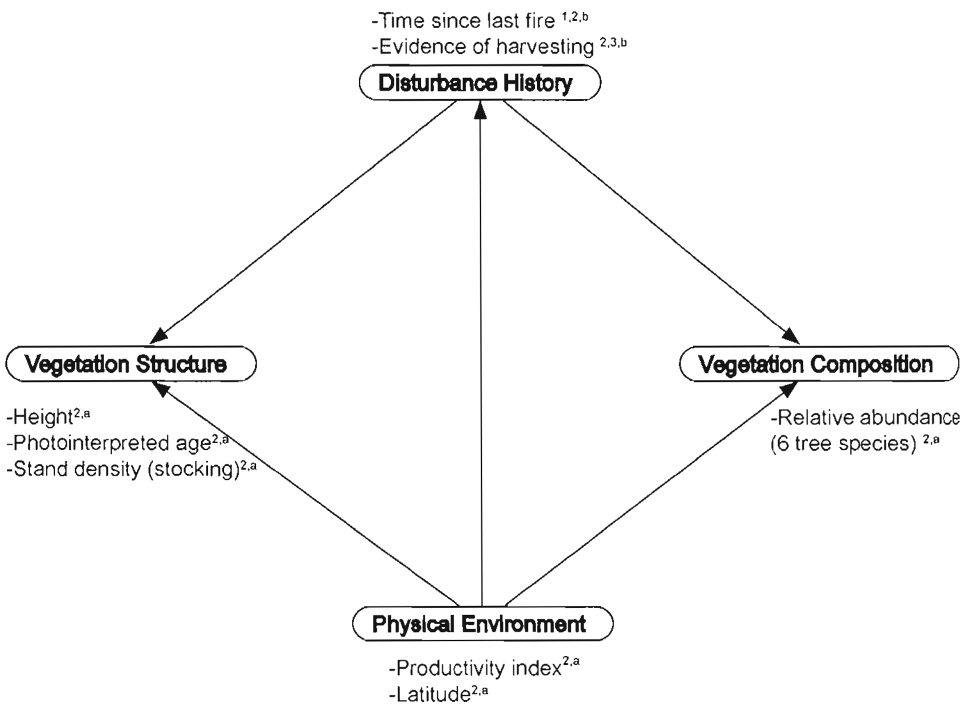


Figure A1.2 Simplified influence diagram showing the general structure of the model and input information provenance. [1]Gauthier *et al.* (2002). [2]Ontario FRI 2002 [3]As provided by operating companies [a]Available in the entire study area [b]Available in the training area and partially available (incomplete data) in the extrapolated area.

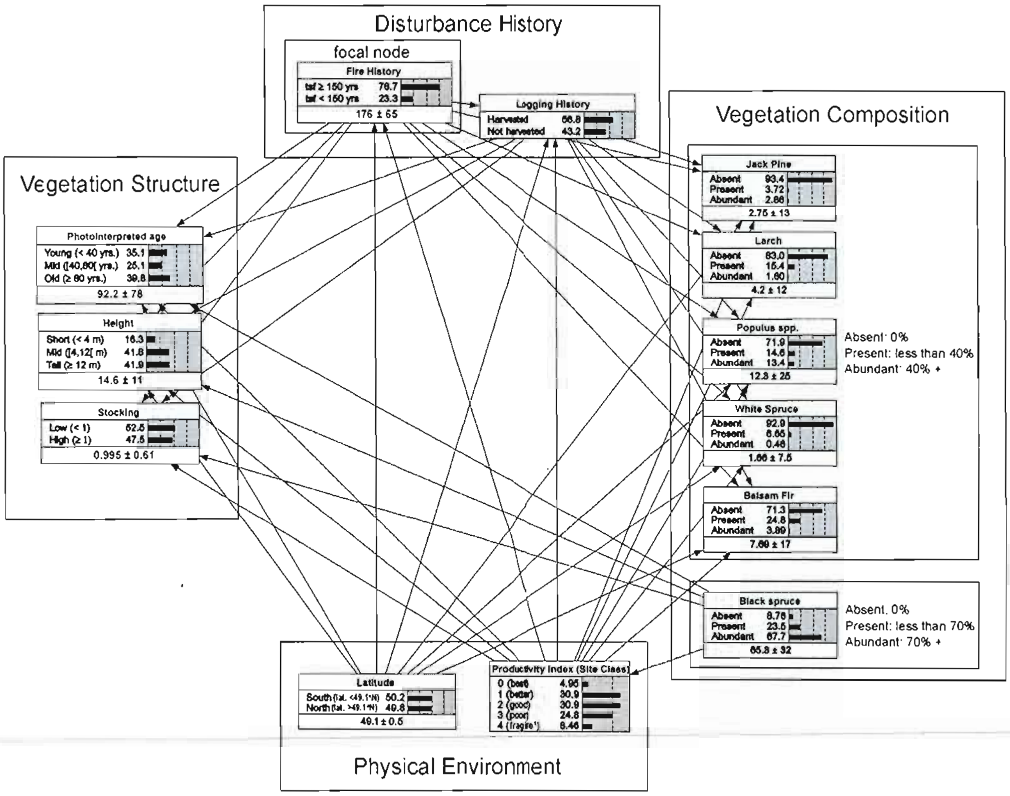


Figure A1.3 Model's complete structure showing each environmental correlate and their global frequency distribution in the training area (in percentage). Mean ± standard deviation are also reported at the bottom of nodes representing continuous variables. Note that mean TSF should be interpreted as a minimum estimate as only a minimum TSF is known for some of the older stands. [1]"Fragile" indicates productive stands on which forest management activities cannot normally be practiced without incurring deleterious environmental effect because of physical limitation such as steep slopes or shallow soils (Ontario Ministry of Natural Resources, 2007).

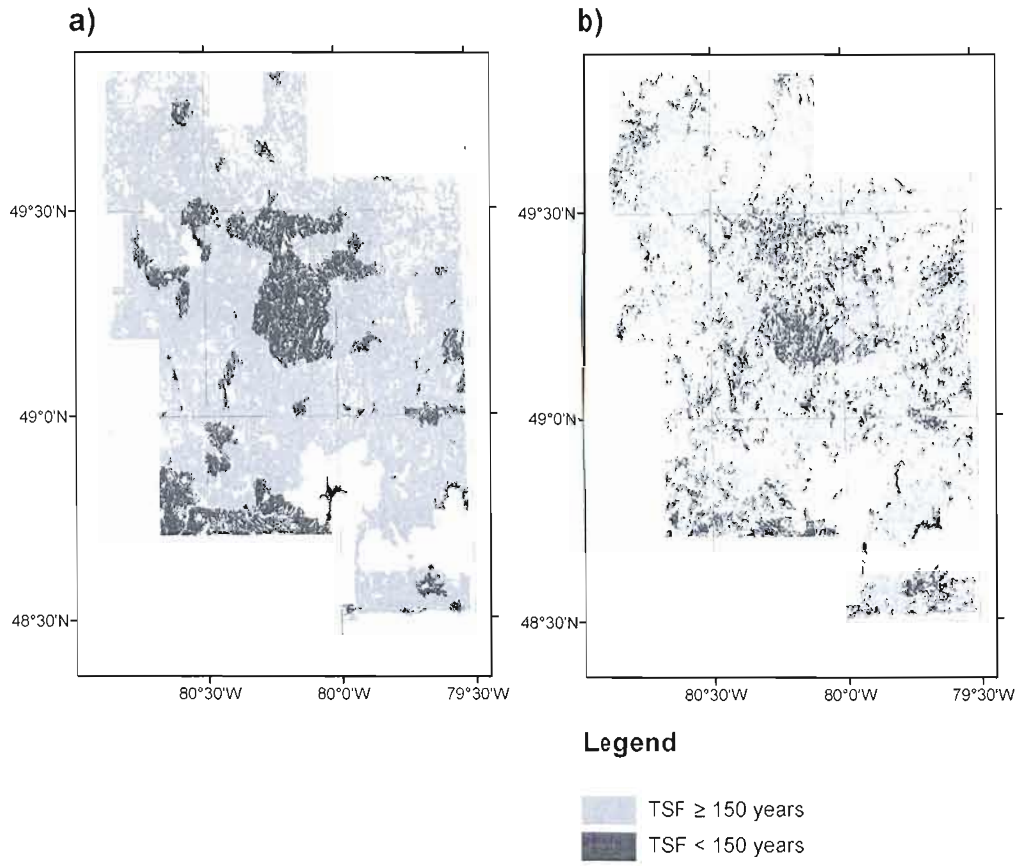


Figure A1.4 Time since fire in the training area (Lake Abitibi Model Forest) as indicated by **a)** the fire map from Gauthier *et al.* (2002) and **b)** a blind run of the Bayesian Belief Network.

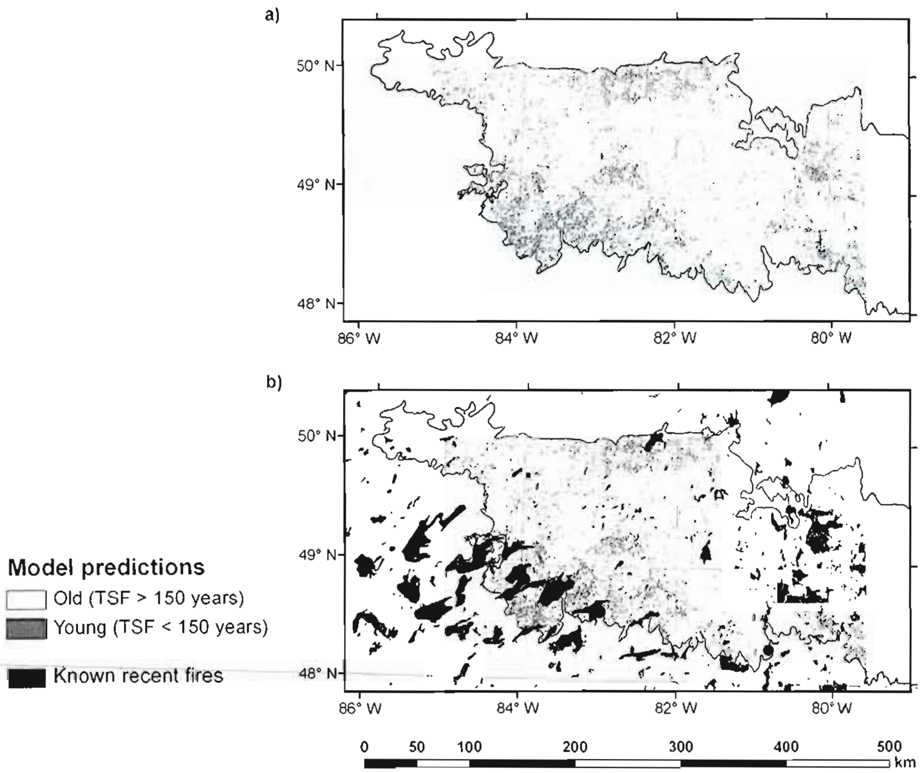


Figure A1.5 Extrapolation a) without known recent burns b) with known recent burns. Model predictions are expressed as a likelihood from 0 to 1 and a threshold of 0.5 is used for discriminating old and young stands. The extrapolation was made without any prior knowledge of fire history. The fire polygons presented in panel b) cover from 1920 to 2002 and are only shown as a simple visual validation. This fire history database is not complete and presents important gaps, especially in remote areas (Stocks *et al.*, 2003).

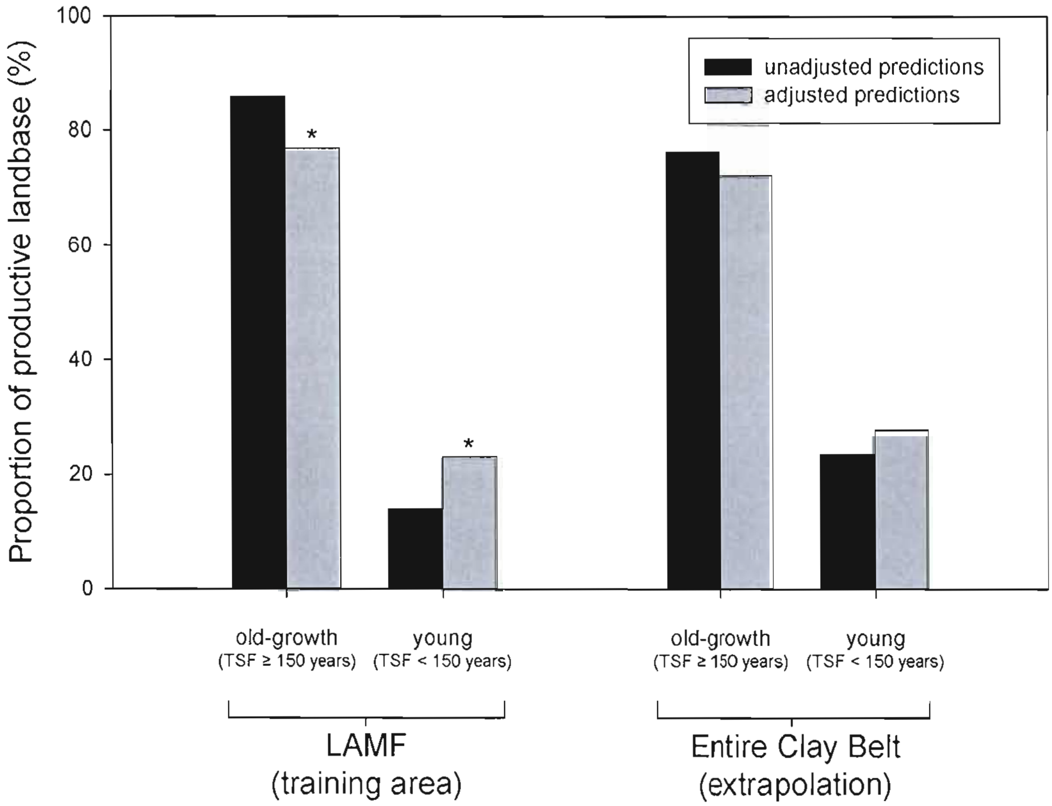


Figure A1.6 Predicted proportions of the productive landbase occupied by old and young stands. *Also as indicated by the fire map from Gauthier *et al.* (2002).

Table A.1 Averaged confusion matrix after 100 train/test random combinations from the training area (N=5393). Absolute values indicate the frequency of cases while percentages in italics are calculated by using the corresponding *row* total. Shaded cells show either type I (false negative) or type II errors (false positive). [a]These percentages constitute the *user probability matrix*.

Actual		
TSF ≥ 150 years 4145 (76.9%)	TSF < 150 years 1248 (23.1%)	**Predicted**
3873 *(83.5%[a])*	765 *(16.5%[a])*	TSF ≥ 150 years 4638 (86.0%)
272 *(36.0%[a])*	483 *(64.0%[a])*	TSF < 150 years 755 (14.0%)

Table A1.2 Sensitivity of time since fire classification to other environmental correlates in the training area. [a]The average time since fire prior to the incorporation of knowledge of any other correlates is 176 years in the training area. [b]Minima and maxima are the mean TSF after incorporating knowledge of only one environmental correlate. The state of the correlate corresponding to the minimum or maximum is in parentheses (also refer to Fig. A1.3).

Environmental correlates (ranked by decreasing order of variance reduction)	**Mean Time Since Fire**[a]		**Variance Reduction (%)**
	Minimum *a posteriori*[b]	**Maximum *a posteriori***[b]	
Jack Pine	124 (abundant)	179 (absent)	3.91
Populus spp.	157 (abundant)	180 (absent)	1.91
Balsam Fir	171 (absent)	189 (abundant)	1.79
Photointerpreted age	168 (mid)	185 (young)	1.53
Productivity index	152 (good)	192 (best)	1.19
Stocking	170 (high)	181 (low)	1.04
Height	170 (tall)	181 (mid)	0.83
Larch	174 (absent)	184 (present)	0.41
White spruce	159 (abundant)	186 (present)	0.32
Harvesting history	174 (harvested)	177 (not harvested)	0.06
Latitude	175 (north)	177 (south)	0.03
Black spruce	176	176	0