An integrated model of stand dynamics, soil carbon and fire regime:

Applications to boreal ecosystem response to climate change

Thèse

Yosune Miquelajauregui Graf

Doctorat en sciences forestières
Philosophiæ doctor (Ph. D.)

Québec, Canada

Résumé

Les forêts d'épinettes noires (*Picea mariana* (Mill.) BSP) contiennent de grandes quantités de carbone stockées dans la biomasse vivante et dans le sol. Les feux de forêt et leur régime (ex. l'intervalle de retour de feu, l'intensité, la saisonnalité et la sévérité) jouent un rôle central dans le stockage et le flux du carbone, en modifiant la distribution et le transfert de carbone. Il y a peu de doute dans la communauté scientifique que le changement climatique provoquera des modifications dans les variables temporelles et spatiales qui contrôlent la fréquence et la sévérité des feux. Un modèle démographique structuré par classes de diamètre a été développé pour simuler le stockage du carbone sous divers régimes de feu. Cette approche intègre l'effet de l'intensité du feu et les mesures de la structure du peuplement sur la sévérité mesurée par la proportion de la mortalité des arbres. Le modèle permet aussi de quantifier et de cartographier les estimations régionales du carbone actuelles et futures pour le domaine bioclimatique de la pessière à mousses du nord du Québec. Les résultats de simulations suggèrent que la sévérité du feu augmente avec l'intensité initiale du feu. La variation de la structure du peuplement est l'un des facteurs qui explique la variation observée dans la sévérité du feu des régions boréales. Nous avons simulé les stocks et fluctuations de carbone sous sept niveaux d'intervalle de retour de feu et deux saisons de feu. Nous avons testé pour un effet de ces paramètres sur la moyenne des stocks de carbone. Les stocks de carbone étaient sensibles aux intervalles entre 60 et 300 ans. Le stock de carbone dans le sol fut plus faible pour les incendies d'été qui se produisaient durant de plus courts IRF. Finalement, les impacts à court terme du changement climatique ont été investigués au cours de quatre périodes climatiques : 1980-2010, 2010-2040, 2040-2070 et 2070-2100. Des cartes d'intervalle de retour du feu historique et futur et des données météorologiques projetées par CanESM2 RCP8.5 ont été utilisées pour simuler la croissance des forêts, le taux de décomposition, le régime du feu et la dynamique du C. Dans nos expériences de simulation, l'accumulation de carbone dans l'écosystème était réduite de 11% d'ici à la fin de 2100. Les forêts d'épinette noire du Québec seraient possiblement en train de perdre leur capacité à séquestrer et à stocker le carbone organique durant les prochaines décennies, à cause des effets du changement climatique sur le régime de feu et la croissance des forêts.

Abstract

Boreal black spruce forests (*Picea mariana* (Mill.) BSP) store great amounts of carbon in the living biomass and in the soil. Fire regime characteristics (e.g. fire return interval, fire intensity, fire season and severity) play a central role in the storage and flow of carbon, by modifying the distribution and transfer of material among pools. There is little doubt in the scientific community that climate change will cause changes in the temporal and spatial variables that control the frequency and severity of fires. A demographic diameter-class structured model was developed to simulate boreal carbon storage under different fire regimes. This approach incorporates the effect of fire intensity and stand structure measures to simulate fire severity, measured as the proportion of overstory tree mortality. The model allows quantifying and mapping average regional estimates of current and future carbon stocks for the black spruce-feathermoss bioclimatic domain of northern Québec. Simulation results suggest that fire severity increases with fire the intensity. Stand structure is one of the factors that explains the observed variation in boreal fire severity. We simulated carbon stocks and fluxes under seven levels of fire return interval (FRI) and two fire seasons. We tested for an effect of these parameters on average carbon stocks. Carbon stocks were sensitive to IRF's between 60 and 300 years. Soil C stocks were lower for summer fires that occurred during shorter IRF. Finally, we investigated the short-term impacts of climate change under four climatic periods: 1980-2010, 2010-2040, 2040-2070 and 2070-2100. Historical and future FRI maps and historical and forecasted weather data estimated by CanESM2 RCP8.5 were used to drive the growth of forests, decomposition rates, fire regime and C dynamics. In our simulation experiments, the accumulation of carbon in the ecosystem was reduced by 11% by the end of 2100. The results of this study suggest that black spruce forest could be losing their capacity to sequester and store organic C over the next coming decades due to climate change effects on the fire regime and on forest growth.

Table of contents

List of tables

List of figures

Acknowledgements

This research was supported by funding from NSERC (Natural Sciences and Engineering Research Council of Canada) Strategic grant to A.D. Munson, R.L. Bradley, S.G. Cumming, S. Gauthier, D. Paré and S. Quideau. Financial support was also obtained from a NSERC-CGS D-Alexander Graham Bell Graduate scholarship to Y. Miquelajauregui. The author also received financial support from Produits forestiers Résolu and F.K. Morrow Foundation. I specially thank the Centre d'étude de la forêt (CEF) for financial and logistic support.

I would like to express my sincere gratitude to my supervisor Dr. Steve Cumming for his support and guidance during the time this thesis was completed. My co-supervisor Dr. Sylvie Gauthier who always provided important insights and comments on my work, thanks. I also want to thank the members of the C*Fire team at Université Laval for their important intellectual role during my Ph.D studies. My special gratitude to the CEF for providing important support which allowed me to improve my skills. I would like to acknowledge the help of Dr. Changhui Peng during my research stage at his laboratory.

This work was completed with the help of many people and institutions. I thank the Ministère des Ressources Naturelles for providing access to the Québec forest inventory data and to the Société de protection des forêts contre le feu (SOPFEU) for the historical forest fire database. I want to thank D. Boucher for her help with the stand structure classification, Y. Boulanger for allowing access to the fire regime maps, J. Marchal for his help with coding, M. Fortin for his guidance with the use of ARTEMIS and to R. Saint-Amant for his help with BIOSIM. I want to thank F. Raulier and N. Dhital for their assistance during the completion of the last chapter of this thesis. I also want to recognize the great support of Dr. Luis A. Bojórquez Tapia from the National Laboratory of Sustainability Sciences, UNAM for allowing me to work on my thesis and complete it on time.

Specially, I want to express my gratitude to my beautiful family, to mom, dad, Unai, Bartholomew, Julia, Bambas and Max who despite the distance, were always close to my heart. Their presence has helped me overcoming the challenges of life. In the memory of those who are not here with me anymore, Tita and abuelito, Amona and Aitona, Tere, Nandito, Nico and Akira, you are all part of me. Special thanks to my friends and loved ones who have allowed me to grow with them.

Preface

This thesis entitled “An integrated model of stand dynamics, soil carbon and fire regime: Applications to boreal ecosystem response to climate change” is composed of three chapters written in English which are presented in the form of scientific papers. All the papers and information presented in this thesis are my original contributions aimed at obtaining a Ph.D in Forest Sciences at Université Laval, Québec, Canada. The model presented here, including its framework and modules was developed and coded entirely by the author.

Chapter 1- Miquelajauregui,Y., Cumming, SG and Gauthier, S. 2016. Modelling variable fire severity in boreal forests: effects of fire intensity and stand structure PLoS ONE 11(2).

Chapter 2- Miquelajauregui, Y., Cumming, SG and Gauthier, S. Sensitivity of boreal carbon stocks to fire return interval and seasonality of head fire intensity: a simulation study of black spruce (submitted to Ecosystems in May 2016; revised in July 2016).

Chapter 3- Miquelajauregui, Y., Cumming, S.G and Gauthier, S. Short-term responses of boreal carbon stocks to climate change: a simulation study of black spruce forests.

In addition to the papers mentioned above, a book chapter entitled “Simulation models of C dynamics/ Modelos de simulación de la dinámica del carbono” was published in 2013 by OmniaScience. The book chapter was the product of my attendance to the 6th annual summer course in Flux Measurements and advanced Modelling which took place at the University of Colorado Mountain Research Station, Boulder, Colorado.

This thesis has been directed by Dr. Steve Cumming, who is coauthor in all the chapters of this thesis. Sylvie Gauthier provided the fire intensity data and helped with the experimental design of all chapters. She also participated in the drafting and organization of all chapters. I want to acknowledge the help of the coauthors.

General Introduction

The Canadian boreal forest is a vast region of mostly coniferous forest dominated by black spruce (*Picea mariana* (*Mill. B.S.P*)), the most important fuel type in the region (Hirsch 1996). In Québec, the black spruce boreal forest represents 28% of terrestrial surface area (Rowe 1972, Saucier et al. 1998) and 52% of commercial forest (de Groot et al. 2003). The primary natural disturbance in coniferous boreal landscapes is fire, and large, high-intensity crown fires have long been regarded as characteristic of the region (Van Wagner 1983, Harper et al. 2005, Kashian et al. 2006). The boreal fire regime is mainly driven by regional climate along with fuel and ignition characteristics (Kasischke et al. 1995, Kafka et al. 2001, Aakala et al. 2007, Boulanger et al. 2013). Fire regime parameters, including the fire return interval, fire intensity, size, season of burning and fire severity largely determine patterns of boreal ecosystem structure and function (Oliver and Larson 1996, Johnstone 2011, Boulanger et al. 2013). Therefore, variations in the fire regime could lead to changes in stand structure and successional trends (Harper et al. 2005, Brassard and Chen 2006), forest productivity (Johnstone and Chapin 2006) and flammability (Van Wagner 1983), and the regional carbon balance (Bergeron et al. 2004, Kashian et al. 2006).

Fire return interval is defined as the mean number of years between successive fires at a given location, over a given time period (Li 2002). In eastern boreal forests of Quebec, historical fire return intervals range from 100 years in the western regions to more than 500 years in the eastern ones (Boucher et al. 2003, Bouchard et al. 2008, Chabot et al. 2009). In black spruce forests an initial cohort of spruce establishes immediately after a fire, giving rise to a dense, largely uniform, single-layered canopy forest with stems that are relatively homogeneous in diameter (Brassard and Chen 2006). As the stand develops, this stand structure gradually develops into a more open, multi-sized forest containing stems that originated from seed after the fire or from layering (Bergeron et al. 2002). In the prolonged absence of fire, black spruce canopy dominance is maintained through time by disturbances other than fire (e.g. gap dynamics, defoliating insects, wind; Harper et al. 2003, Forest et al. 2006, Rossi et al. 2009). Long fire return intervals lead to stands with an uneven distribution of tree sizes, whereas even-sized stands with a regular distribution of tree sizes are formed under shorter fire return intervals (Kasischke et al. 1995, Boucher et al. 2003, Bouchard et al. 2008, Gauthier et al. 2009).

Fire intensity is a descriptor of forest fire behaviour which is correlated with fire return interval through fuel loading (Weber and Flannigan 1997). Fire intensity is defined as the rate of heat energy released per unit length of fire front (Byram 1959). Fire intensities in the boreal forest range from <10 kWm^{-1} for smouldering fires, from 10 to 2,000 kWm^{-1} for surface fires, and up to 150,000 kWm^{-1} for high-intensity crown fires (Alexander 1982; Johnson 1992). The season of the year when a fire occurs may affect intensity through differences in surface and crown fuel moisture content (Weber and Flannigan 1997). Modelled or measured fire intensity can be used to assess the likelihood of crown fire initiation (Alexander and Cruz 2012), predict the scorching height of conifer crowns (Van Wagner 1973), and estimate the biophysical impacts of fire (Alexander 1982, Keeley 2009, Johnstone 2011, Alexander and Cruz 2012). Fire severity refers to the general effect of fire on the forest environment, usually measured as the proportional overstory tree mortality (Kafka et al. 2001, Ryan 2002), but also by the consumption of soil organic layers and the mortality of belowground propagules (Ryan 2002). Fire severity is related to the amount, nature, and successional trajectory of regeneration vegetation through seedbed availability and canopy mortality (Greene et al. 2004; Johnstone 2011), post-fire tree fall patterns (Boulanger et al. 2011), nutrient cycling (Ryan 2002), and to the carbon stocks and fluxes of boreal ecosystems (Kasischke et al. 1995, Boby et al. 2010).

Boreal black spruce forests are considered a highly flammable fuel type due to their crown architecture: deep crowns with relatively low crown base heights (Johnson 1992), high crown bulk density (e.g. twigs and branches; Johnson 1992, Alexander et al. 2004), and their high resin and low crown moisture contents (Johnstone 2011). These stand structure attributes describe the availability and distribution of canopy fuels and so influence the development of high intensity crown fires (Cruz et al. 2003, Stocks et al. 2004). According to Van Wagner (1977) crown fire initiation and vertical spread occur when fire intensity attains a critical value that is a function of crown base height. Once the fire has reached the canopy, a crown fire can be sustained as long as a minimum density of fuels is present (Van Wagner 1973, Cruz et al. 2005, Cruz and Alexander 2010). Despite the fact that boreal forest fires are generally described as severe, stand-replacing crown fires, recent findings have drawn attention to important variation in fire severity both within and among fires (Thompson and Spies 2009, Kafka et al. 2001, Amoroso et al. 2011). This variability could be explained by underlying spatial variation in fire weather, soils, physiography, and vegetation (Thompson and Spies 2009). However, much work is still required to understand how spatial variation in severity can emerge at multiple scales. The assessment of fire severity is relevant in the context of fire management, especially where forest landscape management intends to emulate natural disturbance regime by maintaining a mosaic of stand structures (Harvey et al. 2003, Sikkink and Keane 2012).

Boreal ecosystems store large amounts of carbon in the live plant biomass and soil (25 and 75% of the total stored carbon respectively; Kasischke et al. 1995, 2013). The extensive accumulation of carbon in boreal soils is possible due to the low decomposition rates which result from the cold temperatures characteristic of these forests (Kasischke 2000). The C dynamics in the boreal forest is mainly affected by the regional climate, soil characteristics, stand structure and composition, and the fire regime (Kurz and Apps 1999, Wang et al. 2003). In the boreal forest, individual fires typically kill most of the conifer live biomass (Brassard and Chen 2006, Kashian et al. 2006). They release carbon to the atmosphere via organic matter combustion (Kashian et al. 2006, Boisvenue et al. 2012), alter the thermal and moisture regime (van Bellen et al. 2010), re-initiate succession (Kasischke 2000), and modify the distribution of forest C stocks (Gower et al. 1997; Laganière et al. 2013). The key role of Canada´s boreal forests in the global C cycle has significant implications for forest management strategies (Kurz and Apps 1999, Boisvenue et al. 2012, Lemprière et al. 2013). For example, existing guidelines for ecosystem management consider landscape-level assemblages of forest stand attributes (e.g. diameter distribution, basal area, height distributions) but not forest carbon (Boisvenue et al. 2012). It is of interest to explicitly account for carbon in order to improve current C stocks assessments and to increase our capacity to deal with boreal forest C responses to climate change (Kasischke et al. 1995, Boisvenue et al. 2012). In Canada, sustainable boreal ecosystem management regimes aimed at improving carbon sequestration potential and mitigating and adapting to the effects of future climate change are underway but remain at an early stage (Peng et al. 2002, Boisvenue et al. 2012, Lemprière et al. 2013, Gauthier et al. 2014).

Predictive models which are grounded in ecological theory can be used to guide management decisions (Cuddington et al. 2013). Forest C dynamics models, for example, can be applied to study the relationships between fire regime and climate, forest growth and C dynamics (Peng et al. 2002, Kurz et al. 2008). These models may be grouped into those where forest growth is driven by empirical and yield models (e.g. CBM-CFS3, Kurz et al. 2009; CO2FIX, Masera et al. 2003); process-based models where forest growth depends on a number of ecological processes such as photosynthesis, respiration, water fluxes and nutrient cycling (e.g. BIOME-BGC, Thornton et al. 2002; FOREST-BGC, Running and Gower, 1991); and hybrid models which link key elements of empirical forest growth to different underlying ecological processes (Mäkelä et al. 2000). All approaches can be used to study and predict C sequestration and storage under altered conditions (Peng et al. 2002, Keane et al. 2004 , Cuddington et al. 2013). However, some approaches are more suitable for application in forest management within the context of global change (Gustafson 2013). For example, empirical models provide information on stand characteristics basal area, height, stand density which can be easily constructed and incorporated into management analyses. However, extrapolation beyond known data is challenging (Cuddington et al. 2013). Process-based models are suitable tools to simulate climate change impacts on forest and to assess adaptive forest management strategies (Gustafson 2013). However, they are not designed to predict stand characteristics such as basal area, making them difficult for forest managers to use (Peng et al. 2002). Hybrid models are better suited to guide forest management practices because they integrate both ecological mechanisms and correlational components into easy-to-use modelling platforms. Their application allows evaluating forest C sequestration and dynamics under alternate responses to climate, fire and harvesting regimes (Peng et al. 2002).

The climate in many parts of the boreal forest is warming rapidly as a result of anthropogenic climate change (IPCC 2007). Although temperature is the climate variable in which the anthropogenic changes are expected to be strongest, other aspects of climate such as precipitation will change as well (Räisänen and Tuomenvirta 2009). The potential impact of climate change on the fire regime has been shown in several studies (Flannigan and Van Wagner 1991, de Groot et al. 2003, Girardin et al. 2009, Boulanger et al. 2013). Variations in the fire regime will lead to changes in forest structure and function (Kurz et al. 1995), forest productivity, and consequently in C sequestration and storage (Boulanger et al. 2013). For the boreal forest of Canada, shorter fire return intervals, more intense fires and an extended fire season peaking towards the late summer are expected under projected climatic scenarios (Kurz et al. 2008, van Bellen et al. 2010). In many areas of the boreal forest, climate change is also expected to reduce black spruce tree growth (Girardin et al. 2008, Dhital et al. 2015, Girardin et al. 2015). Forest soils will likely be affected by changes in both site water balance and temperatures as these affect soil organic matter decomposition rates and nutrient cycling (Boisvenue and Running 2006, Gavin et al. 2007). Under the United Nations Framework Convention on Climate Change (UNFCCC), Canada is obligated to prepare and submit an annual national report on total national emissions and removals of CO_2 and non-CO_2 greenhouse gases (Brown 2002). However, Canada lacks critical information about boreal carbon dynamics necessary for reliable reporting, specifically about the stability of soil carbon stocks under different fire regimes. Thorough knowledge on boreal C dynamics and the immediate and long-term impacts of wildfires is necessary if we are to model and forecast regional or national C balances.

In this thesis, I develop a new hybrid-model of forest growth and C dynamics that links fire regime parameters and stand structure to simulate carbon stocks in boreal black spruce forests of northern Québec, Canada. The model uses a diameter-class structured demographic tool (Caswell 2001) to simulate stand dynamics based on empirical models of stem growth and mortality. We coupled this with an adapted version of the CBM-CFS3 boreal soil carbon module (Kurz et al. 2009), which contains explicit links between standing biomass and DOM carbon pools via mortality and living biomass turnover. A model of fire occurrence and severity driven by two key parameters of boreal fire regimes, intensity and fire return interval, allows us to simulate the effects of fire and fire regime on canopy tree mortality, combustion of organic matter, and resulting changes C stocks. This model can be easily applied as a management tool to assess short- and long- term climate change effects. It could also be used in other regions of the boreal given appropriate data and recalibration of parameters to determine the long-term effectiveness of Canadian forests in meeting the goals stipulated in international agreements and policies.

This dissertation has been developed in the form of a collection of three articles already published, submitted or in the process of submission for publication in peer reviewed scientific journals. Therefore, some resemblance among chapters can occur.

Chapter 1

Modelling variable fire severity in boreal forests: effects of fire intensity and stand structure[1]

[1]Complete version of a published manuscript: Miquelajauregui Y, Cumming SG, Gauthier S (2016). Modelling variable fire severity in boreal forests: effects of fire intensity and stand structure. PLoS ONE 11(2).

Abstract

It is becoming clear that fires in boreal forests are not uniformly stand-replacing. On the contrary, marked variation in fire severity, measured as tree mortality, has been found both within and among individual fires. It is important to understand the conditions under which this variation can arise. We integrated forest sample plot data, tree allometries and historical forest fire records within a diameter class-structured model of 1.0 ha patches of mono-specific black spruce and jack pine stands in northern Québec, Canada. The model accounts for crown fire initiation and vertical spread into the canopy. It uses empirical relations between fire intensity, scorch height, the percent of crown scorched and tree mortality to simulate fire severity, specifically the percent reduction in patch basal area due to fire-caused mortality. A random forest and a regression tree analysis of a large random sample of simulated fires were used to test for an effect of fireline intensity, stand structure, species composition and pyrogeographic regions on resultant severity. Severity increased with intensity and was lower for jack pine stands. The proportion of simulated fires that burned at high severity (e.g. >75% reduction in patch basal area) was 0.80 for black spruce and 0.11 for jack pine. We identified thresholds in intensity below which there was a marked sensitivity of simulated fire severity to stand structure, and to interactions between intensity and structure. We found no evidence for a residual effect of pyrogeographic region on simulated severity, after the effects of stand structure and species composition were accounted for. The model presented here was able to produce variation in fire severity under a range of fire intensity conditions. This suggests that variation in stand structure is one of the factors causing the observed variation in boreal fire severity.

Keywords

Canada; boreal forest; fire intensity; canopy base height; canopy bulk density; inventory plots; crown scorch; fire severity; stand structure

Résumé

Il est de plus en plus clair que les feux de forêt boréale ne brûlent pas avec la même intensité et sévérité. Tout au contraire, une variation significative au niveau de la sévérité du feu, mesurée par le taux de mortalité des arbres, a été découverte tant au niveau d'un feu particulier qu'entre différents feux. Il est important de comprendre les conditions sous lequelles cette variation peut se produire. Nous avons intégré, des données d'inventaire forestier, des données historiques de feux de forêts et des allométries d'arbres à un modèle démographique structurée en classes de diamètre. Nous avons appliqué ce modèle aux placettes d'un hectare avec des peuplements purs d'épinette noire et de pin gris pur dans le nord du Québec, au Canada. Le modèle simule l'initiation des feux de cime et la propagation verticale dans la canopée. Ce dernier utilise les relations empiriques entre l'intensité du feu, la hauteur des flammes, la proportion de la cime brûlée et la mortalité des arbres pour simuler la sévérité du feu, en particulier la proportion de réduction de la surface terrière en raison de la mortalité due au feu. Des analyses d'arbre de classification et de régression ont été utilisés pour tester l'effet de l'intensité de feu, la structure du peuplement, la composition des espèces et des régions pyro-géographiques sur la sévérité résultante. Nous avons trouvé que la sévérité augmente avec l'intensité du feu et qu'elle était plus faible dans les peuplements de pins gris que dans eux d'épinette. La proportion des feux simulés qui ont brûlé avec une forte sévérité (c'est-à-dire, ayant une réduction de plus de 75% de la surface terrière) était de 0.80 pour l'épinette noire et de 0.11 pour le pin gris. Nous avons identifié des seuils d'intensité en dessous desquels il y avait une sensibilité marquée de la sévérité du feu simulée à la structure des peuplements, et aux interactions entre l'intensité et la structure. Nous n'avons trouvé aucune preuve d'un effet résiduel de la région sur la sévérité simulée, après avoir tenu compte les effets de la structure du peuplement et la composition en espèces. Le modèle présenté ici est capable de produire des variations dans la sévérité du feu sous une gamme de conditions d'intensité initiale du feu. Ceci suggère que la variation de la structure du peuplement est l'un des facteurs à l'origine de la variation observée dans la sévérité du feu des régions boréales.

Mots clés
Canada; forêt boréale; intensité de feu; hauteur de la base de cime; densité de combustible; inventaire forestier; proportion de la cime brûlée; sévérité; structure du peuplement

I. Introduction

A fire regime is a quantitative description of the characteristics of the fires that occur in a region (Whelan 1995), including frequency, size, cause, season of burning and the general type of fires (i.e. ground, surface or crown). In boreal North America, the fire regime is characterized by infrequent, high intensity lightning-caused crown fires that are both large and severe (Van Wagner 1983). Fireline intensity (fire intensity, hereafter) as defined by (Byram 1959) is the rate of energy release per unit length of fire front, currently measured in units of kW m^{-1} (Alexander 1982). It is one of the most important descriptors of fire behaviour to be used in explaining aboveground fire impacts (Alexander and Cruz 2012). Fire severity, on the other hand, refers to the biophysical or ecological impacts of a fire (Ryan 2002). Severity is inherently multifactorial. Some aspects that can be readily quantified are the proportion of foliage consumed or killed, and fire induced tree mortality (Johnstone and Chapin 2006, Boby et al. 2010). In forested ecosystems, fire intensity has been directly related to scorching height of conifer crowns (Keeley 2009). Scorch height is defined as the height at which the heat of a fire is lethal to living foliage; it is correlated to the proportion of foliage consumed (Peterson 1985). Low-intensity surface fires yield lower scorch heights that cause little or no tree mortality, whereas higher scorch heights characteristic of high-intensity fires can kill large trees resulting in nearly 100% tree mortality (Van Wagner 1973). In the boreal forest, variation in fire severity can have long lasting effects on the post-fire vegetation community structure and dynamics and on their flammability (Van Wagner 1983, Johnstone and Chapin 2006).

Boreal tree species have adaptations for survival and persistence in fire-dominated environments. For example, black spruce (*Picea mariana* (Mill.) BSP) and jack pine (*Pinus banksiana* Lamb.), both possess, in different degrees, clumped aerial seedbanks protected by cone serotiny that ensure a seed source for regeneration after a crown fire. However, the two species respond differently (e.g. in terms of mean fecundity and seedling survival rates) to variation in fire severity, as measured by overstory tree canopy mortality and duff consumption (Greene et al. 2004, Boiffin and Munson 2013). These differences in responses to fire severity can in turn affect post-fire regeneration densities and structural development

(Lecomte et al. 2007). Low-to moderate-severity fires typically leave most of the large trees alive, which results in structurally complex stands with a broad range of tree diameters (Bergeron et al. 2002). These fires tend to leave on the ground a thick layer of partially charred organic matter, a substrate that negatively affects recruitment and early seedling growth of both species, although with a less important effect on jack pine (Johnstone and Chapin 2006, Boiffin and Munson 2013). In contrast, severe fires that kill most trees are likely to regenerate as dense stands with relatively low levels of structural complexity (Amoroso et al. 2011). This is because such fires expose mineral soil, an optimal regeneration seedbed for both black spruce and jack pine (Greene et al. 2004, Boiffin and Munson 2013).

Boreal conifer forest stands present a highly flammable configuration of fuels because of their crown architecture (e.g. deep crowns with relatively low crown base heights; Johnson 1992), their high canopy bulk densities with large amounts of fine twigs and needles, high resin and low foliar moisture contents (Van Wagner 1983). From the point of view of the quantity of crown fuels, boreal conifer stands are architecturally easier to burn than other fuel types (Van Wagner 1977). During high latitude summers, longer daylight hours and lack of turgid new plant growth are conducive to drying of canopy fuels and thus high fire intensity (Alexander and Cruz 2012). It is for these reasons that high intensity crown fires with high flame length, high levels of consumption of the soil organic layers (Johnson 1992), and corresponding high severity have been considered characteristic of these ecosystems (Boby et al. 2010). However, recent findings have drawn attention to important variation in fire severity both within and among fires (Bergeron et al. 2002, Amoroso et al. 2011), even within boreal conifer stands. It is important then to understand the conditions under which such variation in fire severity can arise. One potentially contributing factor is variation in stand structure (Keeley 2009). In forest sciences, “stand structure” refers to the within-stand distribution of vegetation such as the horizontal and vertical arrangement of trees (Bacaro et al. 2014). Horizontal structure can be measured by stem density and diameter distribution, and vertical structure can be measured by factors such as the height to crown base and tree height (Smith et al. 1997). These variables are related to the quantity of available fuels and to their vertical distribution between the surface and top of the canopy (Cruz et al. 2003, Alexander and Cruz 2012). Stand structure influences the probability of transition between surface and crown fires (Van Wagner 1977). Thus, stand structure is an important factor determining fire behaviour, fire severity, and forest ecosystem resistance and resilience in response to disturbances (Cruz et al. 2003, Gauthier et al. 2009, Thompson and Spies 2009).

The purpose of this study was to explore and quantify the effects of stand structure and, secondarily, of tree species composition and region, on the stem-mortality component of fire severity within the boreal conifer forests of northern Québec, Canada. We focused on simulated stands of black spruce and jack pine, the two most abundant and important boreal coniferous species (Boiffin and Munson 2013). Our objectives were to: 1) quantify the relationship between fire intensity and stand structure on fire severity; and 2) compare severity between black spruce and jack pine stands and among pyrogeographic regions of the study area. We expected that the effect of stand structure on severity will be of greatest importance at lower fire intensities associated with surface fires. High intensity fires almost always become crown fires, where close to hundred per cent tree mortality is the usual outcome. We also hypothesized that severity in pure jack pine stands will be lower than in pure black spruce stands mostly due to dissimilarities in stand structure, including the higher crown base height characteristic of pine. We tested these expectations using a simulation model where fires of varying intensity were applied to a “static” diameter class-structured model of forest stands. Static means there is no growth, mortality or recruitment. Our approach integrates physical models of fire behaviour with empirical models of fire effects (e.g. severity). The model was calibrated with data representative of our study area derived from inventory plots and historical fire intensities (1994-2010) estimated from spatially interpolated meteorological data. This study conducts a simulation experiment that evaluates the effect of fire intensity (reflecting weather) and stand structure variables on fire severity in 1.0 ha patches of mono-specific black spruce and jack pine stands in northern Québec, Canada. The results of these simulations provide insight into the causes of variable fire severity in boreal forests.

II. Materials and Methods

1. *Study area*

Our study area is contained within the black spruce feather moss domain (49° to 52° N, 57° to 79°W), of Québec, Canada, a vast region of approximately 412,000 km^2 (Saucier et al. 1998; Fig. 1). The domain lies within the Canadian Shield, a large area of exposed Precambrian rock (Rowe 1972). It is characterized by a flat topography with surficial deposits of glacial till that are predominantly thin and discontinuous (Laganière et al. 2011). Fire is the most common natural disturbance in the domain (Johnson 1992). Short fire cycles (<180 years; Bélisle et al. 2011) predominate in the western and central portions of the domain, influenced by a continental climate, whereas longer fire cycles (>300 years) are found in the eastern part of the domain due to the humid maritime climate (Lecomte et al. 2007). Chabot et al. (2009) identified relatively homogeneous pyrogeographic regions -henceforth termed "fire regions"- of Québec forest (Fig. 1) based on levels of two fire regime parameters, namely fire cycle, which is estimated as the reciprocal of the mean annual proportional area burned (Van Wagner 1978), and the number of fires per unit area and time (Simard 1975). Four fire regions with contrasting fire regimes within the domain were chosen: A2, B3, C3 and D4 (names represent combinations of the two fire regime parameters following Chabot et al. (2009). These regions were expected to capture systematic factors such as climate or soils that potentially influence fire severity independent of stand structure.

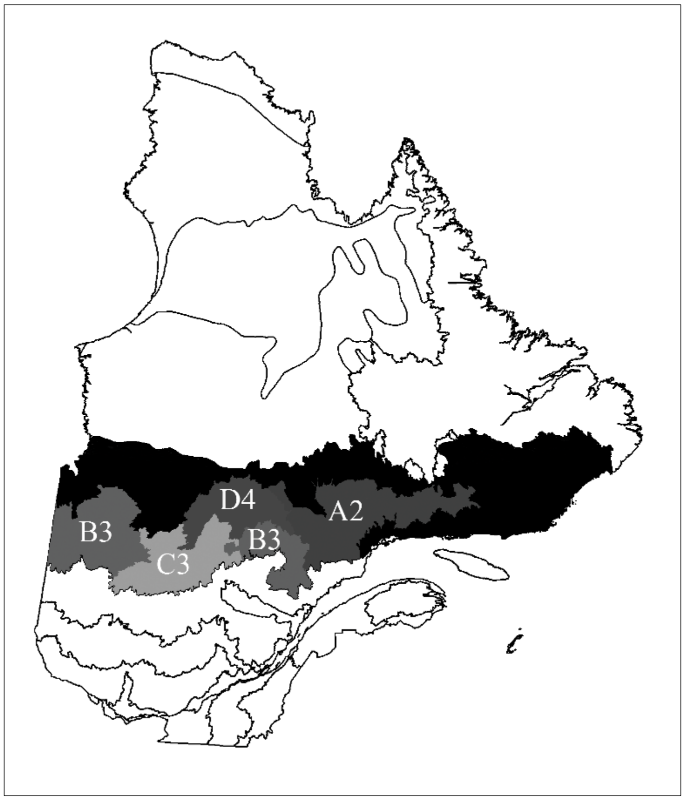


Figure 1. The black spruce feathermoss bioclimatic domain in Québec, Canada (shaded area), divided into pyrogeographic regions based on two parameters of the fire regime: the fire cycle and the fire frequency in low, medium and high frequency categories (Chabot et al. 2009). The four fire regions chosen are shown: A2 (>1100 yrs; low-medium), B3 (500-1100 yrs; medium), C3 (200-500 yrs; medium), D4 (100-200 yrs; medium-high). Map created using ArcGIS 10.0 software.

2. *Model design*

We developed an integrated, size-class structured model of stand structure and fire effects (Fig. 2). Our methodology relies on several existing fire modelling systems and empirical allometric equations and models of fire effect and biotic response (Table 1) linking fire intensity, scorch height, the percent of crown scorched and tree mortality to derive one aspect of fire severity, specifically the percent reduction in patch basal area due to fire-caused mortality. The model can simulate the transition from a low intensity surface fire to a high intensity crown fire, as a process of vertical spread into the canopy. The vertical propagation of a fire in the patch is simulated using approximations of the physical conditions limiting the initiation and vertical spread of a crown fire. These critical factors are the surface fire intensity, the canopy base height, and the bulk fuels density in the canopy (Van Wagner 1977, Cruz et al. 2003, Alexander and Cruz 2012). We do not model spatial propagation of a fire line or the interactions between surface fuel bed structure and fire behaviour. The model operates at the 1.0 ha patch level. We defined a "patch" as a homogenous spatial unit with respect to stand composition and structure. A patch is represented by counts of live trees within fifteen diameter at breast height (DBH) classes of 2.0 cm in width, from 1-3 to 29-31 cm. The class quadratic mean diameters were used to calculate stand basal area and other diameter class-level attributes (Van Wagner 1982; Table 1). Tree heights and crown ratios were calculated using species-specific allometries (Holdaway 1986, Peng 1999). Crown base height class was derived from calculated class top heights and class crown ratios (Cruz et al. 2003). Tree crown biomass (TCB; kg) was calculated using diameter-based crown fuel equations for black spruce (Stocks 1980) and jack pine (Lambert et al. 2005). Based on Alexander et al. (2004), crown biomass included the needles and the live branchwood material <0.5 cm in diameter and from 0.5 to 1.0 cm in diameter (Table 1).

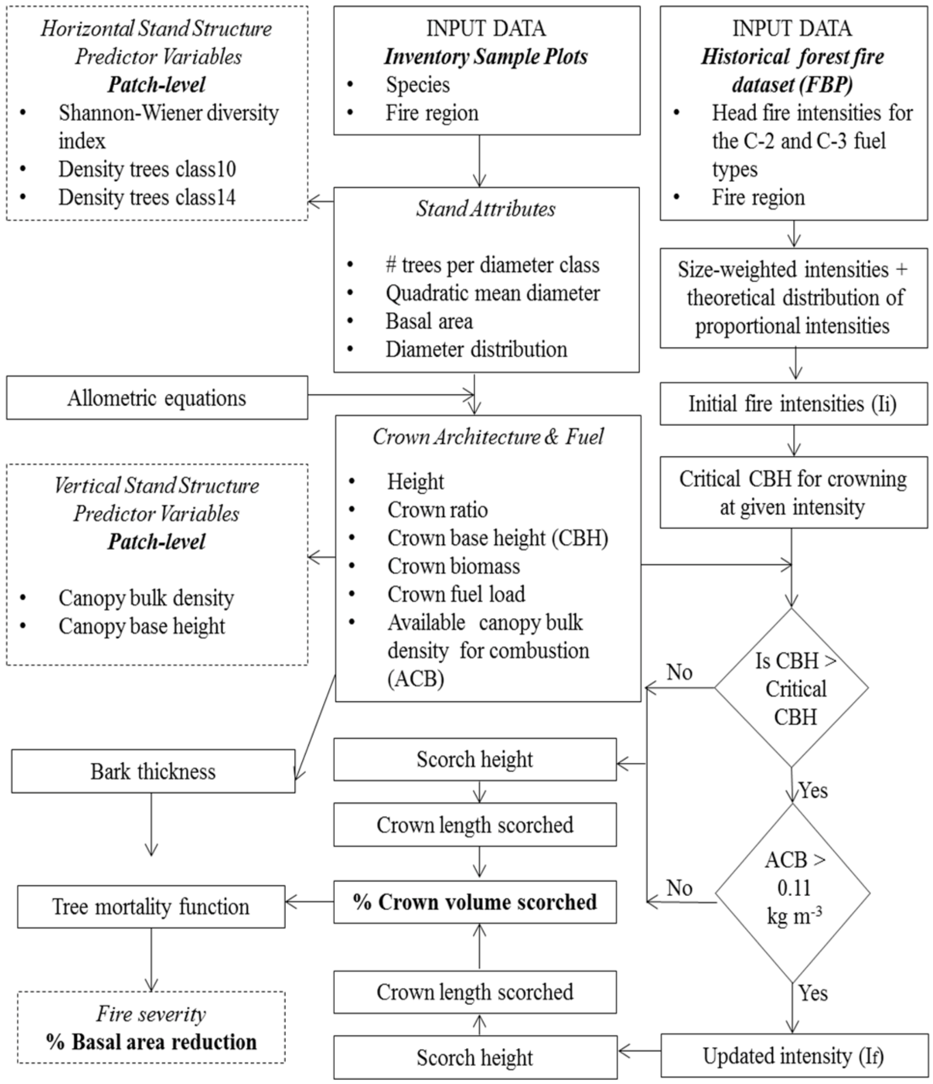


Figure 2. Flow diagram of the fire severity model, relating geographically stratified samples of initial fire intensities and forest patch diameter distributions to perform the simulation experiment. Diameter distributions were used to derive fuel and stand structural measures. Crown fire initiation and vertical propagation of a fire was evaluated given the initial fire intensity distribution and the patch canopy fuel characteristics. If crowning occurs, fire intensity is updated and corrected for crown fires (Byram 1959). Foliage consumption or scorching is calculated from flame height and foliage profiles. This allows us to calculate size-class specific mortality rates, leading to a patch-level severity measure of basal area loss.

Table 1. Names, definitions, units, equations, and sources of the variables used in the fire severity model. Equations and parameters are for (a) black spruce and (b) jack pine. * denotes stand structure variables estimated at patch-level.

Name	Definition	Units	Equation	Reference
QMD	Quadratic mean diameter per diameter class	cm	sqrt((X_2^3- X_1^3)/((X_2-X_1)(3))) where X_2=upper DBH class limit X_1= lower DBH class limit	Van Wagner (1982)
BA	Basal area of the average tree	m^2 ha^{-1}	$(QMD/2)^2$ (3.14)/10,000	-
H	Top height per diameter class	m	(**a**) (1.3+1.065) (QMD^0.886) (**b**) (1.3+1.306) (QMD^0.834)	Peng (1999)
CR	Crown ratio. The ratio of live crown length to tree height	unitless	(**a**)(5.54/(1+((0.007)(BA)))+(4.20)(1-exp((-0.053)(QMD)))-0.45)/10 (**b**) (6.64/(1 + ((0.013)(BA)))+(3.20) (1-exp((-0.052)(QMD))) -0.45)/10	Holdaway (1986)
TCB	Tree crown biomass per diameter class. Living needles and branchwood <0.5 cm and from 0.5 to 1.0 cm in diameter	kg	(**a**) 0.63+ (0.02)(QMD^2.2) (**b**) (0.0079)(QMD^2.41) +(0.0389)(QMD^ 1.729)	(**a**) Stocks (1980) (**b**) Lambert et al. (2005)
FM	Available fuel masses per diameter class	kg	(TCB)(TEF$_i$) where TEF$_i$ = No. trees in each ith DBH class	Alexander et al. (2004)
CBH$_c$	Critical crown base height	m	(I ^ 0.667) ((460+26)(FMC)) ^1.5 where FMC is the fine moisture content assumed to be 100%	Van Wagner (1987),Alexander and Cruz (2012)
Ii	Initial fireline intensity	kW m^{-1}	Corrected initial surface fire intensities	-
I$_f$	Updated fireline intensity corrected for crown fires	kW m^{-1}	(259.833)(H$_i$ +(H$_i$*0.5) ^2.174) where H$_i$ is the height of the i^{th} DBH class sustaining crowning assuming no effect of wind speed	Byram (1959), Alexander and Cruz (2012)
SH	Scorch height. The vertical height of the highest point in the crown where fire damage occurs	m	(0.1483) (I ^ 0.667) where I is the fireline intensity (I$_i$ or I$_f$)	Van Wagner (1973),Alexander and Cruz (2012)
CLS	Crown length scorched	m	SH-(H-((H)(CR))) if SH>H then CLS=(H)(CR)	Andrews (2009)
CS	Percentage of tree crown volume that is consumed or scorched	%	(100)((CLS/H)(CR))	Modified from Reinhardt and Crookston (2003), Andrews (2009)
BT	Bark thickness	cm	(**a**) (0.032)(2.54)(QMD) (**b**) (0.040)(2.54)(QMD)	Andrews (2009)
M	Mortality probability	unitless	(**a,b**) 1/(1+exp(-1.941+6.316 (1-exp(-0.3937)(BT))-(0.000535)(CS^2)))	Reinhardt and Crookston (2003), Hood et al. (2007)
S	Live overstory basal area reduction. Measure of fire severity	%	(100) (1- (BA after / BA before))	-
CBH*	Stand mean canopy base height. Average height from the ground to the bottom of the live stand's canopy	m	sum (((H$_i$)(1-CR$_i$))(TEF$_i$))/sum(TEF$_i$) where TEFi= # trees in each i^{th} diameter class	Cruz et al. 2003
CFL*	Canopy fuel load	kg ha^{-1}	sum((TCB)(TEF$_i$))	Cruz et al. 2003
CL*	Average length of the canopy fuel stratum	m	sum(((H$_i$)(CR$_i$))(TEF$_i$)))/sum(TEF$_i$)	Cruz et al. 2003
CBD*	Canopy bulk density. The available canopy fuel per unit canopy volume	kg m^{-3}	CFL/CL	Van Wagner (1977), Cruz et al. (2003)
SWDI*	Shannon-Wiener diversity index	unitless	$-\sum p_i (\ln (p_i))$ where p_i = relative proportion of trees in each DBH class	Boucher et al. (2003)

The diameter-class specific tree crown biomass values were multiplied by the number of trees in each diameter class to obtain fuel mass load (kg, Table 1). A vertical fuel profile for each patch was obtained by summing fuel masses in thin (1 m) vertical layers along the tree canopy, across all DBH classes and dividing by the volume of that layer (plot area x layer depth; Reinhardt et al. 2006). We computed the "available" canopy bulk density for combustion using the running mean approach (Reinhardt et al. 2006). The "available" CBD provides information on the height of the densest layer within the canopy and is an appropriate measure to model crown fire behaviour (Keane 2015). When a fire of a given surface intensity (I_i) is initiated in the patch, there is a minimum crown base height that will allow for vertical propagation of a surface fire into the canopy (Van Wagner 1977, Reinhardt and Crookston 2003, Alexander and Cruz 2012; Fig. 2, Table 1). If crowning is initiated, the "available" canopy bulk density for combustion is compared to a critical bulk density threshold of 0.11 kg m^{-3} (Cruz et al. 2005), to determine if a crown fire could be sustained. This "available" CBD (ACB) is a target value for assessing the rate of spread (R_0) to sustain active crown fires (Reinhardt and Crookston 2003) and has been empirically determined by Cruz et al. (2005) from experimental crown fire data covering a wide range of Canadian boreal coniferous fuel types, and a diversity of crown fuel structures (Van Wagner 1977, Cruz et al. 2005); therefore it can be applicable to any fuel type included in the FBP System prone to crown fires. This threshold is supported by similar wildfire case studies (Alexander et al. 2004) and used in other fire behaviour modelling frameworks (e.g. FFE-FVS; Reinhardt and Crookston 2003). For the purpose of this study, the same CBD threshold was assumed for both the C-2 and C-3 fuel types.

If both conditions apply, crowning is assumed and the fire intensity is updated (I_f) and corrected for crown fires as suggested by Byram (1959), Alexander (1982) and Alexander and Cruz (2012), to reflect a flame length consistent with the top height of the deepest canopy stratum capable of sustaining combustion. This assumes no effect of wind speed on flame's geometry (Alexander 1982; Table 1). Otherwise, the initial fire intensity (I_i) is used for further computations. Scorch height is calculated as a function of intensity, after accounting for vertical propagation (Van Wagner 1973, Alexander and Cruz 2012). The percentage of crown volume scorched per DBH class is determined from calculated scorch height, class top heights and class crown ratios by approximating the crown shape as a cylinder (Hood et al. 2007, Andrews 2009). The probability of tree mortality following fire per DBH class was modeled as a function of stem diameter, bark thickness and the percentage of crown volume scorched (Hood et al. 2007; Table 1). The number of trees killed in each DBH class is sampled from a binomial distribution given the predicted class mortality and the number of trees prior to the fire. From this, the model calculates pre- and post-fire basal area. Fire severity is measured as the percent basal area reduction due to mortality (Fig. 2, Table 1).

3. *Historical forest fire and forest mensuration data*

To run the model we required head fire intensities and tree diameter distributions. Head fire intensities representative of our study area, were selected from an historical forest fire database (1994-2010) provided by the Société de protection des forêts contre le feu (SOPFEU 2012), the province of Québec's forest fire management agency. Database attributes for each recorded fire include the date when the fire was detected, the location and fuel type at detection, a final size, and the head fire intensity for the first day of burning. These head fire intensities were estimated according to the Canadian Forest Fire Behaviour Prediction (FBP) System from the assigned fuel type, and interpolated local solar-noon temperature, relative humidity, wind speed, and precipitation data (Forestry Canada Fire Danger Group 1992, Wotton et al. 2009). The geographical coordinates were used to select fires within one of the four regions (Fig. 1). We then classified fires as black spruce or jack pine if their fuel types were C-2 and C-3, respectively. The C-2 fuel type is characterised by pure, moderately well-stocked black spruce stands, with a low crown base. The C-3 fuel type is characterized by pure fully-stocked jack pine stands that have matured to the stage of crown closure closed (Forestry Canada Fire Danger Group 1992, Wotton et al. 2009). Fires of other fuel types were excluded, as were fires whose final size was recorded as zero. A total of 1,290 fire records were selected, of which 1,111 were classed as black spruce (C-2), and 179 as jack pine (C-3). SOPFEU is required to actively suppress all fires when first detected (SOPFEU 2012), and this policy was in place over the entire study interval. Fire management objectives in Québec are that fires be contained within a final size of 3.0 ha (SOPFEU 2012). Not all fires can be successfully contained given their size and intensity at initial attack (Hirsch et al. 1997): approximately 43% (n=556) of the historical forest fires (1994-2010) in our study area exceeded the 3.0 ha target, and can be regarded as having escaped initial attack. We found a significant relationship ($F_{1,1288} = 6.06$, $p = 0.013$) between fire intensity and fire size in our study region, meaning that low intensity fires are associated with smaller fires.

Diameter distributions and stem counts were obtained from Québec's extensive network of inventory sample plots (Ministère des Ressources Naturelles du Québec, 2008). The plot data contain descriptive and quantitative information at the plot level (e.g. geographical coordinates, altitude, slope, drainage class, surficial deposit type) and at the tree level (e.g. species and diameter at breast height). Plots are circular with an area of 400 m^2 and a small circular subplot of 40 m^2 at the center. Tree species and measured DBH are recorded for all live trees with a DBH greater than 9.1 cm. Height and age are recorded only for a subset of sample trees (Ministère des Ressources Naturelles du Québec, 2008). Saplings (trees with a DBH lower than 9.1 cm; Ministère des Ressources Naturelles du Québec, 2008) are measured within the 40 m^2 subplot. Each inventory plot was associated with a list of measured tree diameters which are binned into the size-class structures. The inventory plot level data was scaled up to 1.0 ha. Inventory plots were spatially stratified by fire regions (Fig. 1), and then by soil drainage class and superficial deposit, two soil properties related to surface fuel moisture content that reflect the growing conditions of trees within the stand (Mansuy et al. 2010). Plots with "mesic-glacial till" soils, most characteristic of the domain, were kept for the modelling exercise (6,956 of 11,454). These were then classified by species composition (Ministère des Ressources Naturelles du Québec, 2008). Mono-specific plots were defined as those where a single species contributed more than 75% of the total basal area. We finally retained 3,428 mono-specific plots of black spruce (n=3,195) and jack pine (n=233) from which to sample simulated stands distributed among the four fire regions.

4. *Simulation experiment*

To evaluate the relationship between stand structure, fire intensity and severity, we simulated the severity of fires of randomly chosen intensity on randomly chosen patches, stratified by fire region and dominant tree species. We ran 3,000 simulations for each combination of four fire regions and two dominant tree species, for a total of 24,000 runs. The replicate plots were sampled randomly with replacement from the subset of inventory plots for the given species within the fire region, and scaled to 1.0 ha. Stand attributes and the horizontal and vertical stand structure variables were calculated for each patch.

Fire intensities were sampled by a three-stage process. First, head fire intensities were selected from the historical forest fire database for the appropriate region and fuel type. Given the association between head fire intensity and fire size in our study area, we used a size-weighted sampling scheme to sample with replacement 3,000 head fire intensity records. For this procedure we considered fires with a minimal final size of 0.1 ha. By accounting for area burned, the low fire intensities that were associated with smaller fires were less likely to be sampled (Bessi and Johnson 1995). As a result, we expected the range of intensity values used in the modeling experiment to be more representative of the distribution of intensities over area burned. The estimated head fire intensities represent a mix of surface and crown fires, and overestimate the average fire intensity within the burn, even assuming constant burning conditions and elliptical growth (Catchpole et al. 1992). Fire severity is related to rate of spread (Keeley 2008), which varies along the perimeter of an ellipse, and is asymmetric along the major axis (Alexander 1985). Under this model of elliptical fire growth, the theoretical distribution of intensity within the burn can be derived from well-established principles of fire behaviour (Catchpole et al. 1992). We used this approach to account for variation in intensity within fires, assuming elliptical shapes (Catchpole et al. 1992). The average length-to-breadth ratios characteristic of jack pine and black spruce wildfires (Alexander 1985) were used to determine the shape of the ellipsoids.

We then sampled 3,000 proportional intensities from the Catchpole's theoretical distribution and multiplied them by the size-weighted head fire intensity to provide a patch-level initial fire intensity (I_i). For each simulation, an initial intensity was applied to a sampled patch and updated to account for crown fire initiation. Fire severity was then calculated within the sample patch given the fire intensity (Fig. 2). Following Purdon et al. (2004), we classified fires as low, medium or high severity according to severity values of <25%, between 25 and 75%, and >75%, respectively. Although there seems to be no real consensus in terms of the meaning of these categories, such classifications can be useful for forest managers because they can be easily applied in aerial surveys of post-fire crown scorching (Purdon et al. 2004).

5. *Stand structure variables*

For each sampled patch, we calculated a set of horizontal and vertical stand structure variables that were used as predictors of fire severity in statistical analysis (Fig. 2). We used three horizontal structure variables that have been shown to effectively discriminate among stand structure types within this system (Boucher et al. 2003). These measures were the Shannon-Wiener diversity index (SWDI) of the diameter-class counts, and the percent density of trees in the 10- and 14-cm diameter classes. The SWDI (Table 1) measures the unevenness of the diameter distribution and can be related to the time elapsed since the last major disturbance (Smith et al. 1997, Boucher et al. 2003, Harper et al. 2003, Bacaro et al. 2014). Lower values of this index (1.2-1.7) are characteristic of stands with an even distribution of tree sizes that were affected by a recent disturbance, while higher values (1.8-2.4; Boucher et al. 2003, Harper et al. 2003) are characteristic of uneven-sized stands where the time since the stand-initiating disturbance is probably long compared to the lifespan of the dominant tree species. The percentages of live stems in the 10- and 14-cm diameter classes are also important stand structure attributes (Boucher et al. 2003). An increased density of small stems (e.g. 10-14 cm DBH) within the patch could contribute to an overall increase in fire intensity, thus in severity, as the canopy base height decreases and the abundance of ladder fuels increases (Van Wagner 1977, Mruzik 2001, Cruz et al. 2005).

The vertical stand structure covariates included in the analysis were the patch-level canopy base height (CBH, m; Table 1) and the canopy bulk density (CBD, kg m^{-3}; Table 1). These variables are related to the quantity and vertical distribution of fuels within the canopy; therefore are important in estimating the potential of surface fires to transition to crown fires (Cruz et al. 2003, Keane 2015). Canopy base height was estimated from calculated class top height and class crown ratios and weighted over diameter classes (Cruz et al. 2003; Table 1). The canopy bulk density was estimated using the load-over-depth approach by Van Wagner (1977) and Cruz et al. (2003), that simply divides canopy fuel load by canopy length (Table 1). This straightforward approach allows relatively simple estimation of CBD, without the need to account for individual tree variations (Reinhardt et al. 2006, Hall and Burke 2006). To obtain the canopy fuel load (CFL, kg ha^{-1}), the tree crown biomass values were multiplied by the number of trees in each diameter class and summed over classes (Table 1). Canopy length, defined as the average length of the canopy fuel stratum, was estimated by subtracting the calculated class crown base from the class top height and weighted over diameter classes (Cruz et al. 2003). Our patch-level CBD differs from the "available" canopy bulk density used in evaluating crowning, in that the former represents an average across all canopy layers and the latter the variability of canopy fuel over horizontal space (Keane 2015).

6. *Statistical analysis*

Associations among the stand structure variables were determined, within species, using the Pearson product moment correlation coefficient (R package "stats"). We tested for differences in the stand structure variables and compared the mean fire severity among the four fire regions and between species using ANOVA's and Tukey's HSD tests. We compared historical and initial fire intensities among fire regions and fuel types. To model relationships between fire severity and the covariates of fire intensity, stand structure, species composition and fire region, we used a two-step approach based on nonparametric decision trees. A random forest analysis (RFA; R package "randomforest") was first used to rank the potential covariates in terms of the strengths of their relationships to the response variable, and select a parsimonious subset based on this ranking. Then, a regression tree analysis (RTA; R package "party") was used to classify the burned plots into groups of similar severity using the subset of covariates identified in the previous step. Both the RFA and the RTA are non-parametric methods suitable for ecological data with complex non-linear and interacting relationships between the predictors and the response. The random forest analysis outperforms many other statistical methods in terms of classification accuracy and is very useful when, as here, the true model is not known (Thompson and Spies 2009).

Once the important variables were identified by the RFA, an implementation of RTA called a conditional inference tree was applied. RTA recursively partitions the data into subsets, called nodes, which are relatively homogeneous in the response. Partitions or "splits" are determined by a threshold value of a single covariate, selected to maximise dissimilarity between the two new nodes. In conditional inference trees, covariates are selected by permutation-based significance tests. This reduces variable selection bias and overfitting (Hothorn et al. 2006, Thompson and Spies 2009) in comparison to similar methods such as

Classification and Regression Trees. Nodes that cannot be further split are called terminal nodes (Hothorn et al. 2006). For each terminal node, we calculated the mean, the median, and the coefficient of variation of fire severity. Separate trees were built for black spruce and jack pine stands. We used R version 2.15.0 (R Development Core Team 2012) for all statistical and graphical analysis.

III. Results

Historical head fire intensities did not differ among the four fire regions (Fig. 3a; $F_{3,1286}$ =2.1, p = 0.094) but did differ among fuel types (Fig. 3b; $F_{1,1288}$ =122, p < 0.001). Mean initial fire intensities (I_i) differed among fire regions (Fig 3c; $F_{3,23996}$ = 194, p < 0.001) and fuel types (Fig. 3d; $F_{1,23998}$= 6885, p < 0.001). For both fuel types, we found a significant and marked negative correlations between the SWDI and the % density of trees in the 10-cm diameter class (r= -0.83 and -0.68, respectively; $p \leq .0001$), and a weak but significant positive association between the former and the CBH (r= 0.35 and 0.38, respectively; $p \leq .0001$). Very weak correlations were found for the rest of the horizontal and vertical stand structure variables. A significant species and fire region interaction ($p \leq 0.001$) was found for the stand attributes listed Table 2.

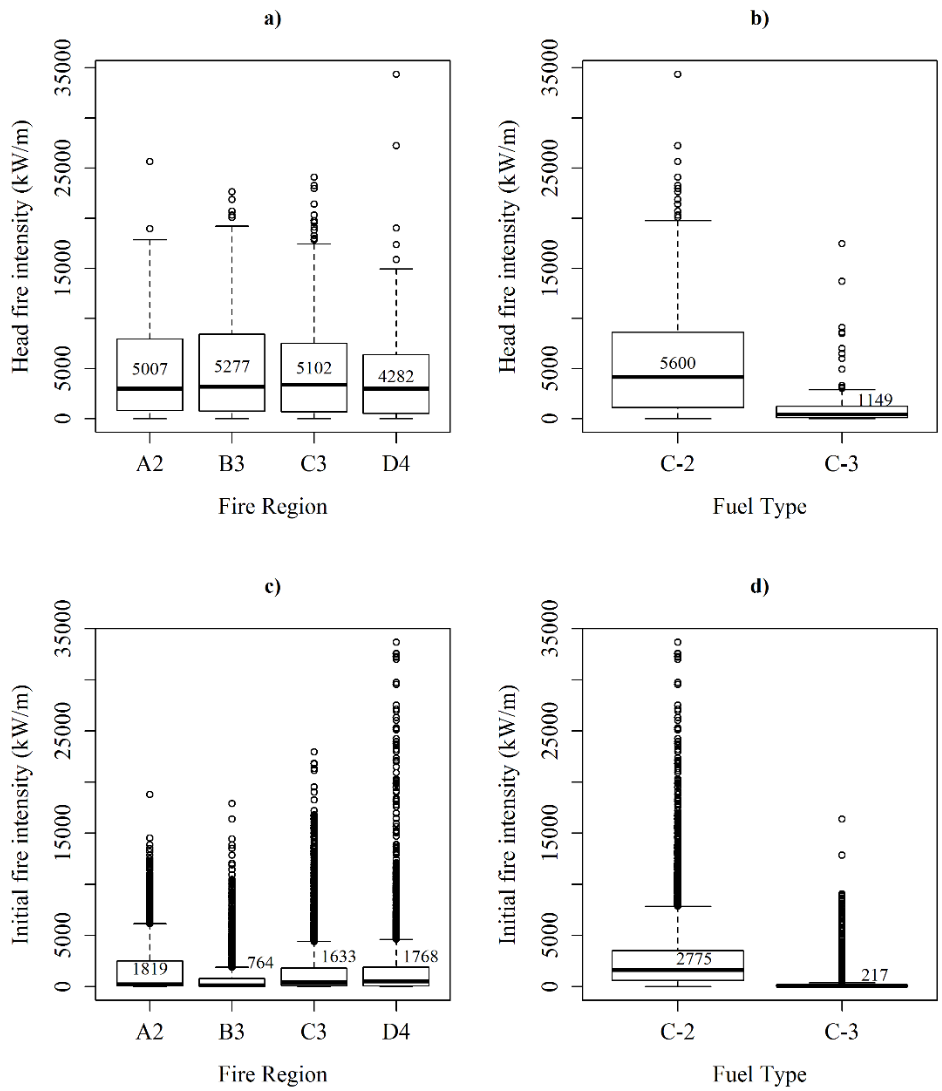


Figure 3. Boxplots summarizing the distribution of the recorded historical head fire intensities (kW m^{-1}, n=1,290) for a) fire region, b) fuel type, and the distributions of initial fire intensities (Ii, kW m^{-1}, n=3,000) for c) fire region, and d) fuel type. Mean values are shown within the boxes. Boxes represent the inter-quartile ranges; horizontal lines within the boxes represent medians; whiskers extend to the most extreme data point that is no more than 1.5 times greater than the 3rd quartile or less than the 1st quartile. Dots above whiskers represent extreme values.

Table 2. Descriptive statistics of the stand characteristics and structure attributes (mean±sd) in 24,000 simulated 1.0 ha patches summarized by species and fire region. The number of available inventory sample plots per species and fire region are shown. Different letters (in parenthesis) for the stand structure variables tested (*) represent significant differences within rows obtained from a Tukey's multiple comparison test (α=0.05). Highest values for each variable tested are shown in bold. The number of fires in the historical record that escaped the management target size of 3.0 ha for each species and within each fire regions is also reported.

Stand and structure attributes	**Fire regions**							
	A2		**B3**		**C3**		**D4**	
	BS	***JP***	***BS***	***JP***	***BS***	***JP***	***BS***	***JP***
No sample plots	1007	6	539	25	1184	138	465	64
Total density	4154± 2577	1374± 417	4250± 3408	2400± 1335	4209± 3304	3244± 2853	3987± 3030	2132± 2160
Basal area	24.6±8.4	14.4±3.2	22.6±10.0	18.1±6.4	22.3±9.6	18.5±7.4	19.4±8.8	9.9±5.1
CBD*	**0.31**± 0.14 (a)	0.12± 0.03(e)	**0.30**± 0.18(a)	0.18± 0.10(d)	0.30± 0.17(a)	0.20± 0.12(c)	0.27± 0.16(b)	0.10± 0.07(f)
CBH*	3.0± 0.63(c)	3.4± 0.22(b)	3.0± 0.71(d)	**3.5**± 0.57(a)	3.0± 0.72(e)	3.4± 0.78(b)	2.8± 0.60(g)	2.8± 0.59(f)
SWDI*	**1.7**± 0.32(a)	1.6± 0.31(b)	1.6± 0.40(c)	1.5± 0.31(e)	1.6± 0.42(c)	1.4± 0.46(f)	1.6± 0.39(d)	1.1± 0.45(g)
% trees class 10*	23.6± 15(e)	22.3± 16.4(f)	27.0± 19.2(d)	27.4± 15.3(d)	27.8± 19.3(d)	32.5± 23.1(b)	29.5± 18.9(c)	**35.0**± 22.9(a)
% trees class 14*	17.2± 7.1(a)	16.9± 6.3(ab)	16.0± 8.5(de)	**18.2**± 7.4(a)	15.7± 8.7(e)	16.1± 8.9(cd)	16.8± 8.8(bc)	14.2± 12.2(f)
No. fires ≥ 3.0 ha	50 (35%)	10 (76%)	155(38%)	16 (44%)	127 (37%)	35 (39%)	134 (59%)	29 (72%)

1. *Variation in fire severity among species and fire regions*

The proportion of simulated fires that burned at high severity was 0.80 for black spruce and 0.11 for jack pine (Fig. 4). This difference was significant (χ^2_1=11577, $p \leq .0001$). Mean severity was significantly affected by the interaction between species and fire region ($F_{3,23992}$ = 481, $p \leq .0001$). Mean severity was lower in jack pine stands than in black spruce stands (Appendix A-1). Fire region B3 and A2, had the lowest mean severity for black spruce (67%) and jack pine (8%), respectively (Appendix A-1).

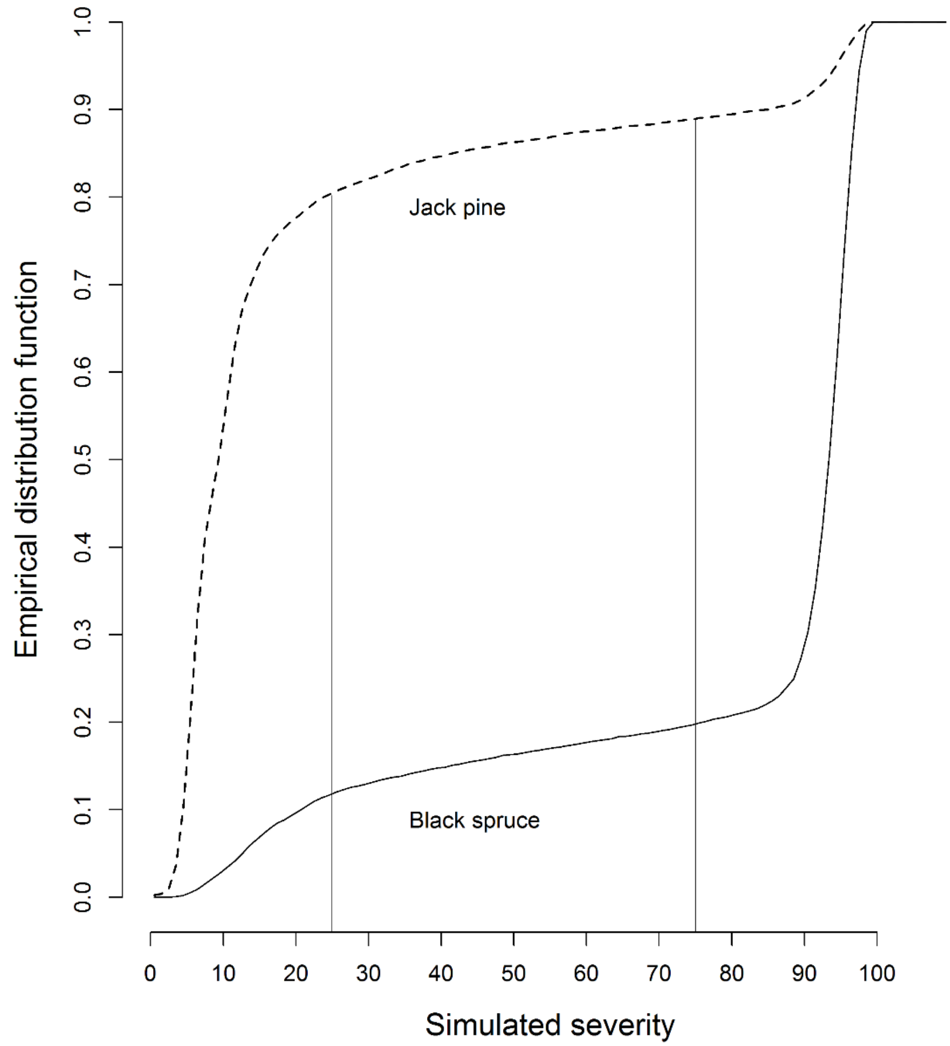


Figure 4. Empirical distribution function of simulated fire severity, measured as percent reduction in patch basal area, within patches of jack pine and black spruce. Fire severity classes of Purdon et al. 2004), are delimited by the vertical lines: low severity (<25%), moderate severity (25-75%), and fire severity (>75%).

2. ***Fire intensity and stand structure effects on fire severity***

The random forest analysis identified a similar set of important severity predictors for jack pine and black spruce stands. Intensity was by far the most important predictor of severity, followed by the canopy bulk density, the Shannon-Wiener diversity index (i.e. for black spruce), and the percent density of trees in diameter class 10 (i.e. for jack pine). High severity fires were predominantly associated to increased fire intensity, greater canopy bulk density values, higher density of trees in the 10-cm diameter class and lower values of the SWDI. The fire region had the weakest association with severity.

The regression tree analysis for black spruce produced a tree with 6 terminal nodes. The model suggests interacting effects of the SWDI, the CBD, and the fire intensity (Fig. 5). The first split was determined by initial intensity ≤ 177 kW m^{-1} (corresponding to a scorch height of 5 m; Table 1). Low fire severity levels (<25%) were associated with intensities below this threshold (terminal node 1). Above this intensity, SWDI showed the greatest association with the response variable. A split at the right side of the tree root was determined by the condition SWDI >1.8 (Fig. 5). This corresponds closely to the value distinguishing stands with even (<1.8) from uneven (>1.8) stem diameter distributions. For stands falling on the left side of this node, where SWDI <1.8, the canopy bulk density had the strongest association with the response variable. Stands where this value was less than 0.2 kg m^{-3} (terminal node 2), experienced a median severity of 94% (Table 3). Greater CBD values yielded higher severity fires (>93%, terminal node 3 and 4), and were particularly high (median severity of 97%) when the SWDI was below 1.5 (terminal node 3). This SWDI value lies within the upper bound estimated for stands with even stem size distributions (1.4 ± 0.2; Boucher et al. 2003).

For stands falling on the right side of the tree root, that is, where SWDI >1.8 (Fig. 5), fire intensity had the greatest association with the response variable. Uneven stands (Boucher et al. 2003) experienced moderate canopy tree fire severities with a median of 57% under intensities > 177 and ≤ 928 kW m^{-1} and corresponding scorch heights between 5 and 14 m, respectively (terminal node 5). Intensities above >928 kW m^{-1} (i.e. scorch height >14 m) in uneven-sized patches, a combination accounting for 24.3% of all simulated black spruce fires, had a median severity of 97% (terminal node 6). Variation in fire severity among the stands within terminal nodes 1, 2 and 5 (CVs. 0.98, 0.25, and 0.57 respectively; Table 3) was greater than among other terminal nodes.

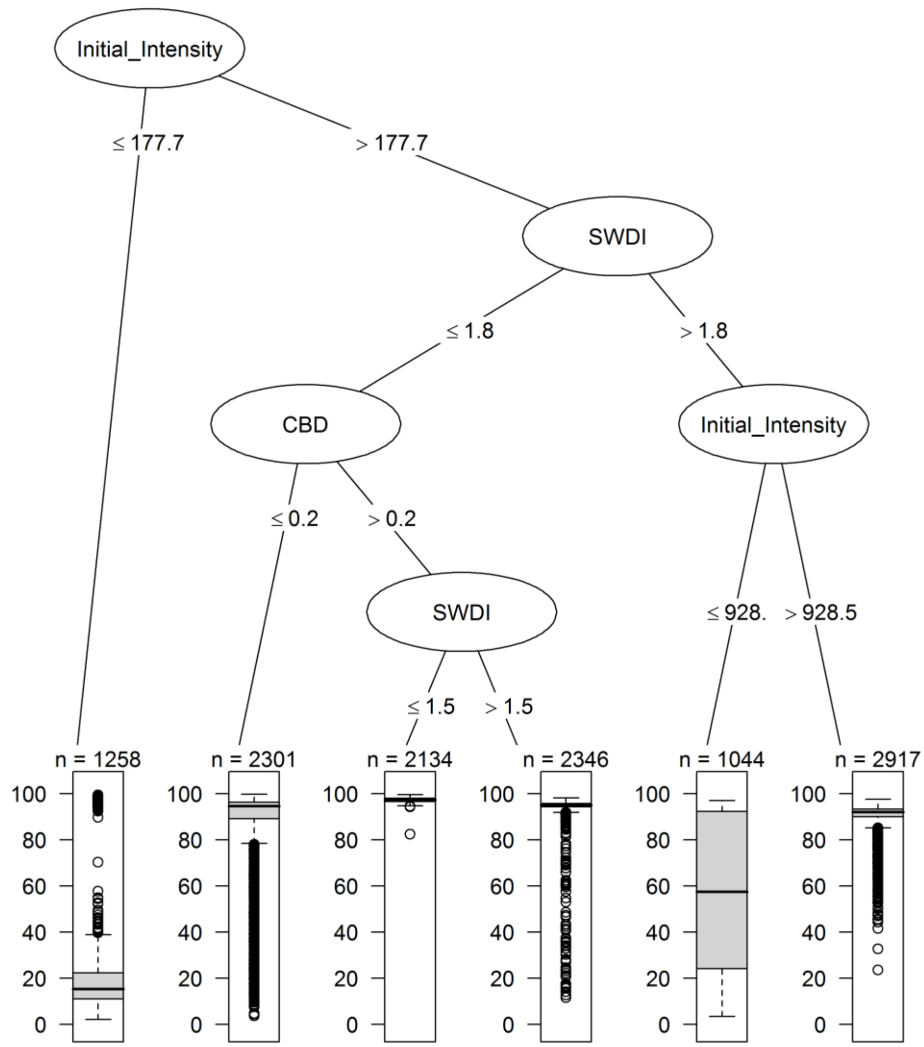


Figure 5. Regression tree for simulated fire severity in black spruce patches. The first split in the tree, or the root, is defined by the covariate with the strongest relationship with severity. Box plots at terminal nodes show the distribution of the fire severity data within each branch of the tree. The number of observations within each branch is shown at the top of each boxplot. The total number of simulated fires was 12,000.

Table 3. Descriptive statistics (fire severity mean, median and coefficient of variation) and mean fuel characteristics (basal area, canopy base height, canopy bulk density, total stem and sapling density) for each of the 6 terminal nodes produced by the regression tree analysis for black spruce and 4 terminal nodes for jack pine. The number of model runs for each node and the percentage of total (%) are shown. The initial fire intensities (Ii) and the updated intensities (If; kW m^{-1}) are reported (mean±sd). The proportion of simulated 1.0 ha patches in each fire region within each terminal node are shown. Significant differences in the proportion of patches within terminal nodes and fire regions were found for black spruce (χ^2_{15}=96.3, $p \leq$ 0.001) and jack pine (χ^2_{9}=126.0, $p \leq 0.001$).

	Fire severity descriptive statistics			**Fuel characteristics (means)**				**No. of model runs**	**Fire intensities (mean±sd)**		**% simulated patches per fire region**			
Terminal node	Mean	Median	C.V	Basal area	CBH	CBD	Total stem density/sapling density	(% total) total=12,000 per species	Initial intensity (Ii)	Updated intensity (If)	A2	B3	C3	D4
Black spruce														
1	21.5	15.2	98.7	21.9	2.9	0.30	4270/3234	1258 (10.5%)	83±50	539±3119	10.2	**57.2**	7.70	24.8
5	57.6	57.4	57.0	25.5	3.2	0.28	3235/2251	1044 (8.70%)	524±222	8994±14049	14.9	**40.0**	28.9	16.0
2	84.8	94.6	25.8	12.8	2.8	0.14	2078/1347	2301 (19.1%)	2921±3162	3303±3855	16.4	22.4	26.2	**34.8**
6	90.2	91.9	7.1	25.5	3.1	0.29	3250/2234	2917 (24.3%)	3862±3154	11068±13413	**38.3**	12.4	26.5	22.7
4	93.6	95.0	9.1	25.5	3.0	0.34	4754/3435	2346 (19.5%)	3013±2971±	16739±14373	**34.1**	20.2	24.2	21.4
3	97.2	97.2	1.0	23.3	2.7	0.42	7330/6148	2134 (17.7%)	2892±3125	18613±15085	19.5	23.9	**30.7**	25.8
Jack pine														
1	9.8	7.7	92.3	15.7	3.3	0.15	2143/1262	8677 (72.3%)	47±42	127±925	**30.3**	29.5	21.6	18.4
2	23.5	13.9	108	14.9	3.2	0.15	2160/1353	1280 (10.6%)	239±51	1566±4260	26.6	8.6	**37.0**	27.6
3	67.6	82.4	47.5	10.3	2.3	0.14	4324/3933	397 (3.30%)	88±93	3566±4558	0.0	0.0	**53.6**	46.3
4	69.9	84.6	40.3	14.2	3.1	0.15	2507/1724	1645 (13.7%)	1196±1416	3229±6368	1.3	19.9	26.3	**52.3**

The conditional regression tree for jack pine is shown in Fig. 6, with basic statistics reported in Table 3. Variation in the % density of trees in the 10-cm diameter class produced detectable differences in the resulting severity at intensities below 348 kW m^{-1} (i.e. scorch height of 7 m). Low severity (<25% basal area reduction) was almost always (91% frequency) observed below this threshold. At intensities below 169 kW m^{-1} (i.e. scorch height of 4.5 m), low severity with a median of 7.7% was found in jack pine stands where the % density of trees in the 10-cm diameter class was less than 69% (terminal node 1; Fig. 6). High severity fires (>75% basal area reduction) with a median of 82% were observed in stands where this value was greater than 69% (terminal node 3). At intensities above 348 kW m^{-1}, high severity (>75% basal area reduction) with a median of 88% was observed (40% frequency; terminal node 4; Fig. 6).

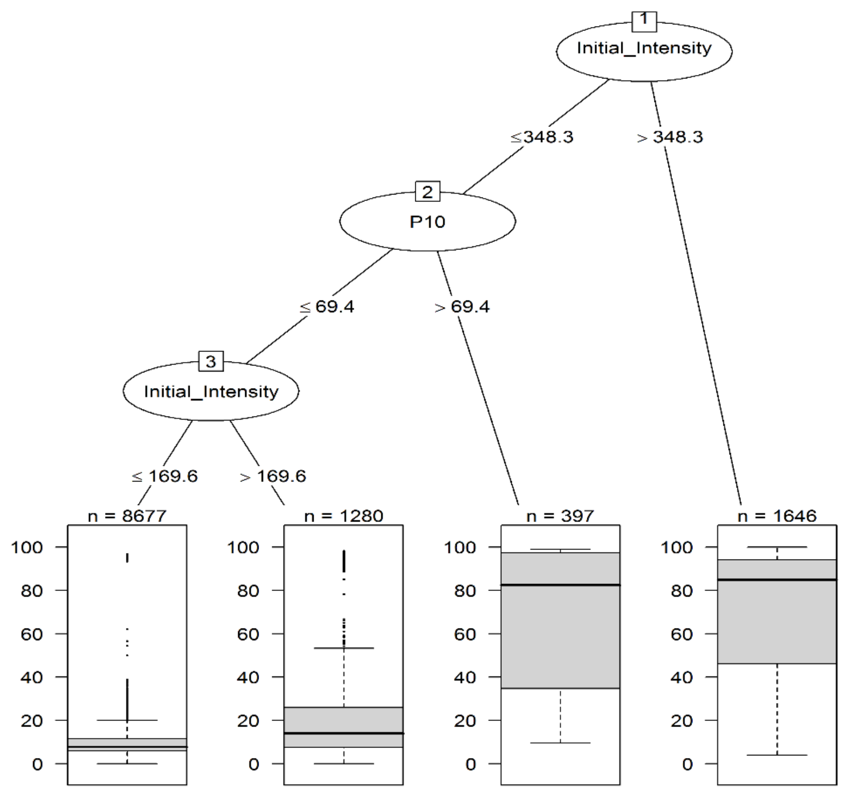


Figure 6. Regression tree for simulated fire severity in jack pine patches. The first split in the tree, or the root, is defined by the covariate with the strongest relationship with fire severity. Box plots at terminal nodes show the distribution of the fire severity data within each branch of the tree. The number of observations within each branch is shown at the top of each boxplot. The total number of simulated fires was 12,000

IV. Discussion

We integrated stand structure characteristics derived from inventory plots and fire intensities, within a diameter class-structured fire severity model that accounts for propagation from a surface fire into the canopy. Fire intensities were sampled as to approximate the unknown distribution of intensities over the historical area burned. The model uses allometric equations to derive stand structure and fuels distribution from diameter-class structures. It uses empirical relations between fire behaviour descriptors and fire effects to evaluate and quantify the influence of the relationship between fire intensity and stand structure on fire severity in 1.0 ha patches of mono-specific black spruce and jack pine stands in northern Québec, Canada.

We found no evidence for a residual effect of pyrogeographic region on simulated severity, after the effects of stand structure and species composition were accounted for. It remains possible that the differences we detected in stand structure among regions reflect differences in fire regime or other geographic factors. The regional implications of these findings would be of interest to pursue in further studies. Our simulations suggest that stand structure is one of the factors causing the observed variation in boreal fire severity. Stand structure exerts its effects primarily through horizontal and vertical structure as reflected in the diameter class distribution and canopy bulk density for black spruce stands and, for pine stands, in the % density of trees in the 10-cm diameter class. We identified thresholds in intensity below which some stand characteristics are conducive to low or moderate severity outcomes. Under high fire intensities associated with crowning and high overstory fuels consumption (Alexander and Cole 1995, Alexander and Cruz 2012), simulated fire severity was independent of stand structure. At lower intensities, we found marked sensitivity to stand structure, and interactions between intensity and structure.

We found that for black spruce, complex structures usually associated to uneven-sized stands (Boucher et al. 2003, Amoroso et al. 2011), tended to have lower severity (terminal node 5 in Fig. 5). This means that, if an uneven-sized stand was burned at low severity, one might expect that it would be temporarily converted to a relatively even-sized stand of predominantly larger trees. This statement is supported by the fact that approximately 47% (n=452) of the mono-specific black spruce inventory plots classified as even-sized (n=951) have basal area values comparable to those found in uneven-sized stands (e.g. mean of 24 m^2 ha^{-1}; Harper et al. 2003, Rossi et al. 2009). As lower severity fires would act as stand-maintaining rather than stand-initiating events, the uneven-sized stands would thus tend to perpetuate themselves as new individuals were recruited beneath the surviving overstory. In other words, stand structure may act as a biotic feedback mechanism, tending to reduce mean fire severity. However, our method for modelling the propagation from surface to crown fire does not account for the spatial distribution of canopy fuel (e.g. clumps of trees) within the patch, which may have an effect on fire behaviour and resulting severity (Staudhammer and LeMay 2001). Therefore, it remains possible that uneven-sized stands with heavy, continuous fuel loading would support the development of severe crown fires under some fire-weather conditions. In that case, the development of heavy fuel loads in such stands would tend to counteract the hypothetical biotic feedback.

The updated intensity values calculated for terminal nodes 1,3,4,5 and 6 of the regression tree for black spruce were substantially higher than the initial intensities (Table 3). However, in the case of terminal node 2, there is a small difference between the initial and updated intensities. Node 2 represents relatively even-sized stands (SWDI<1.8) with low canopy bulk density (CBD<0.2), and they burned primarily at high severity with substantial variation in severity (Fig. 5). A possible reason for this small difference between the initial and updates intensities lies in the stand and fuel characteristics (Table 3). For example, node 2 is characterized by mean basal area values of 12 m^2 ha^{-1}, low amounts of available fuel in the canopy and a low density of stems (Table 3), 64% of which is represented by saplings. As the top height of the canopy stratum capable of sustaining combustion decreases, so do the resulting updated intensities (Table 1).

The fire history archives contain estimated head fire intensities at solar-noon on the day the fire started, interpolated from meteorological data (Forestry Canada Fire Danger Group 1992, Wotton et al. 2009). These intensities do not apply uniformly to the total area burned by the fire. We used a theoretical distribution of proportional intensity by burned area (Catchpole et al. 1992) to correct for this. This correction dramatically reduces the mean intensities relative to the reported values (e.g. in Fig. 3). It is possible that in so doing, we underestimate fire severity. To provide the readers with a general insight into the conditions under which variation in fire severity can arise, an additional set of simulations per species was run in which crown fire development was not modelled; that is fire intensity remained fixed regardless of canopy structure. These results are shown in Appendix A-2 and A-3. Although the regression trees for black spruce and jack pine using the additional set of simulations showed different thresholds in intensity compared to Fig. 5 and Fig. 6, the conclusion that stand structure explains fire severity within the study region is robust to this correction.

The boreal forest of North America has traditionally been characterised by the presence of large high intensity crown fires which resulted in uniform, near 100% mortality (Whelan 1995, Ryan 2002). This view has encouraged the adoption of short rotation clear-cut harvesting as the forest management practice most suitable to the region (Bergeron et al. 2001). However, this view of boreal fire regimes has recently been challenged. For example, significant areas of low or moderate severity fire have also been reported in the western boreal forest (Amoroso et al. 2011). Further, the variation in severity implied by our results is consistent with the findings of Kafka et al. (2001) that revealed heterogeneity in fire impacts, based on visual characteristics of the post-burn landscape within a large wildfire in western Québec. Despite the importance of high intensity crown fires in boreal forest, significant variation in severity clearly occurs. Our results provide a partial biophysical explanation for this phenomenon. Specifically, our results suggest that spatial diversity in stand structure is sufficient to generate variation in fire severity. Other sources of variation in severity include diurnal and longer term variation in fire weather and thus in fire intensity (Beck et al. 2002). The relative importance of these and other factors in generating spatial variation in fire severity remains to be elucidated.

1. *Model limitations and extensions*

Many models have been developed for simulating patterns of fire effects (Sikkink and Keane 2012). Complex models of fire behaviour are capable of describing variation in fire effects in response to stand structure and hourly fire weather conditions, but require very detailed input streams that are not easy to generate (Gardner et al. 1999). In contrast, the diameter class-structured model presented here uses simple forest fire history and mensuration data, linked with empirical relationships between fire intensity and fire effects. Model uncertainties associated to factors inherent to these relationships are somewhat difficult to quantify because our model integrates so many disparate data sources and past mensuration and modelling studies. We do not think it is necessary to explore these many sources of error in detail for the purposes of the present study. This conclusion might be altered if the precise values of the decision variables in the terminal nodes of Fig. 5 and 6 were of great practical importance.

There are some uncertainties in the model assumptions and implementation that could be resolved to improve model predictions. For example, fire severity outcomes are sensitive to assumptions regarding the geometrical representation of the tree's crown, whether cylindrical, parabolic, or otherwise, because these shapes affect the vertical distribution of fuels (Peterson 1985, Hall and Burke 2006). Uncertainty in the calculation of crown fuels, namely canopy base height and canopy bulk density could have an effect on our fire severity results because these variables determine the vertical propagation of flaming combustion from the surface to the canopy. Moreover, the calculation of canopy base height is a weighted mean of diameter size-class values. This definition is not unique, and others might lead to different results (Keane 2015). Model outcomes could perhaps be improved by integrating multiple data sources and approaches when available, such as individual tree measurements from intensive sampling or Light Detection and Ranging (LiDAR) information (Skowroski et al. 2011).

The percentage of crown scorched, an important variable influencing overstory tree mortality and resulting severity, was quantified as function of several variables that were estimated from DBH (e.g. Table 1). The uncertainty involving these quantities and the subsequent effect on the calculation of the percentage of crown scorched, could be reduced by integrating other models that use different crown, stem, and root injury variables to predict tree mortality (Thies et al. 2006). We acknowledge that this improvement might increase post-fire mortality prediction accuracy. However, the lack of available models calibrated for black spruce or jack pine made this integration not feasible for the present study. Similarly, post-fire tree mortality is calculated as a function of the scorch height, the percentage of crown scorched, and the bark thickness. Although originally developed for western conifers (Hood et al. 2007), the generic mortality model such as the one used in our model, are applied in other severity modeling frameworks (Reinhardt and Crookstone 2003, Andrews 2009). We found this equation appropriate because they capture the damaging effect of fire on the stem cambium and the loss of foliage in the crown. Moreover, no alternative models have been developed for our region.

Wind speed and direction are critical influences on fire behavior (Whelan 1995, Alexander 1985, Alexander and Cruz 2012). Wind speed increases the fire energy output and exposes the unburned fuel to additional radiative and convective heating, thus affecting crown fire initiation and fire spread (Moon et al. 2013). However, estimates of wind profiles are complex and tend to vary substantially with height, forest type and stand structure (Moon et al. 2013). In addition, a certain proportion of wind momentum is absorbed by the vegetation, resulting in a wind speed reduction (Moon et al. 2013). Due to the lack of forest wind speed profile data for our study region, it was decided not to include this interaction in the fire severity model presented here. We also acknowledge that our horizontal and vertical stand structure measures do not provide direct information on the spatial heterogeneity of tree crowns within the patch, which may have an effect on fire behaviour and resulting severity (Parsons et al. 2011). The recent development of other stand structural diversity indices that combine a mixture of spatial diversity with tree attribute diversity (Staudhammer and LeMay 2001), could be included in future versions of the model, if sufficient data was available. However, investigating the effect of spatial heterogeneity of forest fuels within the patch was outside the scope of this study.

We think the most significant sources of uncertainty lies in the sampling of fire intensities used to derive the biological responses. Our raw data were head fire intensities from recent historical fires, estimated from interpolated meteorological data. These intensities represent a mix of surface and crown fires. The distribution of fire intensities used to drive the ecological model was derived from these raw data in several steps. Firstly, we used area-weighted sampling to increase the representation of intensities associated with larger fires (Bessi and Johnson 1995). We then applied the distribution of Catchpole et al. (1992) which relates head fire intensity to the distribution of intensities over the areas burned by a single fire. Finally, the intensities could be increased if a crown fire were to develop. The intention of all these steps was to better approximate the unknown distribution of intensities over the historical area burned. We note that the main result of this study, namely that stand structure mediates fire severity within the study region was robust to the way we generated the sample of fire intensities.

In this paper, we evaluated mono-specific patches, but there is no fundamental reason why the model could not be adapted to incorporate two or more tree species. It would also be feasible to incorporate other ecological processes. For example, simulation of snag provision and downed dead wood could be incorporated using empirical falldown and decay rates (Bond-Lamberty and Gower 2008, Angers et al. 2010). In fact, we will show in a subsequent paper how a simple matrix model of carbon pool dynamics (Kurz et al. 2009) can be easily coupled to the present model to simulate ecosystem carbon fluxes under alternate fire regimes.

2. *Implications for forest management*

Spatial and temporal variation in severity within fires can have long-lasting impacts on the stand structure and species composition of post-fire communities, and on the frequency and effects of future disturbances (Ryan 2002). Fire severity can affect the amount, nature, and successional trajectory of regenerating vegetation (Johnstone et al. 2011), alter post-fire tree fall patterns and decomposition rates of snags (Boulanger et al. 2011), affect nutrient cycling (Ryan 2002) and modify the carbon stocks and fluxes of fire-prone ecosystems such as the boreal forest of Canada (Boby et al. 2010). All of the factors are of importance in forest management, especially where forest landscape management intends to emulate natural disturbance regime by maintaining a mosaic of stand structures within the forest landscape (Harvey et al. 2003). Understanding the heterogeneity in fire severity patterns can also have direct, operational implications. For example, fire severity classifications can be used to evaluate prescribed fire success, to assess rehabilitation potential and mitigation of burn impacts (Sikkink and Keane 2012). Linking severity information to post-fire vegetation conditions could also improve estimates of future timber volume (Leduc et al. 2007, Hall et al. 2008).

In this study we addressed near-mono specific stands of black spruce and jack pine, stands associated with the C-2 and C-3 fuel types, respectively. These are two of the sixteen fuel types considered by the FBP System, both of which are well represented in Québec and throughout the boreal Canada (Hirsch 1996, Wotton et al. 2009). Although the FBP System fuel type classification is not intended to cover all variation in black spruce and jack pine stands, our study suggests that stand structure limits fire severity within the C-2 and C-3 fuel types under conditions of low and high-intensity surface fires (Alexander and Cole 1995, Alexander and Cruz 2012). In Québec, the classification of forest stands as fuels according to the FBP System include variables such as species composition, ratio of softwoods, height and age classes and drainage type (Pelletier et al. 2009). The fire intensity thresholds found in this study could help refining fuel types by integrating measures of stand structure.

Acknowledgements

We thank the Ministère des Forêts, de la Faune et des Parcs (MFFP) and the Societé de protection des forêts contre le feu (SOPFEU) for allowing us to use the inventory and historical forest fire archives. This project was funded by the Natural Sciences and Engineering Research Council of Canada (NSERC). We thank also the Centre for Forest Research (CEF) for financial and technical support as well as to all the members of the C*FIRE project at Université Laval. Special thanks to U. Valis for his help with the formatting of the graphs.

Chapter 2

Sensitivity of boreal carbon stocks to fire return interval and seasonality of head fire intensity: a simulation study of black spruce forests[2]

[2]Partially revised version of the paper: Miquelajauregui Y, Cumming SG, Gauthier S. Sensitivity of boreal carbon stocks to fire return interval and seasonality: a simulation study of black spruce forests. Submitted to Ecosystems MS# ECO-16-0157-Decision Revise and Resubmit.

Abstract

Boreal forests store substantial amounts of carbon in vegetation and soil pools. The magnitude of these pools is related to fire regime characteristics. Climate change is expected to alter boreal fire regimes, leading to changes in the amount of stored carbon. Quantifying these changes is of importance to understanding and managing global carbon budgets. We investigate how fire return interval interacts with seasonal variation in fire intensity to affect carbon stocks and fluxes in the boreal black spruce forests of Québec, Canada. A diameter-class structured model calibrated from inventory data that simulates the effect of stand dynamics on forest growth was coupled with an established model of carbon dynamics for the Canadian boreal forest and linked to a fire model. A simplified representation of fire regime allows us to simulate the occurrence of fires and their direct effects on canopy tree mortality and surface fuels combustion. We simulated carbon stocks and fluxes under seven levels of FRI and two fire seasons. We tested for an effect of these fire regime parameters on equilibrium mean C stocks. All dead organic matter and biomass carbon stocks were sensitive to FRI between 60 and 300 years. Dead organic matter C stocks were lower for summer fires that occurred under shorter FRI's. Maximum C uptake occurred under FRI's of 300 years while maximum C storage at FRI's of 700 years. We found a weak but significant effect of stand structure on C indicators. Reduced C storage is forecasted for nearly 1/4 of the study region under expected end-of-century climates.

Keywords

Canada; boreal forest; carbon stocks; inventory plots, head fire intensity; fire return interval; seasonality; CBM-CFS3; stand structure

Résumé

Les forêts boréales stockent des quantités importantes de carbone dans la végétation et le sol. La magnitude des puits de carbone dans ces deux pools est corrélée avec les caractéristiques du régime des feux. Le changement climatique devrait influencer le régime des feux de forêt boréale se faisant, il pourrait entrainer un changement dans la quantité de carbone stocké. La quantification de ces changements est importante à la compréhension et la gestion des réserves du carbone du budget global. Nous étudions comment la récurrence des feux interagit avec la variation saisonnière de l'intensité du feu pour affecter les réserves de carbone et ses fluctuations dans les forêts d'épinette noire du Québec, au Canada. Un modèle démographique structurée en classes de diamètre calibré par les données de l'inventaire qui simule les effets de la dynamique des peuplements sur la croissance de la forêt fut combiné avec le modèle du bilan du carbone du secteur forestier canadien (CBM-CFS3) et lié avec un modèle du feu qui utilise des données historiques d'intensité de feux de forêt. Une représentation simplifiée du régime de feu nous permet de simuler l'intervalle de retour du feu et la variation saisonnière de l'intensité du feu de même que les effets directs du feu sur la mortalité des arbres de la canopée et la combustion des combustibles de surface. Nous avons simulé les stocks et fluctuations de carbone sous sept intervalles de retour du feu et deux saisons de feu. Nous avons testé pour un effet de ces paramètres du régime de feu sur la moyenne d'équilibre des stocks de carbone. Tous les pools de carbone étaient sensibles aux intervalles entre 60 et 300 ans. Le stock de carbone dans le sol fut plus faible pour les incendies d'été qui se produisaient durant de plus courts intervalles. Le taux maximum d'absorption de carbone s'est déroulé sous un intervalle de 300 ans alors que le stockage maximal de carbone sous un intervalle de 700 ans. Nous avons trouvé un effet faible, mais significatif de la structure du peuplement sur les indicateurs de carbone. Une réduction dans le stockage de carbone est prévue pour près du quart de la région étudiée sous les climats anticipés en fin de siècle.

Mots clés

Canada; forêt boréale; stocks de carbone; inventaire forestier; intensité de feu; intervalle de retour du feu; saisonnalité; CBM-CFS3; structure du peuplement

I. Introduction

The boreal forest of North America stores substantial amounts of carbon (C) in above- and belowground biomass and as dead organic matter (DOM) carbon pools, making this biome one of the largest terrestrial C reservoirs (Laganière et al. 2013, Kurz et al. 2013). The magnitude of boreal forest C pools is related to the rate of forest growth, the rate of decomposition of dead organic matter, and to carbon losses caused by decomposition and natural disturbances such as wildfires (Kasischke et al. 1995, de Groot et al. 2003, Manies et al. 2005(W J de Groot et al. 2003)(W J de Groot et al. 2003)(W J de Groot et al. 2003)). Forest fire is the dominant disturbance regime in boreal forest ecosystems. The boreal fire regime is characterized by high-intensity crown fires, which are usually large and severe (Johnson 1992). The regional distribution of site-level carbon stocks depends in part on characteristics of the fire regime (Kashian et al. 2006, Boulanger et al. 2013). For the purposes of this paper, we will define the fire regime as having three components: fire return interval, fire intensity and seasonality (Johnson 1992, Ryan 2002). The fire return interval (FRI) is defined as the expected number of years between successive fires at a given location (Ryan 2002). Fire intensity is the rate of energy released per unit length of fire front in units of kWm^{-1} (Byram 1959). Seasonality refers to the time distribution of fire events within years (Ryan 2002).

The fire regime is an important driver of boreal carbon dynamics as it alters the magnitude and composition of forest C stocks both directly, by tree mortality, organic matter combustion and post-fire carbon accumulation, and indirectly, by changing the quantities of C transferred between pools (Kashian et al. 2006). For example, the fire return interval may influence boreal C sequestration and storage through controls over post-fire plant succession, forest stand age and structure (Kurz et al. 1995, Brassard and Chen 2006, Lemprière et al. 2013), soil respiration and forest productivity (Boulanger et al. 2013), fuel dynamics, carbon combustion (de Groot et al. 2003), and dead wood accumulation (Manies et al. 2005, Brassard and Chen 2006). The season of the year when a fire occurs can also alter boreal C dynamics through modifications in surface and crown fuel moisture content, which in turn affects fuel flammability, head fire intensity, fire size and severity (Weber and Flannigan

1997, Ryan 2002). In early spring, crown foliar moisture content is lowest leading to drier crown fuels, which are more likely to burn (Ryan 2002, DeLuca and Boisvenue 2012). However, deep duff moisture content is generally higher in the spring, resulting in fires than are usually less severe than summer ones. Summer fires tend to be more severe as combustion fuels accumulate and drying of the deep duff continues, allowing for more intense fires that usually consume greater amounts of C compared to spring fires (Ryan 2002, Amiro et al. 2009, DeLuca and Boisvenue 2012).

Climate change will likely decrease fire return interval throughout the boreal forest (Flannigan and Van Wagner 1991, Bergeron et al. 2006). Earlier snowmelt, longer droughts and a lengthening in fire season may affect fire seasonality. Increases in severe summer fire weather conditions are expected to increase fire intensity and fire size which in turn might affect boreal C storage (Ryan 2002, Kurz et al. 2008, van Bellen et al. 2010). The effect´s magnitude is expected to vary regionally (Boulanger et al. 2013), which would lead to regionally variable changes in mean C stocks (Kashian et al. 2006). Large quantities of stored C could be released to the atmosphere in areas where, for example, FRI became too short for biomass re-accumulation (van Bellen et al. 2010). However, shorter return intervals could reduce fuel load (Manies et al. 2005), partially compensating for the frequent carbon emissions. Changes in the fire regime due to climate change are expected to have long-lasting effects on boreal C stocks (Ryan 2002). Given the key role of boreal forest in the global C cycle and the importance of boreal soils as a sink for atmospheric C (DeLuca and Boisvenue 2012, Bona et al. 2013), the quantitative understanding of the relationship between current and future fire regime characteristics and boreal forest carbon stocks is needed.

Models of forest C dynamics are important research tools used to study these relationships. These models also allow identifying sensitivities associated with the estimation of boreal C stocks (Peng et al. 2002, Kurz et al. 2008). In this article, we present a diameter-class structured demographic model coupled with the Carbon Budget Model of the Canadian Forest Sector (CBM-CFS3; Kurz et al. 2009) boreal soil carbon module, and linked to an existing model of patch-level fire severity model (Miquelajauregui et al. 2016). This model accounts for the relationship between boreal fire return interval and seasonality in head fire intensity on boreal C stocks and fluxes. The model operates at the 1.0 ha patch level. A "patch" was defined as a homogenous spatial unit where individual-level processes of stem growth, competition, mortality and recruitment predominate (Caswell 2001). The patch growth component is a diameter-class structured demographic model (Caswell 2001) suitable for projecting stands where the diameter size distribution of stems is not uniform (Peng 2000). We coupled the patch model with an established model of boreal soil carbon dynamics based on the CBM-CFS3 (Kurz et al. 2009), which links standing biomass to DOM carbon pools via mortality, living biomass turnover, and temperature-dependent decay rates. The fire module simulates the transition from a surface to a crown fire as a process of vertical spread into the canopy (Van Wagner 1977). The fire module explicitly accounts for the effects of fire on overstory tree mortality, DOM carbon consumption and black spruce post-fire regeneration. The model is driven by a simplified description of a fire regime in terms of FRI and a seasonal distribution of head fire intensities. We use the model to estimate the relations between fire regime parameters and carbon stocks and fluxes in 1.0 ha patches of monospecific black spruce stands in northern Québec, Canada. Specifically, we quantify the effect of fire return interval and seasonal variation in head fire intensity on the mean aboveground and belowground carbon stocks and fluxes and evaluate the residual effect of stand structure on these indicators after accounting for fire regime parameters. Finally, we use forecasted changes in FRI over the 21st century (Boulanger et al. 2013) to forecast and map changes in total ecosystem carbon over 412,400 km^2 of Québec boreal forest.

II. Materials and Methods

1. *Study Area*

The study area is the boreal black spruce-feather moss bioclimatic domain of northern Québec, Canada (48°56'-52°24' N, 79°49'-62°79' W), which covers an area of 412,400 km^2 (Fig. 7; Saucier et al. 1998). Black spruce (*Picea mariana* (Mill.) B.S.P.) is the dominant tree species, occurring mainly in mono-specific stands (Saucier et al. 1998). The domain lies within the Canadian Shield ecozone, a large area composed mostly of Precambrian rocks covered by glacial tills of various thicknesses (Rowe 1972). The black spruce-feather moss domain is characterized by a mean annual temperature ranging from -0.7ºC in the north to just above zero in the south; and receives in average 995 mm of precipitation throughout the year (Environment Canada 2015). Fire is the most common natural disturbance in the domain (Johnson 1992). Historical (1961-1990) fire return intervals vary from 51 to 780 years in the western portion of the domain to more than 900 years in the eastern portion (Appendix B-1; Bouchard et al. 2008; Boulanger et al. 2013). Most of the soils in the domain are Humo-Ferric Podzols (Soil Classification Working Group 1998). They are characterized by a thick organic layer and deep mineral soil horizons that contain large quantities of organic carbon (Tremblay et al. 2002, Laganière et al. 2013).

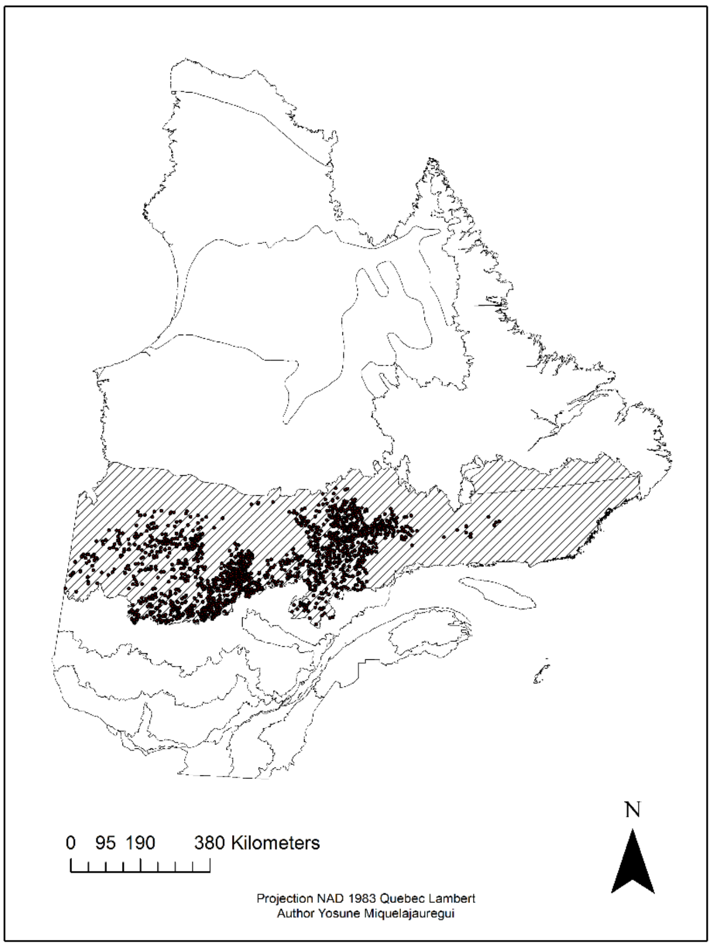


Figure 7. The black spruce feathermoss domain (shaded area) in Québec, Canada showing the location of the 3,249 mono-specific black spruce patches used for the modelling exercise.

2. ***Data***

Stem counts and diameter distributions used to drive the model simulations were obtained from an extensive network of forest inventory plot data completed by the Québec government agency Ministère des Forets, de la Faune et des Parcs Naturelles (MFFP 2008). Inventory plots are circular with a fixed area of 400 m^2 (MFFP 2008). Plot data was scaled up to 1.0 ha. Inventory plots were stratified by soil drainage class and surficial deposit. Mono-specific black spruce plots were defined as those were black spruce contributed more than 75% of the total basal area (MFFP 2008). A total of 3,249 mono-specific black spruce plots growing on characteristic “mesic-glacial till” soils were kept for the modelling exercise (Fig.7).

A historical forest fire database (1994-2010) was provided by the Société de protection des forêts contre le feu (SOPFEU 2012); the province of Québec’s forest fire management agency. Database attributes for each recorded fire include the date when the fire was detected, the location and the fuel type at detection, a final size, and the head fire intensity for the first day of burning. These head fire intensities were estimated according to the Canadian Forest Fire Behaviour Prediction (FBP) System from an assigned fuel type, and interpolated local solar-noon temperature, relative humidity, wind speed, and precipitation data (Forestry Canada Fire Danger Group 1992, Wotton et al. 2009). A total of 1,228 fires for the C-2 fuel type were kept for the modelling exercise. The C-2 fuel type is characterized by pure, moderately well-stocked black spruce stands, with a low crown base (Forestry Canada Fire Danger Group 1992, Wotton et al. 2009). Selected fires were then classified as “spring fires” (n=821) when occurring in May and June and “summer fires” (n=407) from July to September (Le Goff et al. 2009).

3. ***Model Description***

The model has three interacting modules: patch dynamics, fire and carbon dynamics (Fig.8). The three modules were developed and coded in R version 2.15.0 (R Development Core Team 2012).

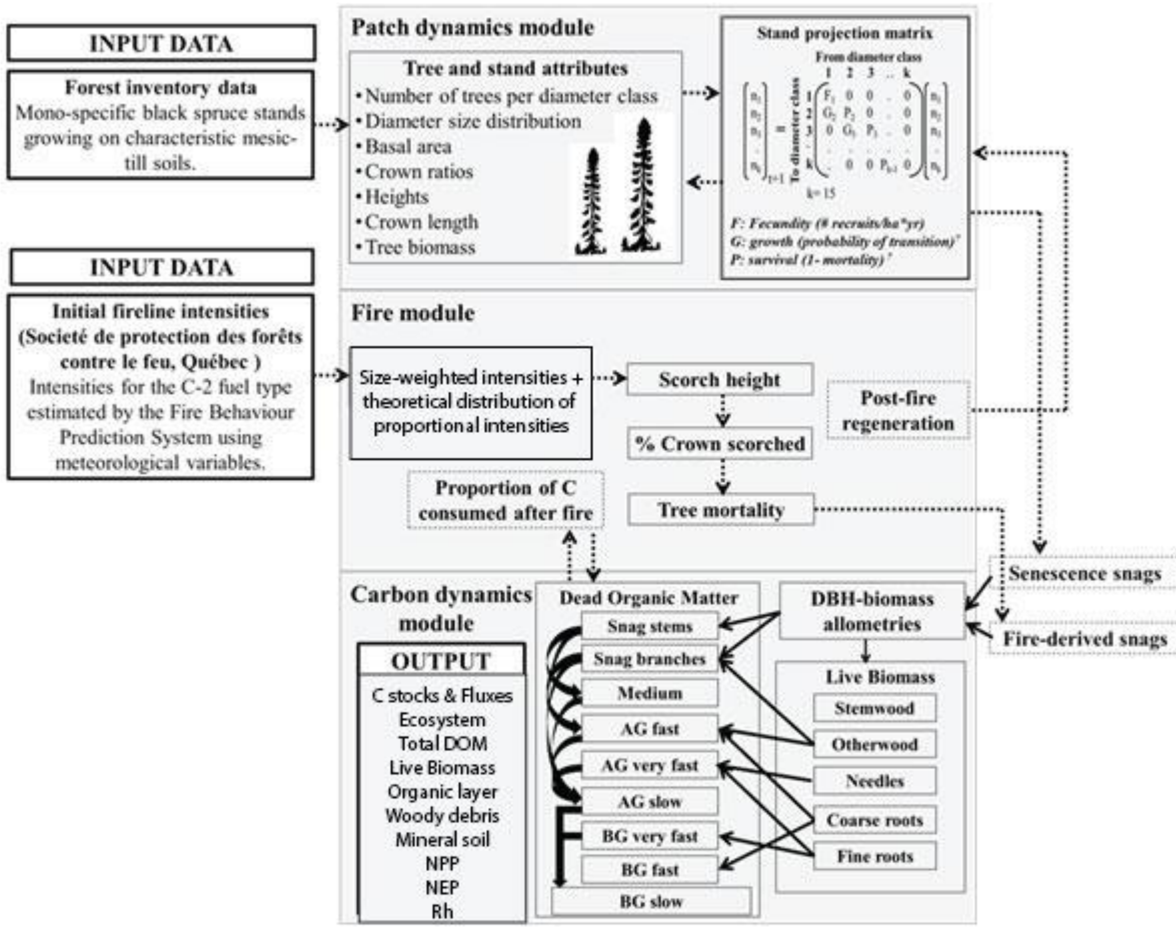


Figure 8. Diagram illustrating the three modules of the diameter-class structure model developed to simulate carbon dynamics for mono-specific black spruce stands of northern Québec, Canada. Biomass inputs and carbon transfers among pools are represented with solid arrows. Interactions among and within modules are represented with dashed arrows.

3.1 Patch Dynamics Module

We developed a diameter class-structured model with annual time steps. There were fifteen diameter at breast height (DBH) classes of 2.0 cm in width, from 1-3 to >29 cm. The largest diameter class was an absorbing state which is impossible to leave until the time of death (Caswell 2001). Patches are initialised from inventory sample plots. The state of the patch at time step t+1 is calculated by multiplying the number of live trees in each diameter class at time t by a matrix of time-varying transition probabilities that incorporate class-specific growth and mortality rates. These rates are themselves functions of time-varying patch properties.

3.1.1 Growth Rates

Annual transition probabilities from one size-class to the next are estimated from the expected size-class duration assuming a geometric waiting time (Caswell 2001). Expected size-class durations are estimated by dividing the stage width (2.0 cm) by mean annual diameter increments (cm yr^{-1}). The number of trees in each DBH class that advanced to the next class was sampled from a binomial distribution given the predicted annual transition probability and the number of trees in the class. Annual diameter increments for trees of DBH > 9.1 cm (9-11 to >29 DBH class) were estimated using an individual-tree distance independent diameter growth model (ARTÉMIS-2009; Fortin and Langevin 2010) which includes the effect of tree size (DBH) and the total patch basal area (m^2 ha^{-1}) on black spruce tree growth. For small diameter trees (< 9.1 cm; 1-3 to 7-9 DBH class) we used the forest vegetation simulator (FVS) model calibrated for black spruce based on Lacerte et al. (2006). The tree size and the sum basal area of larger diameter classes (m^2 ha^{-1}) drive tree growth in the FVS model.

Tree heights per DBH class were estimated using black spruce height-diameter relations (Peng 1999, their Eqn 1). Live crown ratios were initialised for each DBH class using black spruce-specific allometries in Holdaway (1986, their Eqn. 2), which are functions of DBH and patch basal area. Class crown ratios were updated using the first partial derivative of Holdaway (1986)'s equation with respect to patch basal area and diameter. This allows us to express changes in the crown ratio as an elementary function of changes in the other two quantities, with corrections to prevent biologically infeasible changes due to fire. Crown ratios were also updated by accounting for mortality, growth out of the class and recruitment into the first DBH class. From class heights, crown ratios and the number of trees in each class, we computed the class-specific crown lengths. Crown length (m) is an important canopy fuel variable defined as the average length of the canopy fuel stratum (Cruz et al. 2003). We used crown length as one predictor of post-fire tree mortality.

3.1.2 Background Mortality Rates

Annual mortality probabilities are a function of DBH and the basal area in larger classes (Fortin and Langevin 2010). For small diameter trees (< 9.1 cm; 1-3 to 7-9 DBH class), the annual mortality probability was fixed at 0.02, based on survival analysis of boreal black spruce saplings of different initial sizes (Matthias et al. 2003). The number of trees killed in each DBH class was sampled from a binomial distribution given the predicted class mortality probability and the number of trees in the diameter class.

3.1.3 Understory Recruitment Rates

Recruitment occurs when a new stem enters the first diameter class. We modelled the annual recruitment into the smallest size class as a Poisson process defined by the parameter lambda (λ), which represents the mean annual recruitment rate of black spruce stems per hectare. Lambda was estimated by simulation. Patches were randomly sampled from the inventory plots, characterized as even- or uneven sized (Boucher et al. 2003), and projected forward by the patch dynamics model for 500 years, without external disturbance, for varying values of λ. We compared initial and final diameter class distributions by a chi-square statistic. We chose λ that minimised the statistic while maintaining reasonable basal areas (e.g. 24 m^2 ha^{-1}; Bouchard et al. 2008). The resultant values of λ were 60 for even- and 55 for uneven-sized stands.

3.2 Fire Module

At the end of each time step, a fire is initiated with probability p=1/FRI. When a fire occurs, a single patch-level fire intensity is sampled from the historical forest fire database. We used an area-weighted sampling to increase the representation of intensities associated with larger fires (Bessie and Johnson 1995). We then applied the distribution of Catchpole et al. (1992) which relates head fire intensity to the distribution of intensities over the areas burned by a single fire. The intention of all these steps was to better approximate the unknown seasonal distribution of head fire intensities over the historical area burned. Finally, the sampled simulated fire intensity is applied to the 1.0 ha patch and allowed to increase if a crown fire develops. Fire algorithm details and supporting material are provided in Miquelajauregui et al. (2016).

The immediate impacts of fire on tree mortality, DOM carbon consumption and post-fire regeneration are derived from fire intensity. The fire module can simulate the development of high intensity crown fires from low intensity surface fires, using approximations of the physical conditions limiting the initiation and spread of a crown fire (Van Wagner 1977). Empirical relations between fire intensity, scorch height, bark thickness and the percent of crown scorched are used to calculate fire-caused mortality (Miquelajauregui et al. 2016). Scorch height (m) is defined as the height at which the heat of a fire is lethal to living foliage and is calculated as a function of intensity (Van Wagner 1973). The percentage of crown volume scorched per DBH class (%) is determined from calculated scorch height and crown length, approximating crown shapes as cylinders (Reinhardt and Crookston 2003). The probability of tree mortality per DBH class is modeled as a function of stem diameter, bark thickness and the percentage of crown volume scorched (Reinhardt and Crookston 2003). Finally, the number of trees killed in each DBH class is sampled from a binomial distribution given the predicted class mortality probability and the number of trees prior to the fire.

To simulate the effect of fire on aboveground DOM C consumption, we used carbon pool-specific proportions (Table 6). Proportions remained unchanged with fire seasonality. All pre-fire regeneration cohorts are assumed to be killed by the fire. The fire module also estimates post-fire recruitment using Greene and Johnson´s (1999) black spruce post-fire regeneration model. Post-fire tree recruitment was estimated from pre-fire basal area, seed mass, early survival and optimal seedbed availability (Greene and Johnson 1999). We assumed a 27-year regeneration delay for seedlings to enter the first diameter class (1-3 cm DBH; Van Bogaert et al. 2015).

3.3 Carbon Dynamics Module

The number and type of forest carbon pools, and inter-pool transfer and decay rates were defined following the CBM-CFS3 (Table 4; Kurz et al. 2009). The CBM-CFS3 serves as the core component of Canada's National Forest C Monitoring Accounting Reporting System (Kurz et al. 2009, Boisvenue et al. 2012). The model accurately estimates forest C stocks for different forest regions in Canada (Kurz et al. 2009, Hagemann et al. 2010).

Table 4. Description of the five live biomass and nine dead organic matter (DOM) above- (AG) and belowground (BG) carbon pools. Modified from Kurz et al. (2009).

Carbon pool	**Description**
Live biomass	
Stemwood	Stemwood of > 9.1 cm DBH + bark
Otherwood	Branches, trees < 9.1 cm DBH + bark
Needles	Foliage
Fine roots	Roots < 5 mm diameter
Coarse roots	Roots ≥ 5 mm diameter
Dead organic matter (DOM)	
Snag stems	Dead standing trees > 9.1 cm DBH + bark
Snag branches	Dead branches, dead trees < 9.1 cm DBH + bark
Medium	Coarse woody debris on the ground
AG fast	Fine and small woody debris + dead coarse root
AG very fast	The L horizon + dead fine woody material.
AG slow	F, H and O horizons
BG very fast	Dead fine roots in mineral soil <5mm diameter
BG fast	Coarse roots in mineral soil ≥ 5 mm diameter
BG slow	Mineral soil to 45 cm depth

3.3.1 Carbon Pools

We tracked carbon content (Mg C ha^{-1}) in five live biomass pools and nine dead organic matter (DOM) pools. Both live and dead pools included aboveground (AG) and belowground (BG) components. DOM pools included snags stems and branches, coarse woody debris, all litter and organic horizons, as well as organic carbon in the mineral soil (Table 4). Live pool biomass was calculated by diameter class using DBH-allometric equations (Table 5), multiplied by the number of trees in each class, summed over classes, and converted to mass of C at a rate of 0.5 (Hagemann et al. 2010). Tree component-specific litterfall and turnover rates representative of the Canadian boreal shield ecozone were taken from Kurz et al. (2009) and used to calculate annual biomass C transfers from each living pool to one or more DOM pools (Table 5). Annual C inputs from tree mortality were calculated and allocated to one or more DOM pools as specified in Table 5. When a fire occurs, a proportion of DOM C pools is consumed (Table 6), with loss rates from Boisvenue et al. (2012).

Table 5. Tree component-specific allometric DBH-biomass (kg) equations and sources. Biomass turnover rates (% C yr^{-1}) and turnover transfer (%) to each DOM pool taken from Kurz et al. (2009). ** Empirically-derived by the patch dynamics and fire modules. AG=aboveground, BG=belowground.

Tree component	**Allometric equations**	**Source**	**Live biomass C pool**	**Turnover rate**	**DOM C pool receiving turnover**	**Litterfall transfer rate**
Stemwood	$0.0477 \times \mathrm{DBH}^{2.514}$	Lambert et al. 2005	Stemwood *(> 9.1 cm + bark)*	**	Snag stems	100
Bark	$0.0153 \times \mathrm{DBH}^{2.242}$	Lambert et al. 2005	Otherwood (*Branches + small trees+bark)*	4	Snag branches	25
Branches	$0.0278 \times DBH^{2.083}$	Lambert et al. 2005			AG fast	75
Needles	$0.1648 \times DBH^{1.414}$	Lambert et al. 2005	Needles	16	AG very fast	100
Fine roots	$0.0110 \times DBH^{1.9748}$	Chen et al. 2004	Fine roots	64.1	AG very fast	50
					BG very fast	50
Coarse roots	$(-4.76 + 2.87 \times \ln DBH) - (-6.48 + 2.40 \times \ln DBH)$	Ouimet et al. 2008	Coarse roots	2	AG fast	50
					BG fast	50

3.3.2 Decay Dynamics

Decomposition of every DOM C pool was modelled using a temperature-dependent annual decay rate (Kurz et al. 2009), calculated at a regional mean annual temperature of 0.36ºC (Kull et al. 2011). For every pool, a certain proportion of the material decays given the decay rates (Table 6). A proportion of this decomposed material is released to the atmosphere (Patm). The remainder (Pt = 1-Patm), if any, is transferred to a slow DOM pool, as specified in Table 6. Bulk transfers of C among DOM pools (e.g. from Snag branches to AGfast) are also explicitly simulated (Fig. 8, Table 6) using rates from Kurz et al. (2009).

Table 6. Parameters from Kurz et al. (2009) used to simulate boreal soil C dynamics. Organic carbon consumption after a fire was estimated using parameters from Boisvenue et al. (2012). ** Calculated by the fire module as overstory tree mortality. Decay parameters include: base decay rates at a temperature of 10°C, sensitivity to temperature (Q_{10}), proportion of C released to atmosphere (P_{atm}) or transferred to another DOM pool (P_t).

DOM carbon pool	**Decay parameters**					**Bulk transfer parameter**		**Fire disturbance**
	Base decay rate (yr^{-1})	Q_{10}	P_{atm}	P_t	Pool receiving P_t	Transfer rate (yr^{-1})	Pool receiving transfer	Proportion consumed after fire
Snag stems	0.018	2	0.83	0.17	AG slow	0.080	AG Medium	**
Snag branches	0.072	2	0.83	0.17	AG slow	0.100	AG fast	**
AG Medium	0.034	2	0.83	0.17	AG slow	N/A	N/A	0.3921
AG fast	0.143	2	0.83	0.17	AG slow	N/A	N/A	0.6415
AG very fast	0.355	2.65	0.815	0.185	AG slow	N/A	N/A	0.9685
AG slow	0.015	2.65	1.0	0.0	N/A	0.006	BG slow	0.0901
BG very fast	0.500	2	0.83	0.17	BG slow	N/A	N/A	0
BG fast	0.143	2	0.83	0.17	BG slow	N/A	N/A	0
BG slow	0.003	1	1.0	N/A	N/A	N/A	N/A	0

3.3.3 Carbon Stocks and Fluxes

Total ecosystem carbon storage was estimated as the sum of C in all the live biomass and dead organic matter C pools. The live biomass C stock was quantified as the sum of carbon allocated in the five live carbon pools. Total DOM C stock was calculated as the sum of carbon in the nine dead organic matter C pools, including the mineral soil C. To facilitate model comparisons, we defined the organic layer C stock as the sum of C in the AG very fast and AG slow pools (Hagemann et al. 2010). Mineral soil C stock was calculated as the sum of the BG very fast and BG slow pools (Hagemann et al. 2010). We defined a "woody debris" C stock category which included the standing and dead fallen stems and fallen branches (Manies et al. 2005, Kurz et al. 2009). This was calculated as the sum of the Snag stems, Snag branches, AG fast and Medium pools.

Ecosystem fluxes such as the net primary productivity (NPP), the heterotrophic respiration (Rh) and the net ecosystem production (NEP) were estimated annually at the patch level (Mg C ha^{-1} yr^{-1}). Net primary productivity is the rate of carbon captured by living plants after accounting for losses resulting from plant respiration and other metabolic processes (Boisvenue and Running 2006). In other words, forest NPP measures the net flux of carbon between the atmosphere into plant tissues. Our NPP estimates were based upon measurements of live biomass C gain derived from allometric DBH-relationships. We calculated NPP as the sum of the net biomass difference between consecutive years and the replacement -of above- and belowground biomass turnover (Stinson et al. 2011, Kurz et al. 2013). Rh was calculated as the sum of decomposition losses to the atmosphere from all DOM pools. Net ecosystem production (NEP = NPP-Rh) is the annual net loss, or gain, of carbon from an ecosystem (Chen et al. 2002). An ecosystem is considered a carbon “sink” when NEP > 0 and a carbon “source” otherwise (IPCC 2007, Boisvenue et al. 2012, Kurz et al. 2013). In carbon sources, oxydation exceeds biomass growth (IPCC 2007).

4. *Simulation Experiment*

We simulated two descriptors of the fire regime: the fire return interval (FRI) and the empirical distributions of fire intensity for spring and summer fires. We ran 1000 replicates of seven levels of FRI (No Fire, 1200, 700, 300, 150, 100 and 60 years) and two fire seasons (spring and summer), for a total of 14,000 observations. The spatially varying simulated changes in fire regimes were expected to reveal where, within the study region, climate change might impact C storage the most. For each run, a patch structure was randomly sampled from the inventory plots. Stand attributes and live C pools are initialised from this structure. To initialize patch DOM C pools we used published values when available (Tremblay et al. 2002, Hagemann et al. 2010, Kull et al. 2011). Otherwise, the initial DOM C pool values were obtained by running the model for 300 years, and averaging over all runs and return intervals. The experimental runs lasted for 4,800 years, four times the longest fire return interval under study (Baker 1995) to remove dependence on initial conditions. For each year, the growth model is applied and regeneration and biomass gains are calculated. Carbon losses through overstory tree mortality, litterfall and turnover, carbon combustion and decomposition of DOM are then evaluated, and stand attributes and carbon pools are updated. Fire effects on overstory tree mortality, regeneration and DOM carbon consumption are then calculated from intensity and stand structure, as explained above. At the end of each simulation run, we extracted patch carbon stocks and fluxes. We also classified the final patch structure as even- or uneven-sized according to Boucher et al. (2003) to test for a residual effect of stand structure on the indicators of carbon dynamics after accounting for FRI and fire season effects. Before proceeding with the statistical analysis, all model components were verified. For details on this verification step, please refer to Appendix B-2.

5. *Statistical Analysis*

We used an analysis of variance (ANOVA) to test for significant effects of FRI and fire season on the response variables and to determine their relative influence. Preliminary diagnostic analysis of model residuals showed heterogeneity among levels of FRI. In order to incorporate this pattern in the model, the residual variance structure for each FRI was allowed to differ (Zuur et al. 2009). Candidate models that included interaction terms and different variance structures were fit to data and the optimal one was identified using the Akaike Information Criterion (AIC; Zuur et al. 2009). A mixed effect model with random intercepts associated to each structural type (uneven- and even-sized) was fit to data using the R package nmle (Pinheiro et al. 2015). We then tested for an overall residual effect of stand structure on each response variable, using the intraclass correlation coefficient (ICC; Zuur et al. 2009).

Boulanger et al. (2013) developed maps of historical (1961-1990) and future (2071-2100) fire regime attributes for eastern Canada under the IPCC SRES A2 or “business-as-usual” scenario. Fire return intervals within our study area are predicted to decrease over the 21st century compared to historical estimates (Appendix B-1; Boulanger et al. 2013). We used our results to estimate, by linear interpolation, the mean historical (H) and forecast (F) equililbrium C stocks, under the FRI´s given by Boulanger et al. (2013), of pure black spruce stands within the black spruce-feathermoss domain. From this, we estimated and mapped the expected average changes in these stocks, given the FRI maps provided by Boulanger et al. (2013). The mean percent change (%) in ecosystem C storage due to altered fire regimes was determined by comparing the effect of historical and future FRI on C storage, calculated as 100 %*(*F*-*H*)/*H*. We mapped these results over the black spruce feather moss domain.

III. Results

Historical head fire intensities that occurred in the spring were greater than summer ones ($F_{1,1226}$ = 12.21, p =0.0004; Fig. 9a). After accounting for the historical distribution, correlation between fire intensity and fire size, and heterogeneity of intensity within individual fires, simulated head fire intensities occurring during summer were higher than spring fires ($F_{1,47998}$ = 751.9, p <0.0004; Fig. 9b).

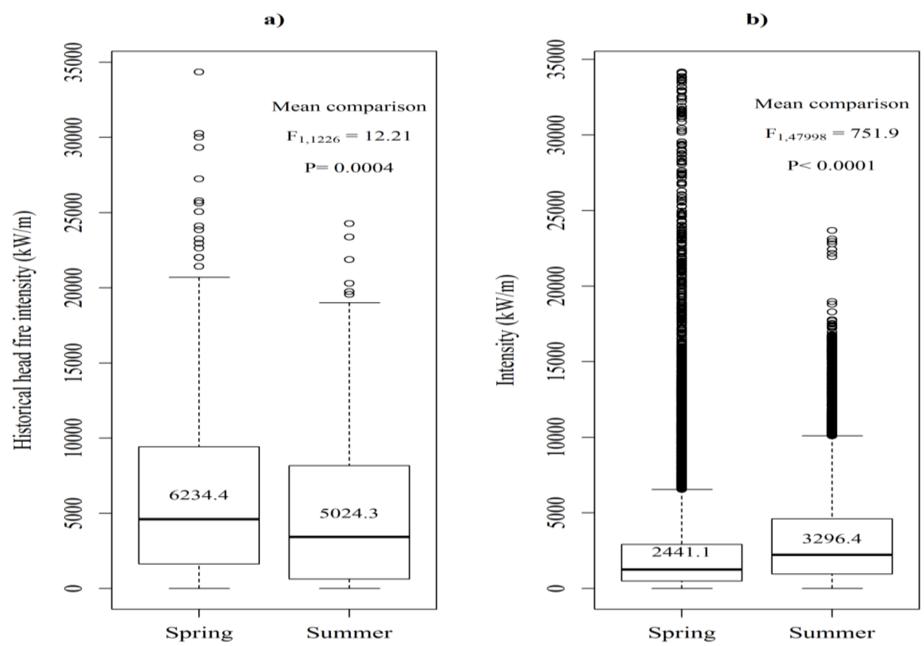


Figure 9. The distributions of fire intensities (kW m^{-1}), by season for: a) the historical fire record and b) the simulated intensities after accounting for the historical distribution, correlation between fire intensity and fire size, and heterogeneity of intensity within individual fires. Spring corresponds to May to June and summer from July to September. Boxes represent the inter-quartile ranges; horizontal lines within the boxes represent medians; whiskers extend to the lowest data point within 1.5 of the 1st quartile and the highest no more than 1.5 times greater than the 3rd quartile. Dots above whiskers represent extreme observations. Fire intensity mean values by fire season are presented within the boxes; ANOVA tests for differences in mean between fire seasons are presented as F statistics and p values.

Total ecosystem, live biomass, organic layer and woody debris C stocks were significantly affected by the fire return interval ($F_{1,6}$ = 536.9, 89.2, 411.7, 459.4, p <0.0001, <0.0001, <0.0001, <0.0001, respectively). For these variables, lowest mean stocks (201.1, 40.3, 39.1 and 31.4 Mg C ha^{-1}) were found under a FRI of 60 years; highest stocks (285.2, 58.6, 52.7 and 51.5 Mg C ha^{-1}) were reached at a FRI of 700 years, and in the case of the woody debris C stocks under the no-fire scenario (Figs. 10a,b,c,d). Intermediate mean ecosystem C stocks were found under a FRI of 1200 years and under the no-fire scenario (283.6 and 280.2 Mg C ha^{-1}, respectively (Fig. 10a). The interaction between FRI and fire season on mineral soil and DOM C stocks was significant ($F_{1,6}$ = 9.4, 5.6, p<0.001, <0.001, respectively; Figs.10e,f). For these pools, mean C stocks were lowest for summer fires under a FRI of 60 years (86.0 and 157.6 Mg C ha^{-1}); whereas highest mean stocks were reached for spring fires under a FRI of 300 years (120.6 and 227.2Mg C ha^{-1}; Figs. 10e,f). Overall, fire return intervals of 60 years reduced mean ecosystem C stocks by 29 % compared to FRI's of 300 and 700 years. For details of mean C stocks by FRI for all tracked DOM C pools, please refer to Appendix B-3.

NPP, NEP and Rh differed among FRI levels ($F_{1,6}$=40.3, 30.6, 157.2, p < 0.0001, respectively). NPP was lowest (3.0 Mg C ha^{-1} year^{-1}) under a FRI of 60 years and greatest (3.7 Mg C ha^{-1} year^{-1}) under a FRI of 150 and 300 years (Fig.11a). Under the no-fire scenario, mean NPP was 3.5 Mg C ha^{-1} year^{-1}, similar to the mean NPP value found for a return interval of 100 years. Heterotrophic respiration (Rh) was highest at a FRI of 300 years and lowest at 60 years (3.6 and 2.6 Mg C ha^{-1} year^{-1}, respectively; Fig.11b). Mean NEP was highest (0.4 Mg C ha^{-1} year^{-1}) under a FRI of 60 years and, as expected close to 0 under the no-fire scenario. Net ecosystem productivity was most variable among FRIs 60 to 300 years (Fig. 11c).

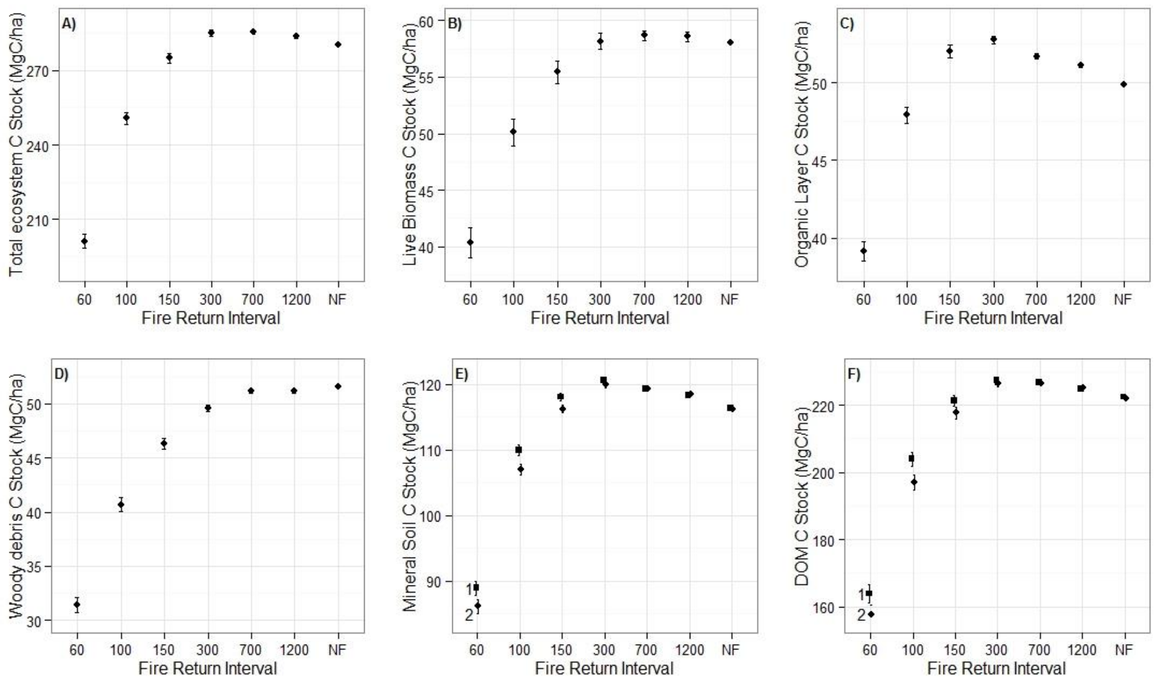


Figure 10. Mean C stocks (Mg C ha-1, mean ± 95%CI) over 1000 replicate simulation runs of 4800 years by FRI (x-axes) and fire season (1: Spring, 2: Summer). A) Total ecosystem, B) Live Biomass, C) Organic layer, D) Woody debris, E) Mineral soil, F) Total DOM.

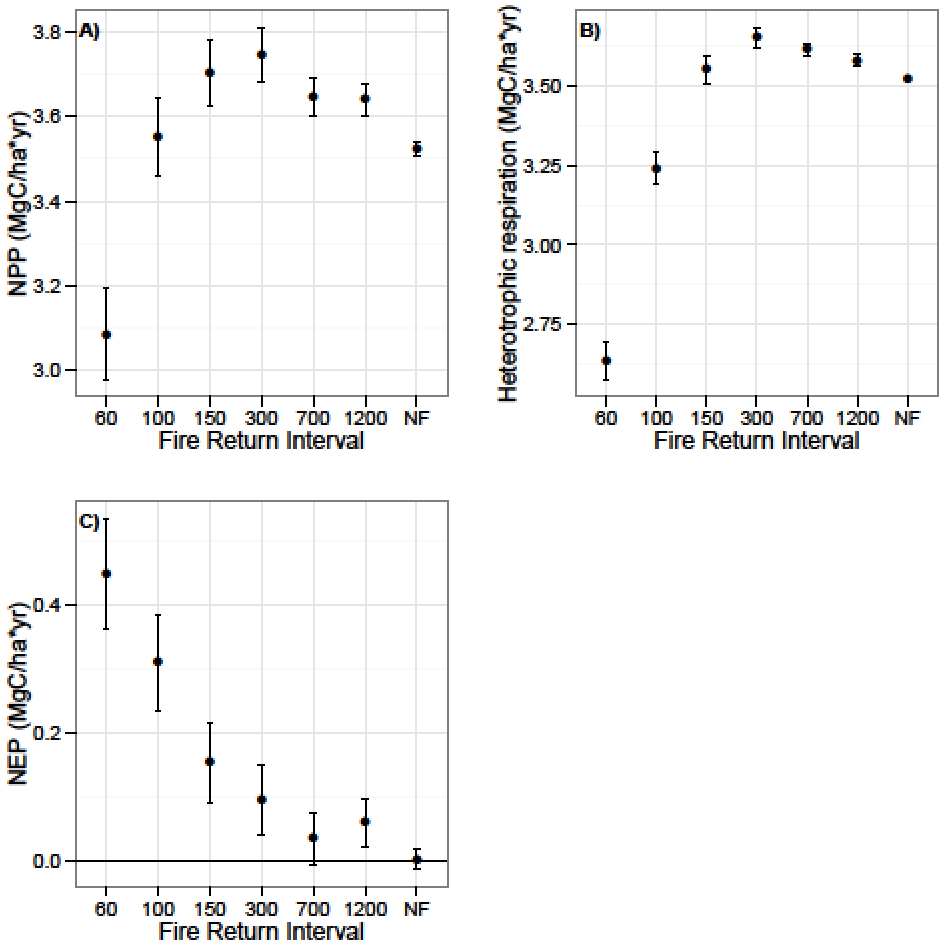


Figure 11. Mean C fluxes (Mg C ha^{-1} year^{-1}, mean ± 95%CI) over 1000 replicate simulation runs of 4800 years by FRI (x-axes). A) Net primary productivity (NPP), B) Heterotrophic respiration (Rh) and C) Net ecosystem production (NEP).

Pinheiro and Bates (2000) suggest that a random term can be excluded from the statistical model when the variability associated to it is less than 0.009. On that basis, residual effects of stand structure were weak but significant for most carbon pools. Approximately 7.9%, 7.9% and 27% of the total NPP, NEP and Rh observed variability was due to stand structure. Stand structure explained 14.0%, 15.5%, 7.1%, 8.0%, 1.9% of the variability found in total ecosystem, DOM, live biomass, organic and mineral C stocks, respectively. The residual effect of stand structure on the woody debris was significant and explained 34.4% of its variability. Total ecosystem C, live biomass and DOM C pools were larger in uneven-sized than even-sized stands (Table 7). The reverse was true for the carbon fluxes. Even-sized stands were roughly 21 percent more productive than uneven-sized stands with an average NPP of 4.3 and 3.4 Mg C ha^{-1} $year^{-1}$, respectively. Even-sized stands were carbon sinks (mean NEP = 1.3 Mg C ha^{-1} $year^{-1}$) while uneven-sized stands were essentially C neutral (mean NEP = -0.02 Mg C ha^{-1} $year^{-1}$). The simulated proportional abundance of the two structural types by fire return interval and season are presented in Appendix B-4.

Table 7. Simulated mean C stocks and fluxes for each structural type.

	Structure	
	Uneven-sized	**Even-sized**
C stocks (Mg ha^{-1})		
Ecosystem	271.7	236.3
Total DOM	215.9	191.2
Live Biomass	55.8	44.7
Organic layer	50.13	44.4
Mineral Soil	113.5	110.0
Woody debris	48.1	34.1
C fluxes (Mg ha^{-1} yr^{-1})		
NPP	3.4	4.3
NEP	-0.02	1.3
Rh	3.4	2.9
# simulated patches	12,298	1702

Our model evaluated under predicted changes in FRI by the end of the 21^{st} century (Boulanger et al. 2013) entails marked changes in the total amount of stored C within the study region (Fig. 12). The magnitude and direction of change varies with latitude. In much of the south of the study region, C stocks would be expected to increase, while decreases are expected in the northern parts (Fig. 12). In approximately 23% of the black spruce domain, C stocks in pure black spruce stands would decrease 4 to 6% by 2071-2100 (Fig. 12).

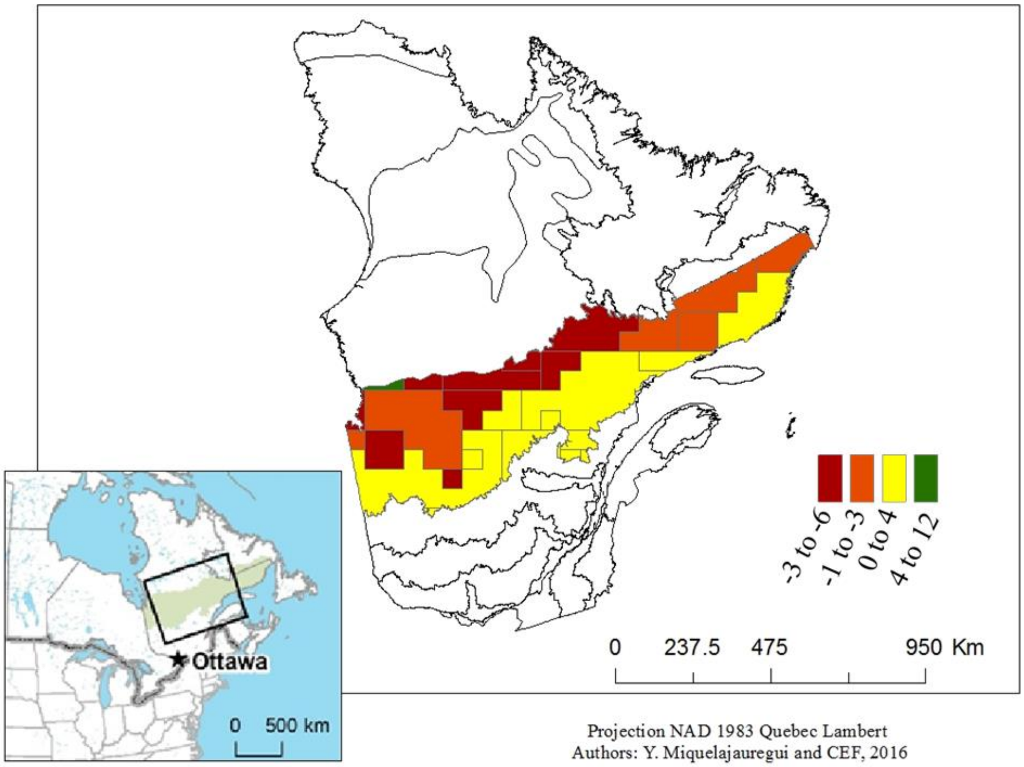


Figure 12. Estimated mean changes (%) in total ecosystem C storage for pure black spruce stands within the study area. We used the results from this study to perform a linear interpolation to estimate C stocks given the historical (H) and projected (F) FRI maps provided by Boulanger et al. (2013). The mean percent change (%) in ecosystem C storage due to altered fire regimes was determined by comparing the effect of historical and future FRI on C storage, calculated as 100 %*(F-H)/H. Map created in ArcGIS by the author.

IV. Discussion

We developed a diameter-class structured demographic model coupled with an established soil carbon model and linked to a fire severity model to simulate boreal black spruce forest C stocks and fluxes under different fire regimes. The fire regime was characterized by varying fire return intervals and seasonal variation in the historical distribution of fire intensities. Our simulated C stocks and fluxes are in good agreement with previous studies reporting measured and modelled C stocks for the boreal black spruce forest. Estimates of net primary productivity in boreal black spruce forests range from 2.6 to 3.4 Mg C ha^{-1} year^{-}

^{1} (Chen et al. 2002, Grant et al. 2010, Boiffin 2014), live biomass C from 47 to 74 Mg C ha^{-1}, and total ecosystem C from 185 to 291 Mg C ha^{-1} (Gower et al. 2001, Hagemann et al. 2010). Boreal podzols are estimated to store approximately 5 to 40 Mg C ha^{-1} in the organic layer and about 10-150 Mg C h a^{-1} in the mineral soil (DeLuca and Boisvenue 2012). Based on the Québec's provincial forest soil database, Tremblay et al. (2002) estimated black spruce organic layer C stocks from 38 to 58 Mg C ha^{-1} and mineral soil C content from 44 to 70 Mg C ha^{-1}. Laganière et al. (2013) quantified organic C content in the mineral soil (0 to 55 cm depth) of boreal black spruce forests of Québec. They reported total mineral C stocks of 62.7 Mg C ha^{-1}. Measured and modelled C content estimates for snags and coarse woody debris (e.g. medium carbon pool) varied between 5.3 to 12.1 and 18-25 Mg C ha^{-1}, respectively (Hagemann et al. 2010, Tremblay et al. 2002). We conclude that our modelling approach has the capacity to reproduce realistic boreal ecosystem C dynamics.

1. *Fire Regime Controls on Black Spruce Forest Carbon Stocks and Fluxes*

In our design experiments, fire return interval was the most important factor affecting simulated black spruce carbon fluxes and stocks. Decreasing FRI significantly decreased mean black spruce C stocks, because the simulated patches were not able to re-accumulate carbon fast enough to compensate for the carbon losses that resulted from overstory tree mortality, carbon combustion and decomposition (Kasischke et al. 1995). We found that the effect of fire season varied with FRI and was more pronounced under shorter return intervals (e.g. 60 years). The higher summer intensities increased post-fire tree mortality because scorch height and the percentage of crown scorched increased (Van Wagner 1973). As competition from neighbouring vegetation is reduced, the growth of the remaining live trees is enhanced. Greater C biomass could lead to higher C inputs into the DOM C pools via turnover of fine roots and needles (Wang et al. 2013). As a result, spring fires that occurred under shorter fire return intervals, allowed for greater C accumulation in the mineral and total DOM C pools compared to summer fires (e.g. Figs. 10e,f). The observed seasonality effect might be the result of the increasing post-fire tree mortality in summer, greater carbon transfers of dead material into the DOM carbon pools, under shorter return intervals, coupled with the assumed regeneration delay of post-fire recruits. We found that C uptake from the overstory was slightly greater for FRI of 300 years, while maximum C storage was at a FRI of 700 years. As suggested by Kurz et al. (2013), boreal forest stands can either be in a phase of C uptake or high C storage but not both, as these phases occur at different times during stand development. The simulated C sequestration and storage dynamics observed in this study is supported by extensive literature on boreal forest C dynamics (Chen et al. 2002, Kashian et al. 2006, Kurz et al. 2013). Our simulations suggest that fire return intervals between 300 and 700 years, are associated with high levels of both uptake and storage.

The simulation results of Bergeron et al. (2006) revealed that the western black spruce forest of northern Québec, a region 170,158 km^2 that covers 41% of the whole black spruce-feathermoss domain area (Saucier et al. 1998), will likely experience a 65% increase in fire frequency for the period 2040-2060, compared to current (1961-1990) estimates (e.g. 200-400 years, Bouchard et al. 2008, Boulanger et al. 2013). Boulanger et al. (2013) identified areas over eastern Canada where greater changes in fire regime are expected under future climate. Their results suggest important increases in fire frequency for most of northwestern Québec by 2041-2070 and some areas in northeastern Québec by 2071-2100. Our results suggest that shortening the fire return interval below 300 years may decrease C storage up to 25%. Evaluating these predicted changes in FRI using our model suggests 4 to 6% declines in stored carbon over nearly ¼ of the black spruce-feather moss domain. The actual effect may be greater, because our estimates did not account for changes in intensity that may accompany reduced FRI's. The sensitivity of black spruce C stocks to FRI is greatest below 300 years. The combined influence of return interval and fire intensity on black spruce ecosystem C stocks could impose challenges for carbon management and climate change mitigation efforts, in particular for the western portion of the black spruce forest of northern Québec.

Boreal forest carbon sequestration and reduction of wildfire hazard are two possible strategies to mitigate the effects of climate change (Lal 2004, Powers et al. 2013). Promoting carbon sequestration implies removal of atmospheric CO_2 by plants and storage of fixed carbon as soil organic matter (Lal 2004, Seedre et al. 2011). Powers et al. (2013) suggested that carbon management and climate change mitigation could be achieved by favouring carbon storage in stable, slow-turnover pools (e.g. woody debris and mineral soil), while minimizing storage in surface fuels (e.g. litter) which tend to decompose more rapidly. In black spruce forests, approximately 75% of the total mineral soil carbon is located within the first 0-15 cm below the organic-mineral interface (Laganière et al. 2013). Although there is not consistent understanding on how fire affects mineral soil C stocks, a post-fire loss of nearly 60% in mineral C stocks has been reported (Seedre et al. 2011). As a result, this carbon pool could be seen as less stable and more susceptible to fire effects than has been previously thought (Laganière et al. 2013).

2. *Stand Structure as an Indicator of C Storage*

With the exception of the woody debris C stock, our study revealed a small but significant residual effect of stand structure on the simulated C stocks and fluxes, after accounting for the effects of FRI and fire season. Such differences in C stocks and fluxes have been observed in both experimental studies and in other modeling exercises exploring the effect of boreal fire regimes on stand dynamics and carbon storage (Kasischke et al. 1995, Bouchard et al. 2008, van Bellen et al. 2010). Our results support the idea that uneven-sized stands store greater amounts of C in both the biomass and DOM carbon pools compared to even-sized ones. However, uneven stands are less productive. Miquelajauregui et al. (2016) suggested that black spruce forest stands associated to uneven-sized structures, tended to burn at low severity compared to even-sized ones. High severity fires would cause greater C losses as overstory tree mortality increases (van Bellen et al. 2010). Our findings also imply that stand structure is not a strong indicator of regional carbon storage and balance. Interacting effects among stand structure and other biotic and abiotic factors could play an important role in regulating carbon accumulation and rates of carbon exchange in the boreal forest. However, exploration of these factors was outside the scope of this paper.

3. *Model Strengths and Limitations*

Few modelling studies to date have coupled empirical models of stand growth, carbon dynamics and fire regime parameters to forecast carbon storage in boreal forest. In one notable example from Québec, Boiffin (2014) applied the spatially explicit model LANDIS-II coupled with a CENTURY succession extension to a boreal black spruce landscape to determine long-term predictions of C storage and fluxes. Her approach included interactions between microclimate patterns, black spruce regeneration, and successional trajectories on C cycling. In this approach, however, fire regime remained relatively homogeneous across the simulated boreal landscape (Boiffin 2014). In the diameter-class structured demographic model presented here, we coupled stand dynamics with an established soil carbon model (CBM-CFS3). We linked it to a fire severity model that accounts for crown ignition, vertical spread and overstory fire severity (Miquelajauregui et al. 2016) to simulate boreal black spruce forest C stocks and fluxes under different fire regimes. Our representation of stands as size-class structured populations is fundamentally different than that of LANDIS-II, and potentially allows for greater mechanistic detail (as in the vertical fire-spread component) and more direct parameterization from forestry mensuration data and tree growth and competition models such as used by the government of Québec. We believe our approach merits further development. Our model was developed for pure stands of black spruce, but many other stand types, both pure and mixed, occur. Parameterizing the model for a more complete suite of stand types would certainly be possible. A synthesis where our model adapted the superior regeneration component of Boiffin´s model, and her empirical findings, was expanded to multi-species stands, and was made spatially explicit would be of interest, as coupling the strengths of these two somewhat different modelling approaches.

Forecast of fire intensity distributions, where available, should also be incorporated in future studies. In addition to the impacts of FRI on black spruce forest C stocks and fluxes, as reported here, other environmental factors such as inter-annual variability in temperature and precipitation, growing season, soil texture and drainage, nitrogen availability and microbial dynamics could affect C fluxes and stocks (Grant et al. 2010, Kurz et al. 2013). None of these factors could be considered here. The matrix structure of the carbon dynamics module is robust enough to yield reasonable C estimates but also allows for improvements or modifications. For example, additional carbon pools could be incorporated to our model version, as long as available data exists, in order to better reflect C dynamics in boreal ecosystem (e.g. bryophyte, understory vegetation, pyrogenic carbon and fire-derived snags). Exploring how sensitive the model predictions are to these new carbon pools could be of interest for further research.

Acknowledgements

This research was funded by an NSERC (Natural Sciences and Engineering Research Council of Canada) Strategic grant to A.D. Munson, R.L. Bradley, S.G. Cumming, S. Gauthier, D. Paré and S. Quideau S.G. Cumming. Financial support was also obtained from a NSERC- CGS D-Alexander Graham Bell Graduate scholarship to Y. Miquelajauregui. The author also received financial support from Produits forestiers Résolu and F.K. Morrow Foundation. I specially thank the Centre d'étude de la forêt (CEF) for financial and logistic support**.** Very special thanks to M. Fortin and J. Marchal for their assistance during the model implementation. I want to thank P. Bernier, H. Chen and C. Boisvenue for the comments they provided to this version of the manuscript. Special thanks to F. Candela for his help with ArcGIS.

Chapter 3

Short-term responses of boreal carbon stocks to climate change: a simulation study of black spruce forests[3]

[3]Manuscript in preparation

Abstract

Boreal forest ecosystems have a significant role in the global C cycle. Over the current century, this ecosystem is expected to undergo one of the largest increases in temperatures. Climate change is expected to affect boreal C storage through changes in fire regimes, tree growth and decomposition rates. We developed a diameter-size structured model, coupled with a boreal soil C dynamics model and a fire model to investigate the short-term responses of boreal carbon storage to climate change. Our modelling approach has the potential of quantifying and mapping the location and timing of changes in boreal black spruce C stocks in northern Québec, Canada. We applied this model to 1.0 ha patches of monospecific black spruce stands under four climatic periods: 1980-2010, 2010-2040, 2040-2070 and 2070-2100. Forest inventory and historical fire intensity records representative of our study area were used to calibrate the model. Historical and future fire return interval (FRI) maps and projected weather data estimated by CanESM2 RCP8.5 climate scenario were used to drive historical and future disturbance frequency, forest growth, decomposition rates, and C dynamics. Black spruce trees showed amplified decreases in growth and temperature-sensitive decomposition rates of soil C pools were enhanced as projected air temperature increased. In our simulation experiments, ecosystem C accumulation was reduced by 11% by the end of 2100. We predicted a marked and widespread change from C sink to C source, which has already started and will persist at least until 2100. C storage differences between climatic periods were most evident towards the first half of the century (2010-2040). The results of this study indicate that black spruce forest of northern Québec could be losing their capacity to sequester and store organic C over the next coming decades due to climate change.

Keywords

Canada; boreal forest; fire return interval; climate change; carbon stocks; forest inventory, fire intensity; CBM-CFS3

Résumé

Les écosystèmes de la forêt boréale ont un rôle significatif dans le cycle global du carbone. Au cours de ce siècle, on anticipe l´une des plus grandes augmentations de températures dans ce biome. Le changement climatique aura un effet sur le stockage boréal du carbone à travers les changements dans le régime de feux, la croissance des arbres et les taux de décomposition. Nous avons développé un modèle structuré par classe de diamètre, couplé avec un modèle du bilan du carbone du secteur forestier canadien (CBM-CFS3). Nous avons lié ça avec un modèle du feu qui utilise des données historiques d'intensité de feux de forêts, afin d'investiguer les effets à court terme sur le stockage boréal du carbone causés par le changement climatique. Nous avons appliqué ce modèle à des régions de 1.0 hectare de peuplements purs d´épinettes noires. Les impacts à court terme du changement climatique ont été investigués au cours de quatre périodes climatiques: 1980-2010, 2010-2040, 2040-2070 et 2070-2100. Des cartes d'intervalle de retour du feu historique et futur et des données météorologiques projetées avec CanESM2 RCP8.5 ont été utilisées pour simuler la croissance des forets, les taux de décomposition, le régime du feu et la dynamique du C. Les simulations indiquent une réduction significative en termes de la croissance des arbres d´épinettes noires. Dans nos expériences de simulation, l'accumulation de carbone d'écosystème était réduite de 11% d'ici la fin de 2100. Nous avons prédit un changement marqué allant de puit de carbone à source de carbone, qui a déjà commencé et qui persistera au moins jusqu'en 2100. Les différences dans le stockage de carbone entre les périodes climatiques fut plus évident dans la première moitié du siècle (2010-2040). Les résultats de la présente étude démontrent que les forêts d'épinette noire du Québec seraient possiblement en train de perdre leur capacité à séquestrer et à stocker le carbone organique durant les prochaines décennies, cela étant causé par le changement climatique.

Mots clés

Canada; forêt boréale; intervalle de retour du feu, changement climatique; stocks de carbone; inventaire forestier; intensité de feu; CBM-CFS3

I. Introduction

Boreal forest ecosystems contain approximately 272 Pg of carbon (1 Pg = petagram = 1 billion tonnes) in living biomass, detritus, and soils (Pan et al. 2011, Kurz et al. 2013). The boreal forest is responsible for ~20 % of the total carbon (C) sequestrated annually by forest ecosystems (Pan et al. 2011) and therefore have the potential to greatly influence the global C balance (DeLuca and Boisvenue 2012; Lemprière et al. 2013, Price et al. 2013). Carbon stocks and fluxes in boreal black spruce forests are sensitive to the mean interval between fires (Kasischke et al. 1995, Boulanger et al. 2013, Miquelajauregui et al. in review) and vary as a function of stand age, stand structure, soil type and drainage, successional trajectories, topography and past fire severity (van Bellen et al. 2010, DeLuca and Boisvenue 2012, Lemprière et al. 2013, Boiffin 2014). Fire alters boreal C storage by killing most of the conifer live biomass (Brassard and Chen 2006, Kashian et al. 2006), and by releasing carbon to the atmosphere via organic matter combustion (Kashian et al. 2006, Boisvenue et al. 2012).

Across the Canadian boreal region, annual mean temperatures are predicted to by 3.3-5.4 ºC compared with current estimates (1961-1990) by 2071-2100 (Bond-Lamberty et al. 2004; Price et al. 2013; Gauthier et al. 2014). The boreal fire regime is also expected to change as a result of climate change (IPCC 2007). Shorter fire return intervals, more intense and severe fires, and a lengthening of the fire season are projected for boreal forest of Canada (Kasischke et al. 1995, Boulanger et al. 2013, 2014, Price et al. 2013). Climate change may affect boreal carbon balance through a number of biophysical mechanisms, some of which can be attributable to increased temperature, changes in water availability (Price et al. 2013, Girardin et al. 2015), and alterations to the fire regime characteristics, including the fire return interval (FRI), fire intensity and severity (Bhatti et al. 2001, Bergeron et al. 2004, Boulanger et al. 2013, 2014). These changes would have direct impacts on ecosystem structure and function (Kasischke et al. 1995, Kashian et al. 2006, Bergeron et al. 2010), leading to changes in the magnitude and distribution of boreal C stocks (Kasischke et al. 1994, Kurz et al. 1995,. 2013).

Climatic patterns and the regional weather regulate C accumulation in boreal ecosystems notably through direct controls on tree growth and microbial decomposition (Boisvenue and

Running 2006, Davidson et al. 2006, DeLuca and Boisvenue 2012, Loudermilk et al. 2013), and indirectly through modifications in the fire regime (Flannigan et al. 2009, Bergeron et al. 2010). Effects of global warming on tree growth and productivity in boreal ecosystems are well documented. For example, empirical studies and growth models results indicate that black spruce growth rates are predicted to increase in some regions of the boreal forest of North America, where precipitation increases could compensate for increasing evaporative stress induced by warmer temperatures (Price et al. 2013, Gauthier et al. 2014, D'Orangeville et al. 2016). In contradiction to these results, Girardin et al. (2008) and Dhital et al. (2015) studies indicate that water limitations and heat stress expected under global warming may reduce boreal black spruce tree growth. Warmer temperatures linked with climate change are likely to have a profound impact on fire activity in boreal forests (Flannigan et al. 2009). Such a warming would lead to drier fuels available for combustion, creating conditions conducive to increased fire activity (de Groot et al. 2003, Flannigan et al. 2009, Bergeron et al. 2010, DeLuca and Boisvenue 2012, Boulanger et al. 2014).

Canada needs to improve information about the magnitude of climate change impacts on boreal forest C stocks and fluxes, and on how such impacts may vary among regions. Understanding these impacts requires knowledge of feedback mechanisms associated with interactions of altered fire regimes, forest growth, decomposition rates and biospheric C pools. In this study we aimed at investigating the expected short-term disequilibria responses of black spruce forest carbon stocks and fluxes to projected climate change. We hypothesized that shorter return intervals, in concomitance with the increased temperatures expected under global warming will decrease black spruce forest C storage due to lower biomass accumulation and higher C losses that result from increased organic matter combustion and fire-related overstory tree mortality, reductions in tree growth rates and enhanced organic C decomposition. In order to investigate this hypothesis, we developed a diameter-class structured demographic model to project forest growth (Caswell 2001), coupled with an established model of boreal soil C dynamics based on the Carbon Budget Model of the Canadian Forest Sector (CBM-CFS3; Kurz et al. 2009), which links standing biomass to DOM carbon pools via mortality, living biomass turnover, and temperature-dependent decay rates. We related these components to an existing model of patch-level fire mortality

(Miquelajauregui et al. 2016), that simulates crown ignition, vertical spread and tree mortality from sampled patch-level fire intensities. We applied this model to 1.0 ha patches of monospecific black spruce stands to simulate short-term C dynamics under four climatic periods: 1980-2010 ("Historical" henceforth), 2010-2040, 2040-2070 and 2070-2100. The model was calibrated with forest inventory records representative of our study area and historical fire intensities. Historical and future fire regime maps (Boulanger et al. 2013) and simulated air temperature and precipitation derived from the weather simulator BioSIM (Régnière et al. 2014) were used to drive historical and future disturbance frequency, forest growth, decomposition rates, and C dynamics. This study is meant to provide insights into which regions within the black spruce-feather moss domain in eastern Canada will experience greatest changes in carbon stocks and how fast this ecosystem will respond to climate change.

II. Materials and Methods

1. Study area

The study area is the boreal black spruce-feathermoss bioclimatic domain of the boreal forest of northern Québec, Canada (48°56'-52°24' N, 79°49'-62°79' W; Fig.12, Saucier et al. 1998). The domain extends over the Canadian Shield, a large area composed mostly of Precambrian rocks covered by glacial tills of various thicknesses (Rowe 1972, Laganière et al. 2011). The black spruce-feathermoss domain covers an area of 412,400 km^2 which represents 28% of Québec's forested land (Saucier et al. 1998). The climate in the domain is boreal with a mean annual precipitation totaling 995 mm and a mean annual temperature ranging from -0.7ºC in the north to just above zero in the south (Environment Canada 2015). The dominant disturbance type is crown fires which are usually large and severe (Johnson 1992). Most of the soils in the domain are Humo-Ferric Podzols (Soil Classification Working Group 1998), characterized by a relatively thin surface organic layer and deep mineral soils (DeLuca and Boisvenue 2012, Laganière et al. 2013).

2. Data

2.1 Forest inventory plot and historical fire intensity data

Stem counts and diameter distributions used to initialise simulated forest patches come from the inventory plot data obtained by the Québec Ministère des Forets, de la Faune et des Parcs Naturelles (MFFP 2008). Inventory plots were stratified by soil drainage class and surficial deposit. Mono-specific plots were defined as those where a single species contributed more than 75% of the total basal area (MFFP 2008). A total of 2,495 mono-specific black spruce forest inventory plots with characteristic "mesic-glacial till" soils were kept for the simulation experiment (Fig.13).

An historical forest fire database (1994-2010) was provided by the Société de protection des forêts contre le feu (SOPFEU 2012); the province of Québec's forest fire management agency. Database attributes for each recorded fire include the date when the fire was detected, the location and the fuel type at detection, a final size, and the head fire intensity for the first day of burning. A total of 1,112 fires for the black spruce fuel type (C-2; Hirsch 1996) within the black spruce-feathermoss domain were selected for this study.

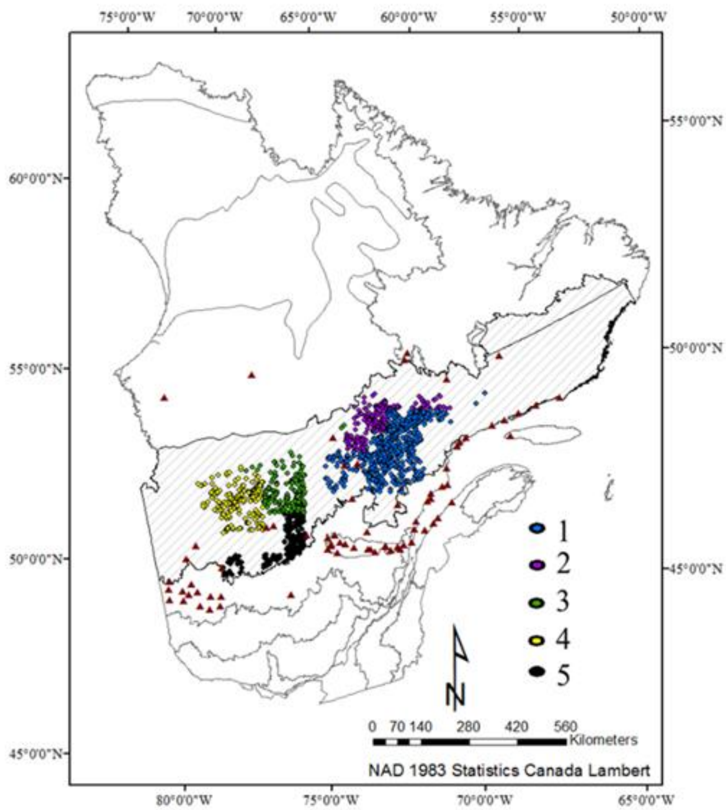


Figure 13. Location of the black spruce-feathermoss bioclimatic domain in eastern Canada (shaded area). The 2,495 mono-specific black spruce forest inventory plots with characteristic "mesic-glacial till" soils used in the simulation experiment are shown. Different colours distinguish inventory plots within each of the five FRI pathways. The location of the meteorological stations used by BioSIM to simulate historical weather data are shown as red triangles.

2.2 Historical and future weather data

Historical (1980-2010) and future weather data (2010-2040, 2040-2070, and 2070-2100) were generated for each inventory plot location using the stochastic weather generator BioSIM v10.3.2.23 (Régnière et al. 2014). BioSIM simulates daily weather data by matching georeferenced sources of historical and simulated future climate normals to a set of locations and adjusting for differences in latitude, longitude and elevation (Boulanger et al. 2013). BioSIM averaged simulated daily data to generate annual weather estimates for each inventory plot. BioSIM monthly historical climate normal data came from 74 meteorological stations in eastern Canada (Fig.13), whereas future weather records were derived by the

Canadian Global Circulation Model 4.0/Canadian Earth System Model 2 (CanESM2) under the IPCC Representative Concentration Pathway (RCP) 8.5 (Moss et al. 2010, Chylek et al. 2011). Under the IPCC RCP8.5 scenario, the greenhouse gas emissions and CO_2 concentration in the atmosphere will continue increasing throughout the 21st century, leading to a radiative forcing of 8.5 W/m^2 by 2100 (IPCC 2007; Riahi et al. 2011). RCP8.5 is called "baseline" scenario that does not include any specific climate mitigation target. In our study area, this scenario projects a 5.2 ºC increase in mean annual temperature (MAT; Appendix C-1) and 24% increase in mean May to August cumulative precipitation by 2100 compared to historical estimates (Table 8).

Table 8. Simulated weather covariates generated by BioSIM for four climatic periods. Averages and standard deviations were calculated over locations throughout the black spruce-feather moss domain. Names in *italics* correspond to the weather covariates names used in equation 2.*Significant differences (alpha=0.05) in means among climatic periods.

Weather variable	**1980-2010 (A)**	**2010-2040 (B)**	**2040-2070 (C)**	**2070-2100 (D)**
Mean annual temp (°C) *MAT*	-0.63±0.12*	1.15±0.15*	3.14±0.16*	5.83±0.18*
February maximum temp (°C) T_{maxFeb}	-10.32±0.65*	-7.84±0.83*	-6.00±0.78*	-2.97±0.78*
August minimum temp (°C) T_{minAug}	8.49±0.30*	9.72±0.37*	11.62±0.39*	14.49±0.32*
June-August min temp (°C) $T_{minJun\text{-}Aug}$	7.93±0.20*	9.26±0.25*	11.35±0.22*	13.79±0.19*
September sum precipitation (mm) $P_{Sep\ t\text{-}1}$	101.0±13.4*	112.4±12.6*	103.6±14.5*	123.6±15.7*
May-August sum precipitation (mm) $P_{May\text{-}Aug}$	372.0±26.5*	395.8±30.9*	417.1±28.0*	463.4±27.2*

2.3 Historical and future boreal fire return interval

Boulanger et al. (2013) developed maps of historical and future fire regime attributes for eastern Canada under the IPCC SRES A2 or "business-as-usual" scenario. We used Boulanger et al. (2013) maps to delineate zones of homogeneous fire return intervals for each climatic period of Table 8. We spatially intersected these maps to define regions with unique temporal FRI "pathways" in terms of changes in fire return interval over the next 100 years. We then assigned a pathway to each inventory plot based on its spatial location. Thirty-two

FRI pathways were identified, but only five were selected for the simulation experiment. We chose these five FRI pathways for three main reasons: their spatial contiguity, their representativeness within the study area (e.g. number of inventory plots within each pathway), and their capacity to capture the historical and projected spatio-temporal variability in fire return intervals within the black spruce-feather moss domain (Boulanger et al. 2013). We acknowledge that the SRES A2 storyline used by Boulanger et al. (2013) to define homogenous FRI zones and the IPCC RCP8.5 scenario used by BioSIM to project future climate represent different approaches used to drive physical climate models (Riahi et al. 2011). However, discrepancies in future emissions, concentrations and temperature tendencies by 2100 between both stoylines represent no concern for the purposes of this study (Riahi et al. 2011).

3. Model Design

The simulation model has three interacting modules: patch dynamics, fire and carbon dynamics. The three model modules were developed and written in R version 2.15.0 (R Development Core Team 2012).

3.1 Patch Dynamics Module

The patch dynamics module is a diameter class-structured demographic model with an annual time step. There are fifteen diameter-at-breast height (DBH) classes of 2.0 cm width, from 1-3 to >29 cm. The model maintains a count of the number of stems in each size class. Patches are initialised from inventory sample plots. The state of the patch at time step t+1 is calculated by multiplying the number of live trees in each diameter class at time t by a matrix of time-varying transition probabilities that incorporate class-specific growth, mortality and recruitment rates.

3.1.1 Black spruce climate-growth modelling

Annual transition probabilities from one size-class to the next are estimated from the expected size-class duration assuming a geometric waiting time (Caswell 2001). Expected durations are estimated by dividing stage widths (2.0 cm) by mean annual diameter increments (cm yr^{-1}). The number of trees in each DBH class that advanced to the next class was sampled from a binomial distribution given the predicted annual transition probability and the number of trees in the class.

Climate-sensitive black spruce annual diameter increments (cm yr^{-1}) were estimated using a modification of the individual-tree basal area growth rate model of NE-TWIGS (Teck and Hilt 1991), that explicitly considers the effect of DBH and of total basal area in larger DBH classes. The growth model´s site index parameter (m), normally fixed in time, was replaced by a growth index (GI, m) that varied annually as a function of climate (Lapointe-Garant et al. 2010, Dhital et al. 2015):

Eqn.1

$$BAGR_t = (GI_t * (b1) * (1 - \exp[(-1) * (b2) * DBH_t])) * (\exp(-b3) * BAL_t)$$

where BAGR is the predicted basal area growth rate, GI is annual climate sensitive growth index, DBH is the diameter at breast height, BAL is the basal area larger than the subject tree. The values of b1, b2 and b3 were fixed to 0.0008, 0.0549 and 0.012, respectively as estimated in Teck and Hilt (1991). Class-specific basal area growth rates were then converted to diameter growth rates using (Teck and Hilt 1991, their Eqn 4).

We used Dhital et al. (2015) model calibrated for black spruce trees in a boreal forest of eastern Canada to estimate climate sensitive annual growth index (GI). Their study identified a set of weather covariates that showed higher correlation with black spruce GI time series. These weather covariates included: the prior-year September (*t*-1) monthly mean precipitation, February (*t*) mean maximum temperature, August (*t*) mean minimum temperature, June to August (*t*) mean periodic temperature, and May to August (*t*) cumulative precipitation:

Eqn.2

$$GI_t = \beta_0 + \beta_1 * T_{maxFeb} + \beta_2 * (T_{maxFeb})^2 + \beta_3 * T_{minAug} + \beta_4 * \ T_{minJun-Aug} + \beta_5 * \ (T_{minJun-Aug})^2 + \beta_6 * \ P_{Sep_{t-1}} + \beta_7 * \ P_{May-Aug}$$

where GI_t is annual climate sensitive growth index, T is maximum or minimum monthly or periodic mean temperature, P is the sum of monthly or periodic total precipitation, and $\beta_0 - \beta_7$ are black spruce-specific parameters (Dhital et al. 2015, their Table 1).

3.1.2 Background Mortality and Understory Recruitment Rates

Background mortality was modeled using the distance-independent individual-tree probability of survival model ARTÉMIS-2009 (Fortin and Langevin 2010). Annual mortality probabilities are a function of DBH and the total basal area in larger diameter classes (Fortin and Langevin 2010). Mortality was not directly influenced by climate, but indirectly by the effect of tree sizes which depends on growth rates. For small diameter trees (DBH<9.1 cm), the annual mortality probability was fixed at 0.02 (Matthias et al. 2003). The number of trees killed in each DBH class was sampled from a binomial distribution given the predicted class mortality probability and the number of tree in the class.

Recruitment occurs when a stem enters the first diameter class. We modelled the annual recruitment into the smallest size class as a Poisson process defined by the parameter lambda (λ), which represents the mean annual recruitment rate per hectare. Lambda was estimated by simulation and used to stochastically estimate the annual recruitment rates for simulation runs without fire. Patches were randomly sampled from the inventory plots, and projected forward by the patch dynamics model for 500 years, without external disturbance, for varying values of λ. We compared initial and final diameter class distributions by a chi-square statistics. We chose λ that minimised the statistic while maintaining reasonable basal areas (e.g. 24 m^2 ha^{-1}; Bouchard et al. 2008). The resultant mean value of λ was 57 stems/ha. When a fire occurs, post-fire tree recruitment is estimated from pre-fire basal area (Greene and Johnson 1999) with a 27-year regeneration delay (Van Bogaert et al. 2015). For more information on the calculation of patch structure attributes from size classes, see (Miquelajauregui et al. 2016). Further details about the growth, mortality and recruitment are given in Miquelajauregui et al. (in review).

3.2 Fire module

The fire module uses a simplified representation of fire regime to simulate the occurrence of fires and their direct effects on canopy tree mortality, surface fuel combustion and post-fire regeneration. Fires are initiated with probability p=1/FRI. When a fire occurs, a single patch-level fire intensity sampled from the empirical data (Miquelajauregui et al. 2016) is applied to the patch. The fire module can simulate the development of high intensity crown fires from low intensity surface fires, using approximations of the physical conditions limiting the initiation and spread of a crown fire (Miquelajauregui et al. 2016). Empirical relations between fire intensity, scorch height, the percent of crown scorched and tree mortality are used to calculate fire severity, measured as the percent reduction in patch basal area due to fire-caused mortality. The fire module also estimates post-fire recruitment using Greene and Johnson´s (1999) model. For details and supporting material, see Miquelajauregui et al. (2016).

3.3 Carbon dynamics module

The C dynamics module calculates patch-level C pools and fluxes at annual steps and integrates these estimates over the study area. The C dynamics module is derived from the Carbon Budget Model of the Canadian Forest Sector (CBM-CFS3; Kurz et al. 2009) which is a C accounting model used by Canada for international reporting purposes (Kurz et al. 2009, DeLuca and Boisvenue 2012, Boisvenue et al. 2012). The CBM-CFS3 accurately estimates forest C stocks for different forest regions in Canada (Kurz et al. 2009, Hagemann et al. 2010).

3.3.1 Carbon pools, biomass turnover and decay dynamics

We tracked carbon content (Mg C ha^{-1}) in five live biomass pools and nine dead organic matter (DOM) pools (Kurz et al. 2009, their Table 1). Aboveground and belowground live biomass components were calculated by diameter class using DBH-allometric equations (Chen et al. 2004, Lambert et al. 2005, Ouimet et al. 2008), multiplied by the number of trees in each class, summed over classes, and converted to mass of C at a rate of 0.5 (Hagemann et al. 2010). Tree component-specific litterfall and turnover rates representative of the Canadian boreal shield ecozone were taken from Kurz et al. (2009) to calculate annual biomass C transfers from each living pool to one or more DOM pools (Kurz and Apps 1999, Kurz et al. 2009, Hilger et al. 2012). Annual C inputs from tree mortality due to senescence and fire disturbance were calculated and allocated to one or more DOM pools (Miquelajauregui et al. in review). When a fire occurs, a proportion of DOM C pools is consumed, with loss rates from Boisvenue et al. (2012).

Decomposition of every DOM C pool was modelled using temperature-dependent decay rates (a_{tki}) that determines the annual proportion of C in the decayed material that is released to the atmosphere of transferred to other C DOM pools following Kurz et al. (2009). To account for the impact of climate change on soil decomposition rates, we replaced the single regional CBM-CFS3 default mean annual temperature (MAT) of 0.36 (Kull et al. 2011) by an annual MAT sampled from the historical and projected temperature distributions. The temperature-dependent decay rates are calculated annually (t) for each DOM pool (k) and for each location (i) as:

Eqn.3

$$a_{tki} = BDR_k * TempMod_{tki} * StandMod$$

where a_{tki} is the carbon-pool specific (k) applied decay rate in time t at location i, BDR_k is the base decay rate for carbon pool k, $TempMod_{tki}$ is a carbon-pool specific (k) temperature modifier in time t at location i, and StandMod is a stand modifier. In the CBM-CFS3 the default value for StandMod is 1. The temperature modifier (TempMod) decreases the decay rate for MAT's below the reference mean annual temperature as:

Eqn. 4

$$TempMod_{tki} = e^{((MAT_{ti} - RefTemp)*\ln(Q_{10k})*0.1)}$$

where MAT_{ti} is the mean annual temperature and time t and location i, RefTemp is the reference temperature, here of 10°C, and Q_{10k} is a temperature coefficient by which the decomposition rate for pool k increases for a 10°C increase in temperature (Davidson and Janssens 2006). For the boreal DOM C pools, the temperature coefficient Q_{10} takes values between 1.0 to 2.65 (Kurz et al 2009, their Table 4). A Q_{10} of 1.0, as for the BG slow carbon pool, indicates thermal independence (Davidson et al. 2006).

3.3.2 Carbon stocks and fluxes

Total ecosystem carbon storage was estimated as the sum of C in all the live biomass and dead organic matter C pools. The live biomass C stock was quantified as the sum of carbon allocated in the five live carbon pools. Total DOM C stock was calculated as the sum of carbon in the nine dead organic matter C pools, including the mineral soil C. We calculated the organic layer C, mineral soil and woody debris C stocks as in Miquelajauregui et al. (in review). Ecosystem fluxes such as the net primary productivity (NPP), the heterotrophic respiration (Rh) and the net ecosystem production (NEP) were estimated annually at the patch level (Mg C ha^{-1} yr^{-1}). We defined NPP as the assimilated patch-level forest C not lost in turnover or patch mortality (Kurz et al. 2009). We calculated NPP as the sum of the net biomass difference between consecutive years and replacement of above- and belowground biomass turnover. Rh was calculated as the sum of decomposition losses to the atmosphere from all DOM pools. Net ecosystem production (NEP = NPP-Rh) was calculated as the annual net loss, or gain, of carbon from an ecosystem (Chen et al. 2002). For more details, please refer to Miquelajauregui et al. (in review).

3.4 Simulation experiment and statistical analysis

We performed a series of simulation experiments that aimed at evaluating short-term changes in boreal ecosystem C storage in response to variation in FRI due to climate change. We did this by starting the model from equilibrium zonal soil carbon values and patch-level live biomass conditions and then applying the expected transitions from one fire regime to another (Table 9). That is, we simulated the change in FRI over 120 years, from 1980 to 2100, and changed the FRI every 30 years (Table 9). We coupled these changes in FRI with the simulated weather covariates of Table 8, which were allowed to change incrementally on a yearly basis over each 30-year climatic period (Historical, 2010-2040, 2040-2070, 2070-2100).

In order to account for zonal variation in DOM C stocks and fluxes within the black spruce domain (Miquelajauregui et al. in revision), we generated initial DOM C conditions under historical FRI and weather data (Table 9) for each of the *n* FRI zones/pathway (Fig. 12). We used a spin-up procedure, in which 1,000 random black spruce forest patches replicates belonging to each FRI pathway in Table 9, were grown and disturbed using the zones historical FRI derived from Boulanger et al. (2013). The model was run for 2,400 years, as in Miquelajauregui et al. (in review), a time length we consider sufficient to reach approximate equilibrium (Hagemann et al. 2010). Carbon stocks were then averaged over all runs for each FRI pathway.

Table 9. Five characteristic temporal pathways (1980-2100) of fire return interval in the black spruce feathermoss domain of northern Québec, derived from Boulanger et al. (2013). The total number of mono-specific black spruce inventory plots within each FRI pathway and the total number of plots are also shown.

Pathway	**Fire return interval (years)**				**No. plots**
	1980-2010 (A)	**2010-2040 (B)**	**2040-2070 (C)**	**2070-2100 (D)**	
1	916	716	458	300	1,080
2	916	304	241	170	339
3	783	212	250	248	365
4	152	182	289	145	327
5	783	1112	735	404	384
				Total	**2,495**

We ran 1,000 replicates for each FRI pathway (Table 9) for a total of 5,000 observations. For each replicate, one inventory plot for the given FRI pathway was selected at random. Stand attributes and live C pools were then initialised from the selected plot as in Miquelajauregui et al. (in review). Dead organic matter C pools were initialised from zonal means, as described above. DOM pools initial values remained the same for all simulations within each FRI pathway. For each plot, one simulated annual weather value of each covariate of Table 8 was selected from the annual data generated by BioSIM, according to the simulation year (e.g. 1980 to 2100). These weather estimates were used in equations 2 and 4 to calculate annual growth and decomposition rates. For each simulation, a fire is initiated with probability p=1/FRI. When a fire occurs, a single patch-level fire intensity is applied to the 1.0 ha sampled forest patch. Fire effects on overstory tree mortality, post-fire regeneration and DOM carbon consumption are then calculated from intensity and stand structure. For each year, the growth, mortality and recruitment submodels are applied and biomass gains are calculated. Carbon losses through overstory tree mortality, litterfall and turnover, carbon combustion and decomposition of DOM are then evaluated, and stand attributes and carbon pools are updated.

At the end of each simulation run (120 years), we extracted patch-level carbon stocks and fluxes. We calculated the mean rate of change in C stocks (Mg C ha^{-1} yr^{-1}) over each 30-year climatic period as (*F*-*I*)/30, where *I* and *F* are the periods' initial and final values, respectively. We calculated the mean percent change (%) in C stocks over each period as 100%*(*F*-*I*)/*I*. Regional boreal C indicators for each period were then calculated as means over the 1,000 replicates within FRI pathways. We used an analysis of variance (ANOVA) to test for significant effects of climatic period and FRI pathway on these C indicators among the 5,000 replicates. To identify where in the study region the greatest changes in black spruce forest carbon stocks may be expected, we mapped the mean % change in ecosystem C for each climatic period. To complement the results from this modelling experiment, we also present results of the effect of historical and future FRI´s on boreal C stocks without accounting for temperature and precipitation effects on growth and decomposition (Appendix C-4). This allowed us to determine the relative effect of historical and projected FRI's on boreal C stocks.

III. Results

Initial conditions (DOM C stocks, growth index, basal area, density and stand structure) for each FRI pathway as well as the mean number of fires per period and pathway are reported in Appendix C-2.

1. Black spruce growth and organic matter decomposition under climate change

Results from the climate-growth modelling approach indicate negative impacts of climate change on black spruce growth (Fig. 14). Simulated average historical growth index was 14 m (GI, Eqn. 2) and declined to an average of 11 m in 2071-2100. Greatest reductions occurred under projected climate conditions for 2040-2100 (Fig.14). Temperature-sensitive decay rate trends for each tracked soil C pool are shown in Appendix C-3. Decomposition rates for the majority of C pools, except for the most stable soil C pool (BG slow; Appendix C-3), increased in response to predicted responses in mean annual temperatures (MAT; Eqn.4).

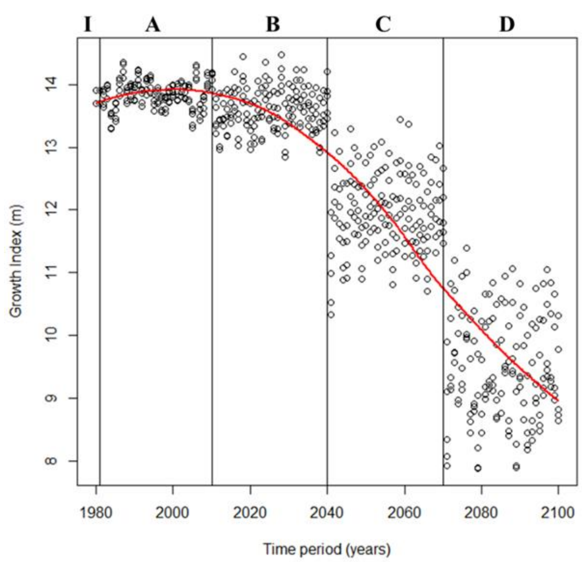


Figure 14. Mean simulated growth index (GI, Eqn.4) calculated over 1000 replicate simulation runs of 120 years at the end of each time period (x-axes). The vertical lines mark the beginning the end of each climatic period. Letters on the top of the plot indicate the initial conditions (I) and the four climatic periods evaluated: A: Historical/1980-2010, B: 2010-2040, C: 2040-2070, D: 2070-2100. Loess curve fitted to data is also shown (red line).

2. Boreal C stocks short-term responses to climate change

Total ecosystem, total DOM, live biomass, organic layer, woody debris and mineral soil C stocks were significantly affected by the interaction between climatic period and FRI pathway ($F_{12,580}$ = 6.2, 2.2, 37.7, 1.5, 4.6, 4.29, p <0.001, p=0.008, p <0.001, p <0.001, p =0.002, p <0.001; respectively). For total ecosystem, total DOM, live biomass, organic layer and woody debris C pools, highest mean stocks (300.5, 243.3, 63.0, 58.1 and 54.8 Mg C ha^{-1}) were found for pathways 1 and 2 under the Historical climate (Fig. 15a,b,c,d,e).Mineral soil C stocks was highest (126.8 Mg C ha^{-1}) for pathway 2 under the Historical climatic period (Fig 15f). For these variables, lowest stocks (215.5, 177.3, 38.2, 36.6, 26.9 and 112.7 Mg C ha^{-1}) were reached for pathways 4 and 5 under the 2070-2100 climatic period (Figs. 15a,b,c,d,e,f).

NPP, NEP and Rh differed among climatic periods and FRI pathways ($F_{12,580}$ =22.6, 8.37 and 3.8, p < 0.0001, p < 0.0001, p < 0.0001, respectively). Net primary productivity was lowest (2.2 Mg C ha^{-1} year^{-1}) for black spruce patches following the FRI pathway 1 under the 2071-2100 climatic period and greatest (3.7 Mg C ha^{-1} year^{-1}) for pathway 5 under the Historical one (Fig. 16a). Heterotrophic respiration was highest for pathway 5 under the Historical period and lowest for pathway 4 under the period 2011-2040 (3.5 and 2.67 MgC ha^{-1} year^{-1}, respectively; Figure 16b). Simulations results suggest positive NEP mean values of 0.21, 0.16, 0.19, 0.10 and 0.24 Mg C ha^{-1} year^{-1} for FRI pathways 1, 2, 3, 4 and 5 under historical climate, respectively. Negative values were obtained for all pathways under the other three climatic periods evaluated (Fig. 16c).

In our simulation experiments, ecosystem carbon accumulation decreased in average 2.2% from 1980 to 2010, with subsequent average reductions in ecosystem C of 6.8, 7.6 and 9.9% by 2040, 2070 and 2100, respectively (Fig. 15a, Table 10). DOM C decreased in average 5% by 2040, for an overall DOM C loss of nearly 9.0% by 2100 (Fig. 15b, Table 10). Live biomass C stocks decreased nearly 13% by the end of 2100 (Fig. 15c, Table 10). Organic and woody debris C stocks had similar average trends. For these pools, the mean cumulative C losses were of 15.2 and 23.0% by the end of 2100, respectively (Figs. 15d,e, Table 10). Mineral soil C stocks decreased by 0.41 and 1.2% under Historical and 2010-2040 climatic periods and decreased by 2.5% during the second half of the 21st century (Fig. 15f, Table 10). Greatest mean percent changes were observed for the fluxes NPP, Rh and NEP for an overall mean C decrease of 1.8, 22.6 and 70% by the end of 2100 (Table 10).

Overall, simulated black spruce patches lost organic carbon in both the living and dead carbon pools at an annual average rate of -0.20 to -0.36 Mg C ha^{-1} year^{-1} during 1980 to 2010 (Fig.17). Subsequent negative mean annual rates of change in ecosystem C were detected for 2010-2040, 2040-2070 and 2070-2100 (Fig.17). However, C storage differences between climatic periods were more pronounced towards the first half of the century (2011-2040) and by the end of it (2070-2100; Fig. 17). Furthermore, our results suggest that black spruce patches located further north within the black spruce feathermoss domain (e.g. FRI pathways 2, 3 and 4; Fig. 18) lost in average from 5 to 8% of the total C stored by 2040-2070, and from 8.0 to 11.0% by 2071-2100, while patches located in the southern portion of the domain lost in average from 5.0 to 8.0% by 2011-2040, and from 8 to 11% by 2071-2100 (e.g. FRI pathways 1 and 5, respectively; Fig. 18).

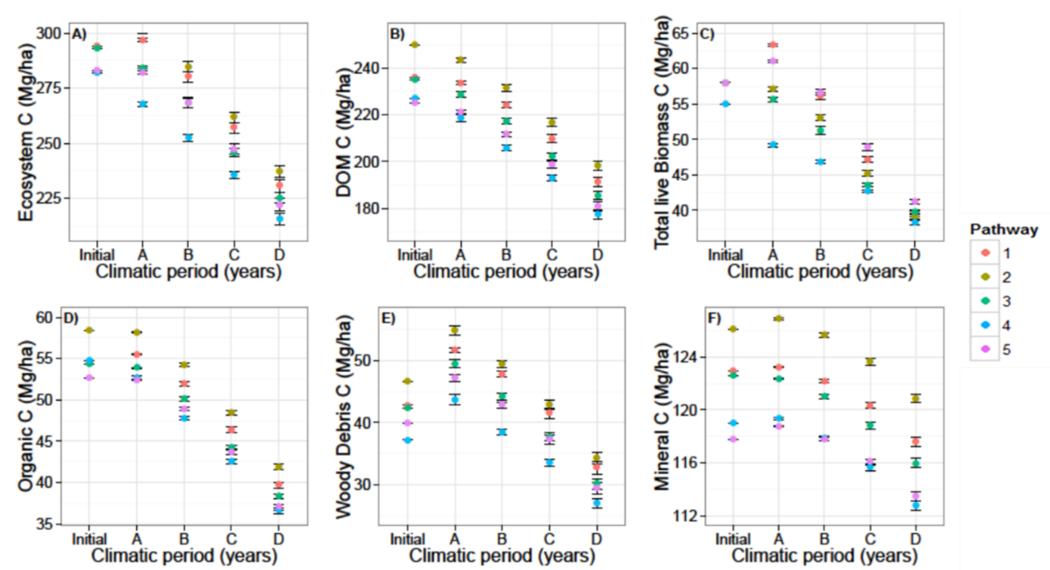


Figure 15. Mean C stocks (Mg C ha^{-1}, mean ± ci) over 1000 replicate simulation runs of 120 years calculated at the end of each climatic period A: Historical, B: 2010-2040, C: 2040-2070, D: 2070-2100 (x-axes) and FRI pathway. Initial zonal mean C stocks values are also reported. A) Total ecosystem, B) DOM, C) Total live biomass, D) Organic layer, E) Woody debris and F) Mineral soil.

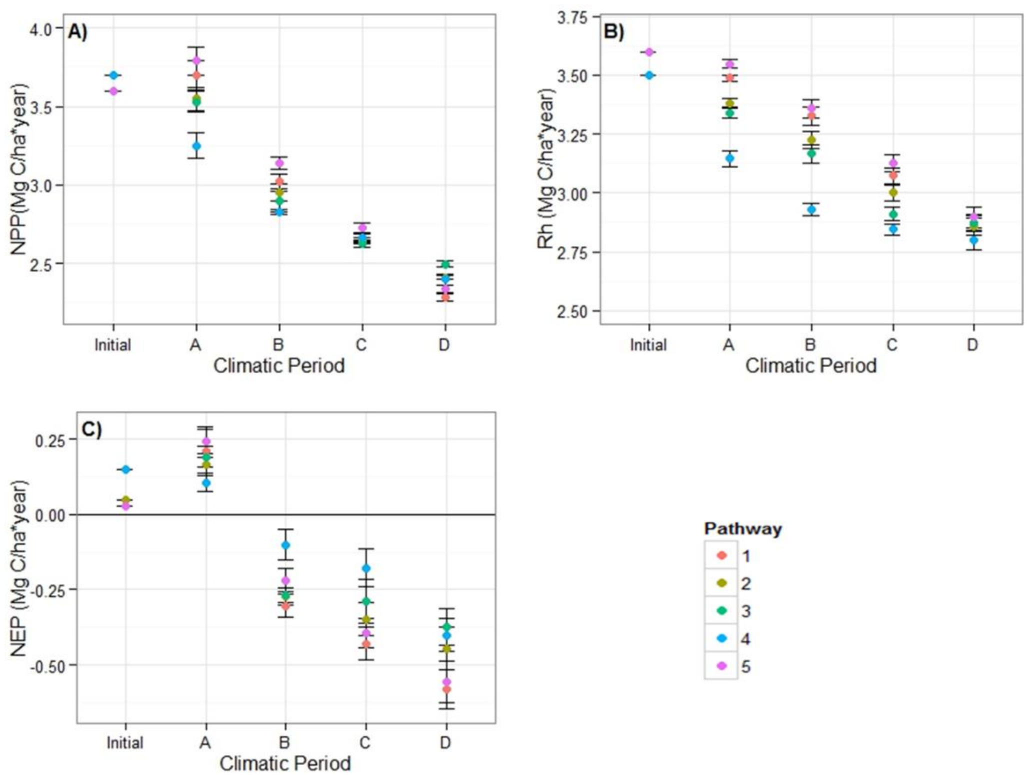


Figure 16. Mean C fluxes (Mg C ha^{-1} year^{-1}, mean ± ci) over 1000 replicate simulation runs of 120 years calculated at the end of each climatic period (x-axes) and FRI pathway. A) Net primary productivity (NPP), B) Heterotrophic respiration (Rh) and C) Net ecosystem production (NEP). A: Historical/1980-2010, B: 2010-2040, C: 2040-2070, D: 2070-2100. Initial zonal mean C fluxes are also reported

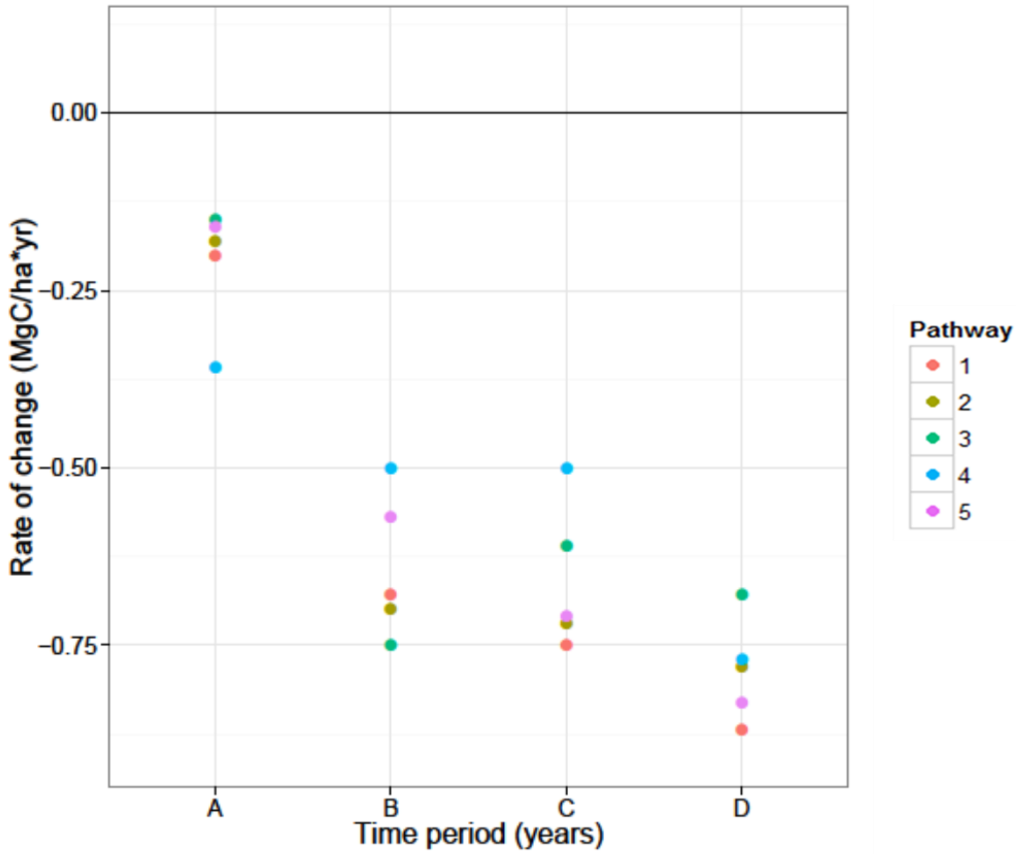


Figure 17. Mean rate of change in ecosystem C (Mg C ha^{-1} yr^{-1}) over 1000 replicate simulation runs of 120 years by climatic period A: Historical/1980-2010, B: 2010-2040, C: 2040-2070, D: 2070-2100 (x-axes) and FRI pathway. Mean rates were calculated over each 30-year climatic period.

Table 10. Mean percent change in black spruce boreal C stocks (Mg C ha^{-1}) and fluxes (Mg C ha^{-1} yr^{-1}) by climatic period A: Historical/1980-2010, B: 2010-2040, C: 2040-2070, D: 2070-2100 and FRI pathway evaluated. Changes were calculated from differences between ending and starting values for each period. Averages were calculated over 1000 replicate simulation runs of 120 years.

		Stocks						**Fluxes**		
FRI Pathway	**Climatic Period**	**Ecosystem**	**DOM**	**Live Biomass**	**Organic layer**	**Mineral soil**	**Woody Debris**	**NPP**	**NEP**	**Rh**
1	A	-2.06	-2.38	-0.80	0.15	-0.16	-6.91	-20.06	-103.52	-4.53
	B	-7.05	-4.95	-15.03	-8.74	-1.15	-9.06	-11.41	-72.04	-20.57
	C	-8.42	-7.01	-14.38	-11.28	-1.75	-15.62	-4.70	-66.43	-19.63
	D	-10.73	-9.63	-15.79	-15.62	-2.56	-24.24	-5.81	-63.91	-23.95
2	A	-1.87	-4.24	9.33	-1.73	-0.35	-11.45	-15.75	-86.63	-9.61
	B	-7.11	-5.28	-14.69	-9.06	-1.23	-9.86	-14.06	-63.74	-20.50
	C	-7.97	-6.87	-13.07	-10.89	-1.81	-15.11	-2.12	-70.59	-18.51
	D	-9.39	-8.96	-11.52	-14.18	-2.49	-22.38	-0.35	-74.92	-21.16
3	A	-1.64	-4.33	10.68	-2.11	-0.52	-11.70	-15.34	-75.77	-9.94
	B	-8.03	-5.69	-17.36	-9.77	-1.44	-11.12	-17.01	-59.26	-22.14
	C	-7.19	-6.92	-8.45	-10.95	-1.96	-15.90	7.35	-90.56	-17.01
	D	-8.74	-8.75	-8.67	-14.32	-2.60	-22.40	-1.11	-76.13	-20.35
4	A	-3.97	-6.17	6.87	-6.76	-0.85	-15.14	-20.08	-85.63	-18.67
	B	-5.85	-5.24	-8.46	-9.54	-1.49	-9.91	-2.11	-114.43	-17.58
	C	-6.14	-6.34	-5.23	-10.68	-2.01	-14.16	6.23	-99.23	-15.19
	D	-10.22	-9.09	-15.29	-15.67	-2.74	-23.28	-8.24	-69.57	-23.94
5	A	-1.78	-3.53	5.07	-1.69	-0.20	-9.77	-18.69	-87.39	-9.43
	B	-6.26	-4.79	-11.55	-8.44	-1.07	-9.49	-10.29	-85.93	-20.12
	C	-8.31	-6.89	-13.96	-11.64	-1.71	-15.41	-6.15	-66.91	-20.11
	D	-10.57	-9.54	-14.92	-16.52	-2.57	-23.96	-5.37	-65.84	-24.01

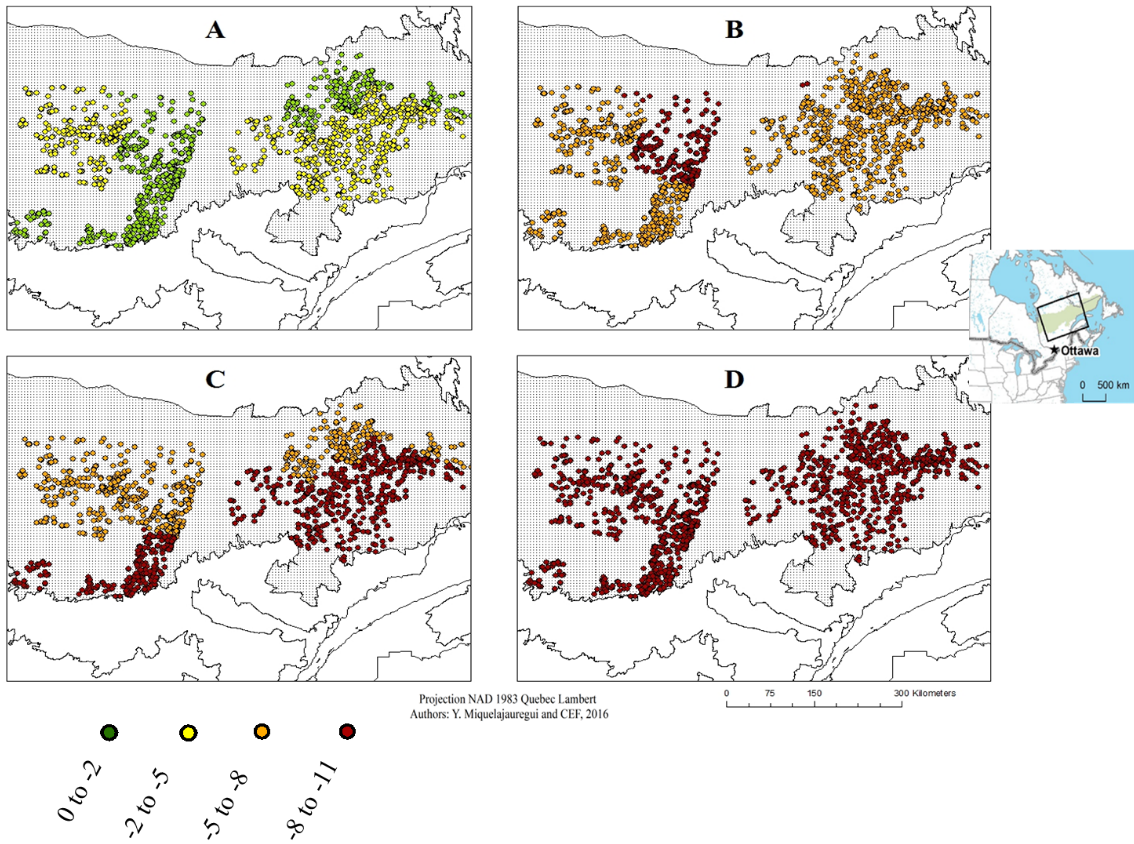


Figure 18. Mean periodic changes (%) in total ecosystem C storage in black spruce stands, by FRI pathway and climatic period. Means were calculated from differences between ending and starting values for each period over 1000 replicate simulation runs of 120 years within each FRI pathway. Letters on the top of the plot indicate the four climatic periods evaluated: A: Historical/1980-2010, B: 2010-2040, C: 2040-2070, D: 2070-2100. The geographic extent of each pathway is indicated by the numbers 1-5 in the first panel. Map created in ArcGIS.

IV. Discussion

The objective of this study was to simulate short-term black spruce forest C storage responses to climate change by integrating climate-growth relationships, temperature-sensitive decay rate functions, historical and projected FRI maps and simulated climatic variables.

1. Short-term responses of boreal forest C stocks and fluxes to climate change

Elucidating forest C dynamics over broad spatial scales requires the use of ecological models. In this paper, we present a diameter-class structured model of black spruce patch dynamics in which live and dead tree biomass are linked to tree measurements while soil organic carbon is simulated as a transfer matrix that determines the annual proportion of C in the decayed material that is released to the atmosphere or transferred to other C DOM pools. A simplified representation of fire regime allows us to simulate the occurrence of fires and their direct effects on canopy tree mortality and surface fuels combustion. Climate change effects on fire regime, tree growth and decomposition rates are explicitly simulated. The inclusion of these relationships allows us to understand how boreal forest C stocks and fluxes might respond to climate change.

Climate change will likely affect C storage in boreal black spruce forest through changes in the capacity of trees to grow and sequester atmospheric carbon (Girardin et al. 2015), the rate of organic matter decomposition (DeLuca and Boisvenue 2012), and through modifications to the fire regime (Boulanger et al. 2013, 2014). In the boreal forest, soil carbon has been reported to account for nearly 85% of the total biome C (DeLuca and Boisvenue 2012). Accumulation of soil C depends on the long-term balance between vegetative C inputs from litterfall and root turnover and C outputs derived from organic matter decomposition (Laganière et al. 2013). Climate change events could potentially influence the boreal soil C balance by altering these ecological processes (van Bellen et al. 2010, Price et al. 2013).

Despite the generally agreed idea that warmer climate and increased precipitation stimulate black spruce tree growth and productivity in many regions of the Canadian boreal forest (Boisvenue and Running 2006, Lemprière et al. 2013, Price et al. 2013, Gauthier et al. 2014, D´Orangeville et al. 2016), no consensus has yet been reached on this matter (D´Orangeville et al. 2016). Empirical studies and model projections have concluded that an increase in summer temperature could lead to greater evaporation and surface water losses, which could hinder the capacity of black spruce to grow and assimilate atmospheric carbon (Beck et al. 2011, Dhital et al. 2015, Girardin et al. 2015). In the boreal forest, the poor plant litter quality and low temperatures are responsible for the low rates of organic matter decomposition, allowing soil C to accumulate (DeLuca and Boisvenue 2012, Laganière et al. 2013, Price et al. 2013). Several lab and field experiments provide evidence of the distinct temperature sensitivities among soil C pools in boreal forest soils (Van Cleve et al. 1990, Davidson and Janssens 2006, Karhu et al. 2010). Decay rates of the most labile soil C pools (e.g. AG very fast and AG slow; Appendix C-3) are temperature sensitive, whereas decomposition rate of the more stable, and recalcitrant soil C (e.g. BG slow; Appendix C-3) is not. Given these assumed relations, the forecast increases in MAT would be expected to increase decomposition rates of the labile soil pools, altering the amount of soil C (Davidson and Janssens 2006, Xu et al. 2014).

Our approach to derive black spruce growth responses to climate is based on a statistical relationship between basal area growth, the growth index and weather covariates (Teck and Hilt 1991, Lapointe-Garant et al. 2010, Dhital et al. 2015). Our results show substantial reductions in black spruce forest growth over the next decades due to climate change. A lack of synchrony between temperature and precipitation increases could also explain such systematic black spruce growth reductions under future climate (Dhital et al. 2015). Subedi and Sharma (2013) climate-growth model results suggest that a wetter growing season, could decrease radiation inputs and increase nutrient leaching, leading to important reductions in black spruce tree growth. Other factors such as carbon dioxide and nitrogen fertilization, and respiration acclimation to high temperature, could potentially modify these growth trends (Beck et al. 2011). A more detailed review of black spruce ecophysiology is beyond the scope of this paper.

A growing body of research suggests that changes in the boreal fire regime can be expected over the forthcoming decades across North America as a result of the more fire-conducive weather linked with climate change (de Groot et al. 2003, Bergeron et al. 2010, Boulanger et al. 2014). In particular, fire return intervals are projected to decrease in many areas of the boreal forest of North America (Boisvenue et al. 2012, Boulanger et al. 2013, Oris et al. 2014). Such a shortening in FRI will affect boreal vegetation dynamics, forest structure, biodiversity patterns and the boreal carbon balance (Kurz et al. 2008, Boulanger et al. 2013). This study indicates that the short-term effects of climate change on black spruce forests productivity and C storage are substantially negative. We predicted a marked and widespread change from C sink to C source, which has already started and will persist at least until 2100. Carbon storage differences between climatic periods were most evident towards the first half of the century (2010-2040), when FRI and temperatures clearly diverge (e.g. Appendix C-1) resulting in a lagged response of patch C dynamics. The expected ecosystem C storage reductions are the result of the decreases in productivity along with the C losses from increasing fire disturbance and increasing decomposition rates (Bunn et al. 2007, Kurz et al. 2008). However, the relative contribution of climate change-related effects on FRI, DOM decomposition and tree growth to changes in ecosystem C storage differed among climatic periods (Appendix C-4). Complementary simulation results without accounting for temperature and precipitation effects on growth and decomposition (Appendix C-4) suggest that FRI is the main driver of ecosystem C change during the first half of the 21st century. Under the 2040-2070 climatic period, the climate change influence on tree growth and DOM decomposition is added to the FRI effects, pattern that continues until the end of 2100.

In our simulation experiments, ecosystem C accumulation was reduced 11% by 2070-2100. Field and modelling studies (Price et al. 1999, Boiffin 2014, Russell et al. 2014) have also shown that increased temperature could increase DOM decomposition rates for an overall decrease in boreal ecosystem C storage by as much as 13-19% over the next 200-500 years. The results of this study suggest that black spruce forest of northern Québec could be losing their capacity to sequester and store organic C over the next coming decades due to climate change. Simulation results suggest that spatial variation in the magnitude and timing of climate change and FRI resulted in spatial variation in carbon storage among zones within the black spruce-feather moss domain of northern Québec, Canada. The manner in which simulated black spruce patches responded regionally to changes in FRI and climate could be explained by the effect of carbon legacies on total carbon accumulation. In this study, higher initial C density levels resulted in lower percentages of ecosystem C loss in the subsequent climatic periods (e.g. Fig.15a and Fig. 18). Loudermilk et al. (2013) examined C sequestration capacity related to the landscape disturbance history in conifer fire-prone forests. Their results results suggest that future forest C cycling may depend more on landscape legacies related to major disturbances than on projected climate change alone.

2. *Boreal forest carbon management under global warming*

In Canada, federal, provincial and local governments have established targets to reduce greenhouse gas emissions (GHG). Canada´s target for 2020 is 17% below the 2005 level (Lemprière et al. 2013). Mitigation strategies could help human societies to better cope with the negative impacts of climate change (Lemprière et al. 2013; Gauthier et al. 2014). Mitigation refers to the implementation of policies aim to limit future growth in net GHG emissions and lessen climate change itself (IPCC 2007, Lemprière et al. 2013, Gauthier et al. 2014). Mitigation involving boreal forest C storage is one response to climate change (Lemprière et al. 2013). Several forest management activities can be implemented to increase boreal C storage (Lemprière et al. 2013). Extending rotations, reduction of regeneration delays, planting, seeding, fertilization, and control of competing vegetation and herbivory, can accelerate the transition from C source to sink (Lemprière et al. 2013). In boreal ecosystems, soil C accounts for nearly 85% per cent of the total biome C (Boisvenue et al. 2012). Soil C is fundamental to ecosystem function since it affects soil physcial properties and microbial activity (DeLuca and Boisvenue 2012). Managing boreal forests for C sequestration will require to explicitly account for soil carbon when developing forest management plans and offseting schemes (Boisvenue et al. 2012; DeLuca and Boisvenue 2012). Increasing C storage in harvested wood products (HWPs) by increasing the use of long-lived HWPs, reducing emissions by substituting wood for fossil-intensive poducts, and using biomass as bioenergy area potential strategies by which the Canadian boreal forest can aid GHG mitigation (Lemprière et al. 2013). Mitigation involving land systems can affect other climate-forcing factors. Therefore, the mitigation potential of forest-related activities should be quantified within a systems perspective (Lemprière et al. 2013).

3. *Model strengths and limitations*

The simulated consequences of climate change on boreal C storage must be treated with caution and there are several important uncertainties and limitations to the work conducted here. Our objective was to evaluate short-term responses of black spruce C stocks and fluxes to climate change by relying on predicted FRIs, historical intensities, simulated weather data, as well as on relationships between regional weather, black spruce growth and decomposition rates of soil organic matter. However, we did not investigate the isolated attribution of each of those factors on changes in boreal C stocks. Future research should focus on deepening our understanding of the relative attribution of changes in FRI, growth and decomposition on boreal C dynamics. We acknowledge that, as we sampled from historical intensities, we might probably be underestimating the contribution of projected changes in fire regime on ecosystem C storage. We incorporated weather variables (e.g. monthly mean temperature and precipitation) to predict the effects of climate change on forest productivity. Historical weather variables were generated from monthly climate normals derived from meteorological stations. However, data from weather stations are point data that represent the specific conditions of the given location, therefore the large spatial variability of weather conditions may not be properly characterized (Kotchi et al. 2016). Moreover, the regional trends in C accumulation present in this study represent 30-yr averages which might obscure year-to year variations in carbon storage. In North America, interannual variability in fire activity, therefore in C storage, has been related to shifts among oceanic/atmospheric circulation regimes since these patterns control climate at regional and continental scales (Tian et al. 1998, Girardin et al. 2009, Boulanger et al. 2013). Accuracy in estimating short-term response in boreal C storage could also be improved by integrating future boreal forest composition patterns (coniferous vs. hardwood), moisture and nutrient regimes and anthropogenic influences such as management regimes, which are important determinants of boreal C storage under a given climate (Girardin et al. 2009, Boulanger et al. 2013). We acknowledge that the IPCC RCP8.5 scenario projection used in this study should not be treated as a prediction of future climate, but rather as an indicator of climate sensitivity to anthropogenic radiative forcing (Price et al. 1999). Therefore, minimizing uncertainties associated with climate forecast could improve estimates of black spruce future growth and temperature-sensitive soil decomposition rates for the boreal forest of Canada. Our modelling approach has the potential of quantifying and mapping the location and timing of changes in boreal black spruce C stocks. The results of this study could help delineating effective mitigation portafolios and develop alternative mitigation strategies (Lemprière et al. 2013).

Acknowledgements

This research was funded by a NSERC (Natural Sciences and Engineering Research Council of Canada) Strategic grant to A.D. Munson, R.L. Bradley, S.G. Cumming, S. Gauthier, D. Paré and S. Quideau, and a NSERC- CGS D-Alexander Graham Bell Graduate scholarship to Y. Miquelajauregui. The author also received financial support from Produits forestiers Résolu and F.K. Morrow Foundation. We thank the Centre d'étude de la forêt for financial and logistic support**.** Very special thanks to R. Saint-Amant for his assistance when performing BioSIM simulations and to Y. Boulanger for kindly providing the historical and projected fire regime maps.

General Conclusion

In the boreal forest, fire is one of the main ecological processes shaping the forest mosaic (Le Goff et al. 2009). Fire strongly influences carbon cycling and storage by altering the distribution of C in boreal ecosystems (Kasischke et al. 1995, Kashian et al. 2006). This redistribution of C includes transfer of live biomass to dead organic matter (DOM) from which carbon (C) is slowly released through decomposition and immediate release of a portion of C which is emitted when a fire occurs (Amiro et al. 2009, de Groot et al. 2009, Kurz et al. 2013). Boreal carbon storage is influenced by a great number of factors including climate, stand age, stand structure, mineral substrate, topography and the fire regime (Ryan, 2002, Kashian et al. 2006, van Bellen et al. 2010). This thesis attempted to quantify the effect of these two factors, stand structure and fire regime, in Quebec boreal black spruce forest. Stand structure is the vertical and horizontal distribution of biomass within a forest stand (Smith et al. 1997). Stand structure influences the probability of transition between surface and crown fires, thus is an important determinant of fire behavior (Stevens-Rumann et al. 2012). Stand structure was expected to affect carbon cycling by influencing fire behavior and the subsequent redistribution of living carbon pools. Changes in the fire regime characteristics, including the length of fire return interval, the fire intensity and severity, may strongly affect the structure and function of boreal ecosystems, with important implications for regional carbon budgets (Boulanger et al. 2013). For example, large amounts of organic carbon stored in biomass, dead organic matter, and soil pools could be released to the atmosphere if the mean interval between fires became too short for biomass re-accumulation (van Bellen et al. 2010, King et al. 2011).

Several modelling approaches can be used to study the relationships between environmental changes such as climate, disturbance and harvesting regimes and forest C balance (Kurz et al. 2008; Peng et al. 2002). Some approaches are better suited than others to address the problem of prediction under global change (Cuddington et al. 2013). Empirical models (e.g. forest growth models), for example, are created by fitting model components using field or experimental data. These models require simple inputs and can be easily constructed and incorporated into management analyses (Peng et al. 2002). However, the correlative rather than the causal nature of these models may limit their ability to determine the sensitivity of model predictions to changing environments (e.g. climate, disturbance and management regimes; Peng et al. 2002, Cuddington et al. 2013). Unlike empirical models, mechanistic process-based models are mathematical representations of how key ecosystem processes interact under environmental change and they usually provide long-term predictions (Peng et al. 2002). They provide a useful framework to incorporate specific management responses (Gustafson 2013); however, they are too complex and require a large amount of information. Process-based growth models are not usually intended to predict stand characteristics (e.g. basal area, height, annual mortality), making them difficult for forest managers to use (Peng et al. 2002). Hybrid models combine both ecological mechanisms and correlational components. They are meant to improve accuracy of predictions while allowing for multiple applications. Hybrid forest ecosystem models incorporate key element of empirical and process approaches to predict forest growth, competition and mortality (Mäkelä et al. 2000), carbon and nitrogen cycling, water fluxes, decomposition and carbon dynamics in both the short and long term (Peng et al. 2002).

In this dissertation, I present a new hybrid-model that links standard forest mensuration data and stand growth modelling to climate and fire-regime characteristics. The model was used to simulate the relations between fire regime parameters and carbon stocks in boreal black spruce forests of Québec, Canada. The model is composed of three modules that interact dynamically: a diameter-class structured demographic model coupled with an established boreal soil C model (CBM-CFS3; Kurz et al. 2009), and a fire model (Miquelajauregui et al. 2016). All model components were developed and coded in R version 2.15.0 (R Development Core Team 2012). This modelling framework incorporates the relationship between fire intensity and stand structure on fire severity into an easy-to-use platform. It also allows evaluating, quantifying and mapping the changes in boreal C stocks, which might result from varying fire regimes. In its present form, the model is sensitive to the climate-change projected variations in temperature and precipitation.

Fire severity is an important aspect of the fire regime that exerts great influence on boreal C storage (van Bellen et al. 2010). In the first chapter, I developed a fire model that uses empirical relationships between fireline intensity, scorch height, crown volume scorched and post-fire tree mortality to calculate fire severity. The fire model accounts for propagation from a surface fire into the canopy. I applied the model to quantify the effects of fire intensity, stand structure and species composition on the stem-mortality component of fire severity. The study revealed specific thresholds in fire intensity at which different stand characteristics are conducive to low, moderate and high severity outcomes in black spruce and jack pine stands of northern Quebec. The model was able to produce variation in fire severity under a range of fire intensity conditions encountered in practice by integrating the effect of stand structure. The fire intensity thresholds found in this study could be used to refine the Forest Fire Behavior Prediction (FBP) System fuel type classification by a better accounting of variation in stand structure within fuel types.

In the second chapter, I developed a diameter-class structured demographic model (Caswell 2001) to empirically simulate the effect of stand dynamics on forest growth. I coupled this with an established boreal soil C model based on the Carbon Budget Model of the Canadian Forest Sector (CBM-CFS3; Kurz et al. 2009), and linked it to the fire model explained above in a very flexible modelling platform. I used the fire return interval and an empirical distribution of head fire intensity for season to simulate the impacts of fire regime on boreal C stocks. Simulated boreal carbon fluxes and stocks were sensitive to the fire return interval (FRI) over the range of 60-300 yrs. The effect of fire season varied with FRI and was more pronounced under shorter return intervals. Simulation results suggest that C storage in pure black spruce patches within the black spruce domain would decrease in average four to six per cent by 2071-2100. The simulated losses of boreal ecosystem carbon found in this study could possibly decrease forest resiliency and long-term sustainability in boreal forests (DeLuca and Boisvenue 2012); therefore, imposing great challenges for carbon management and climate change mitigation efforts for the black spruce forest of northern Québec.

Climate change is already affecting boreal C dynamics in Canada through factors such as increases in temperature, droughts, and modifications to the fire regime (IPCC 2007; Loudermilk et al. 2013; Price et al. 2013; Gauthier et al. 2014). Canada needs to improve the information about the magnitude of climate change impacts on boreal C stocks and fluxes, and on how such impacts may vary among regions. Understanding these impacts requires knowledge of feedback mechanisms associated with interactions of altered fire regimes, forest growth, decomposition rates and biospheric C pools. In the third chapter, I used the model to quantify and map average boreal C stocks and fluxes in response to the short-term effects of climate change in boreal conifer forest of northern Québec over the 21st century. The model predicted a marked and widespread change from C sink to C source, which has already started and will persist at least until 2100. However, the magnitude and timing of these changes differ among regions within the black spruce feathermoss domain of northern Québec, possibly providing some scope for management. My results suggest that black spruce forest could be losing part of their capacity to sequester and store organic C over the next coming decades due to climate change.

The modelling approach I present here can be used to assess transient dynamics and equilibrium levels of boreal C stocks and fluxes. The model can be used directly to evaluate C stocks responses to climate change scenarios. Although many important aspects of the boreal C dynamics were explicitly accounted for in the model, future research needs to focus on improving certain aspects of it. For example, the model operates in a non-spatial way. However, a spatially gridded landscape model could be implemented by incorporating spatial components such as hazard and fire behavior spatial data as well as live biomass and soil C maps. In this thesis, I evaluated mono-specific patches, but there is no fundamental reason why the model could not be adapted to incorporate two or more tree species. It would also be feasible to incorporate other ecological processes such as nitrogen cycling, microbial dynamics, habitat quality and the effects of forest management and forest insects on C stocks and fluxes. Forecasts of fire intensity distributions, should also be incorporated in future studies. Boreal black spruce forests are characterized by a moss-dominated groundcover which represent a significant contributor of C in boreal coniferous forests (Bona et al. 2013). Similarly, pyrogenic carbon (PyC) produced as result of the incomplete combustion of plant material is highly resistant to decomposition, acting as a very stable C pool (Preston and Schmidt 2006). The quantitative and ecological importance of mosses and PyC in the boreal C cycle cannot be ignored when forest C accounting. The inclusion of those two C pools in model simulations has the potential to improve prediction of C estimates in boreal black spruce forests by reducing current uncertainties (Bona et al. 2013).

REFERENCES

Aakala T, Kuuluvainen T, De Grandpré L, Gauthier S. 2007. Trees dying standing in the northeastern boreal old-growth forests of Quebec: spatial patterns, rates, and temporal variation. Canadian Journal of Forest Research 37:50-61.

Alexander ME. 1982. Calculating and interpreting forest fire intensities. Canadian Journal of Botany 60:349-357.

Alexander ME. 1985. Estimating the length-to-breadth ratio of elliptical forest fire patterns. In: Donoghue LR, Martin RE, editors. Eighth Conference on Fire and Forest Meteorology. Bethesda: Society of American Foresters, pp. 287-304.

Alexander ME, Cole F V. 1995. Predicting and interpreting fire intensities in Alaskan black spruce forests using the Canadian System of Fire Danger Rating. Managing Forests to Meet People's Needs. In: Society of American Foresters, editor. Proceedings of the 1994 Society of American Foresters/Canadian Institute of Forestry Convention. Bethesda: Society of American Foresters, pp. 185-192.

Alexander ME, Stefner CN, Mason JA, Stocks BJ, Hartley GR. 2004. Characterizing the Jack Pine—Black Spruce Fuel Complex of the International Crown Fire Modelling Experiment (ICFME). Report No.: NOR-X-393.

Alexander ME, Cruz MG. 2012. Interdependencies between flame length and fireline intensity in predicting crown fire initiation and crown scorch height. International Journal of Wildland Fire 21:95-113.

Alexander ME, Cruz MG. 2012. Modelling the effects of surface and crown fire behaviour on serotinous cone opening in jack pine and lodgepole pine forests. International Journal of Wildland Fire 21:709-21.

Amiro BD, Cantin A, Flannigan MD, de Groot WJ. 2009. Future emissions from canadian boreal forest fires. Canadian Journal of Forest Research 39:383-395.

Amoroso MM, Daniels LD, Bataineh M, Andison DW. 2011. Evidence of mixed-severity fires in the foothills of the Rocky Mountains of west-central Alberta, Canada. Forest Ecology and Management 262:2240–2249.

Andrews PL. 2009. BehavePlus fire modeling system, version 5.0: Variables. 1-124. Available: http://www.fs.fed.us/rm/pubs/rmrs_gtr213.pd

Angers VA, Drapeau P, Bergeron Y. 2010.Snag degradation pathways of four North American boreal tree species. Forest Ecology and Management 259: 246-256.

Bacaro G, Ricotta C, Marignani M, Torri D, Chiarucci A. 2014. Using Shannon's recursivity to summarize forest structural diversity. For Trees Livelihoods 23:211-216.

Baker WL. 1995. Longterm response of disturbance landscape to human intervention global change. Landscape Ecology 10:143-159.

Beck J, Alexander ME, Harvey S, Beaver A. 2002. Forecasting diurnal variations in fire intensity to enhance wildland firefighter safety. International Journal of Wildland Fire 11:173-182.

Beck PSA, Juday GP, Alix C, Barber VA, Winslow SE, Sousa EE, Heiser P, Herriges JD, Goetz SJ. 2011. Changes in forest productivity across Alaska consistent with biome shift. Ecology Letters 14:373-379.

Bélisle AC, Gauthier S, Cyr D, Bergeron Y, Morin H. 2011. Fire regime and old-growth boreal forests in central Québec, Canada: an ecosystem management perspective. Silva Fennica 45:889-908.

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

Bergeron Y, Leduc A, Harvey BD, Gauthier S. 2002. Natural fire regime: a guide for sustainable management of the Canadian boreal forest. Silva Fennica 36:81-95.

Bergeron Y, Flannigan M, Gauthier S, Leduc A, Lefort P. 2004. Past, Current and Future Fire Frequency in the Canadian Boreal Forest: Implications for Sustainable Forest Management. AMBIO: A Journal of the Human Environment 33:356-360.

Bergeron Y, Cyr D, Drever CR, Flannigan M, Gauthier S, Kneeshaw D, Lauzon È, Leduc A, Le Goff H, Lesieur D, Logan K. 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 36:2737-2744.

Bergeron Y, Cyr D, Girardin MP, Carcaillet C. 2010. 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 19:1127-1139.

Bessi WC, Johnson EA. 1995. The relative importance of fuels and weather on fire behavior in subalpine forests. Fuel 76:747-762.

Bhatti JS, Apps MJ, Jiang H. 2001. Examining the carbon stocks of boreal forest ecosystems at stand and regional scales.In :Lal R, Kimble JM, Follet RF, Jiang H., editors. Assessment methods for soil carbon. Lewis Publications, Florida, p 513-532.

Boby L, Schuur E, Mack M. 2010. Quantifying fire severity, carbon, and nitrogen emissions in Alaska's boreal forest. Ecological Applications 20:1633-1647.

Boiffin J. 2014. Résilience des pessières à mousses du Québec aux incendies peu sévères : Impact sur la dynamique du carbone à long terme. Ph.D Thesis. Université Laval. 172p.

Boiffin J, Munson AD. 2013. Three large fire years threaten resilience of closed crown black spruce forests in eastern Canada. Ecosphere 4: 56.

Boisvenue C, Running SW. 2006. Impacts of climate change on natural forest productivity-Evidence since the middle of the 20th century. Global Change Biology 12:862-882.

Boisvenue C, Bergeron Y, Bernier P, Peng C. 2012. Simulations show potential for reduced emissions and carbon stocks increase in boreal forests under ecosystem management. Carbon Management 3:553-568.

Bona KA, Fyles JW, Shaw C, Kurz WA. 2013. Are Mosses Required to Accurately Predict

Upland Black Spruce Forest Soil Carbon in National-Scale Forest C Accounting Models? Ecosystems 16:1071-1086.

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

Bouchard M, Pothier D, Gauthier S. 2008. Fire return intervals and tree species succession in the North Shore region of eastern Quebec. Canadian Journal of Forest Research 38:1621-1633.

Boucher D, De Grandpré L, Gauthier S. 2003. Development of a statistical tool for classifying stand structure and comparison of two territories in the black spruce-moss forest region of Québec. The Forestry Chronicle 79:318-328.

Boulanger Y, Sirois L, Hébert C. 2011. Fire severity as a determinant factor of the decomposition rate of fire-killed black spruce in the northern boreal forest. Canadian Journal of Forest Research 41:370-379.

Boulanger Y, Gauthier S, Gray DR, Le Goff H, Lefort P, Morisette J. 2013. Fire regime zonation under current and future climate over eastern Canada. Ecological Applications 23:904-923.

Boulanger Y, Gauthier S, Burton PJ. 2014. A refinement of models projecting future Canadian fire regimes using homogeneous fire regime zones. Canadian Journal of Forest Research 44:365-376.

Brassard BW, Chen HYH. 2006. Stand Structural Dynamics of North American Boreal Forests. Critical Reviews in Plant Sciences 25:115-137.

Brown S. 2002. Measuring carbon in forests: current status and future challenges. Environmental Pollution 116:363-372.

Byram GM.1959. Combustion of forest fuels. Davis KP, editor. Forest Fire: Control and Use. New York: McGraw-Hill. p. 61-89.

Caswell H. 2001. Matrix Population Models: Construction, Analysis, and Interpretation. Sunderland (MA): Sinauer Associates. 722p.

Catchpole EA, Alexander ME, Gill AM. 1992. Elliptical-fire perimeter- and area-intensity distributions. Canadian Journal of Forest Research 22:968-972.

Chabot M, Blanchet P, Drapeau P, Fortin J, Gauthier S, Imbeau L, et al. 2009. Le feu en milieu forestier. In : MultiMondes, editor. Manuel de foresterie. Québec, Ordre des ingénieurs forestiers du Québec; p. 1037-1090.

Chen W, Chen JM, Price DT, Cihlar J. 2002. Effects of stand age on net primary productivity of boreal black spruce forests in Ontario, Canada. Canadian Journal of Forest Research 32: 833-842.

Chen W, Zhang Q, Cihlar J, Bauhus J, Price DT. 2004. Estimating fine-root biomass and production of boreal and cool temperate forests using aboveground measurements: a new approach. Plant and Soil 265:31-46.

Chylek P, Li J, Dubey MK, Wang M, Lesins G. 2011. Observed and model simulated 20th century Arctic temperature variability: Canadian Earth System Model CanESM2. Atmospheric. Chemistry and Physics Discussion 11:22893-22907.

Cruz MG, Alexander ME, Wakimoto RH. 2003. Assessing canopy fuel stratum characteristics in crown fire prone fuel types of western North America. International Journal of Wildland Fire 12:39-50.

Cruz MG, Alexander ME, Wakimoto RH. 2005.Development and testing of models for predicting crown fire rate of spread in conifer forest stands. 2005. Canadian Journal of Forest Research 35:1626-39.

Cruz, MG, Alexander ME. 2010. Assessing crown fire potential in coniferous forests of western North America : a critique of current approaches and recent simulation studies. International Journal of Wildland Fire 19:377-398.

Cuddington K, Fortin MJ, Gerber LR, Hastings A, Liebhold A, O'Connor M, Ray C. 2013. Process-based models are required to manage ecological systems in a changing world. Ecosphere 4:2.

Davidson EA, Janssens IA. 2006. Temperature sensitivity of soil carbon decomposition and feedbacks to climate change. Nature 440:165-173.

Davidson EA, Janssens IA, Lou Y. 2006. On the variability of respiration in terrestrial ecosystems: Moving beyond Q10. Global Change Biology 12:154-164.

de Groot WJ, Bothwell PM, Carlsson DH, Logan KA. 2003. Simulating the effects of future fire regimes on western Canadian boreal forests. Journal of Vegetation Science 14:355-364.

DeLuca TH, Boisvenue C. 2012. Boreal forest soil carbon: Distribution, function and modelling. Forestry 85:161-184.

Dhital N, Raulier F, Bernier PY, Lapointe-Garant MP, Berninger F, Bergeron Y. 2015. Adaptation potential of ecosystem-based management to climate change in the eastern Canadian boreal forest. Journal of Environmental Planning and Management 58:2228-2249.

D´Orangeville L, Duchesne L, Houle D, Kneeshaw D, Coté B, Pederson N. 2016. Northeastern North America as a potential refugium for boreal forests in a warming climate. Science 352:1452-1455.

Environment Canada. 2015. Canadian climate normal and averages 1971-2000. Environment Canada. http:/www.climate.weather.gc.ca/climate_normals

Flannigan MD, Van Wagner C.1991.Climate change and wildfire in Canada. Canadian Journal of Forest Research 21:66-72.

Forestry Canada Fire Danger Group. 1992. Development and structure of the Canadian Forest Fire Behavior Prediction System. 1–64. Available http://cfs.nrcan.gc.ca/pubwarehouse/pdfs/10068.pdf.

Fortin M, Langevin L. 2010. ARTÉMIS-2009 : un modèle de croissance basé sur une approache par tiges individuelles pour les forêts du Québec. Québec, QC : Direction de la Recherche Forestière, Mémoire de recherche forestière 156.

Gauthier S, Vaillancourt MA, Kneeshaw D, Drapeau P, De Grandpré L, Claveau Y, et al. 2009. Forest Ecosystem Management: origins and Foundations. In: Gauthuier S, Vaillancourt MA, Leduc A, De Grandpré L, Kneeshaw D, Morin H, Drapeau P, Bergeron Y, editors. Ecosystem Management in the Boreal Forest. Québec, Canada: Presses de l'Université du Québec, pp. 15-33.

Gauthier S, Bernier P, Burton PJ, Edwards J, Isaac K, Isabel N, Jayen K, Le Goff H, Nelson EA. 2014. Climate change vulnerability and adaptation in the managed. Environmental Review 22:256-285.

Gavin DG, Hallett DJ, Hu FS, Lertzman KP, Prichard SJ, Brown KJ, Lynch JA., Bartlein P, Peterson DL. 2007. Forest fire and climate change in western North America: insights from sediment charcoal records. Frontiers in Ecology and the Environment 5:499-506.

Girardin MP, Raulier F, Bernier PY, Tardif JC. 2008. Response of tree growth to a changing climate in boreal central Canada: A comparison of empirical, process-based, and hybrid modelling approaches. Ecological Modelling 213:209-228.

Girardin MP, Ali AA., Carcaillet C, Mudelsee M, Drobyshev I, Hély C, Bergeron Y. 2009. Heterogeneous response of circumboreal wildfire risk to climate change since the early 1900s. Global Change Biology 15:2751-2769.

Girardin MP, Hogg EH, Bernier PY, Kurz WA, Guo XJ, Cyr G. 2015. Negative impacts of high temperatures on growth of black spruce forests intensify with the anticipated climate warming. Global Change Biology 22:627-643.

Gower ST, Vogel JG, Norman M, Kucharik CJ, Steele SJ. 1997. Carbon distribution and aboveground net primary production in aspen, jack pine, and black spruce stands in Saskatchewan and Manitoba , Canada. Journal of Geophysical Research: Atmospheres 102:29-41.

Gower S, Krankina O, Olson R. 2001. Net primary production and carbon allocation patterns of boreal forest ecosystems. Ecological Applications. 11:1395-1411.

Grant RF, Barr AG, Black TA, Margolis H, Mccaughey JH,Trofymow JA. 2010. Net ecosystem productivity of temperate and boreal forests after clearcutting - a Fluxnet Canada measurement and modelling synthesis. Tellus 62:475-496.

Greene DF, Johnson EA.1999. Modelling recruitment of *Populus tremuloides*, *Pinus banksiana*, and *Picea mariana* following fire in the mixedwood boreal forest. Canadian Journal of Forest Research 29:462-473.

Gustafson EJ. 2013. When relationships estimated in the past cannot be used to predict the future: using mechanistic models to predict landscape ecological dynamics in a changing world. Landscpae Ecology 28:1429-1437.

Hall RJ, Freeburn JT, De Groot WJ, Pritchard JM, Lynham TJ, Landry R. 2008. Remote sensing of burn severity: experience from western Canada boreal fires. International Journal of Wildland Fire 17:476-489.

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

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

Harvey BD, Nguyen-Xuan T, Bergeron Y, Gauthier S, Leduc A. 2003. Forest management planning based on natural disturbance and forest dynamics. In: Burton PJ, Messier C, Smith DW, Adamowicz WL, editors. Towards Sustainable Management of the Boreal Forest. Ottawa, Ontario: NBC Reasearch Press. p. 395-432.

Hagemann U, Moroni MT, Shaw CH, Kurz WA, Makeschin F. 2010. Comparing measured and modelled forest carbon stocks in high-boreal forests of harvest and natural-disturbance origin in Labrador, Canada. Ecological Modelling 221:825-839.

Hilger AB, Shaw CH, Metsaranta JM, Kurz WA. 2012. Estimation of snag carbon transfer rates by ecozone and lead species for forests in Canada. Ecological Applications 22:2078-2090.

Hirsch KG, Corey PN, Martell, D.1997.Using expert judgment to model initial attack fire crew effectiveness. Forest Science 44:539-549.

Holdaway MR.1986. Modeling Tree Crown Ratio. Forestry Chronicle 62:451-455.

Hood SM, McHugh CW, Ryan KC, Reinhardt E, Smith SL.2007. Evaluation of a post-fire tree mortality model for western USA conifers. International Journal of Wildland Fire 16: 679-689.

Hothorn T, Hornik K, Zeileis A. 2006. Unbiased recursive partitioning: A conditional inference framework. Journal of Computational and Graphical Statistics 15:651-74.

IPCC : Intergovernmental Panel On Climate Change. 2007. Contribution of Working Group I to the fourth assessment report of the Intergovernmental Panel on Climate Change. Cambridge, UK: Cambridge University Press.

Johnson E.1992. Fire and vegetation dynamics-studies from the North American boreal forest. Cambridge, UK: Cambridge University Press. 144p.

Johnson KD, Harden J, McGuire AD, Bliss NB, Bockheim JG, Clark M, Nettleton-Hollingsworth T, Jorgenson MT, Kane ES, Mack M, O'Donnell J, Ping CL,Schuur EAG, Turetsky MR, Valentine DW. 2011. Soil carbon distribution in Alaska in relation to soil-forming factors. Geoderma 167-168:71-84.

Johnstone JF, Chapin FS. 2006. Effects of soil burn severity on post-fire tree recruitment in boreal forest. Ecosystems 9:14-31.

Johnstone JF. 2011. Fire Interval Trajectory Effects in Boreal on Successional Forests of Northwest. Ecosystems 9:268-277.

Johnstone JF, Rupp TS, Olson M, Verbyla D. 2011. Modeling impacts of fire severity on successional trajectories and future fire behavior in Alaskan boreal forests. Landscape Ecology 26:487-500.

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

Kashian DM, Romme WH, Tinker DB, Monica G, Ryan MG, Turner MG. 2006. Carbon storage on landscapes with stand-replacing fires. Bioscience 56:598-606.

Kasischke ES, Christensen NL, Stocks BJ.1995. Fire, global warming, and the carbon balance of boreal forests. Ecological Applications 5:437-451.

Kasischke ES. 2000. Boreal Ecosystems in the Global Carbon Cycle. In: Kasischke ES, Stocks B., editors. Fire, climate change and carbon cycling in the Boreal Forest. Springer-V. New York. p. 19-30.

Kasischke ES, Amiro BD, Barger, NN, French, NHF, Goetz SJ, Grosse G et al. 2013. Impacts of disturbance on the terrestruial carbon budget of North America. Journal of Geophysical Research: Biogeosciences 118:303-316.

Keane RE, Cary GJ, Davies ID, Flannigan MD, Gardner RH, Lavorel S, Lenihan JM, Li C, Rupp TS. 2004. A classification of landscape fire succession models: spatial simulations of fire and vegetation dynamics. Ecological Modelling 179:3-27.

Keane RE. 2015. Wildland Fuel Fundamentals and Applications. Switzerland: Springer,189 p.

Keeley JE. 2009. Fire intensity, fire severity and burn severity: a brief review and suggested usage. International Journal of Wildland Fire 18:116-126.

King KJ, de Ligt RM, Cary G. 2011. Fire and carbon dynamics under climate chaange in south-eastern Australia: insight from FULLCAM and FIRESCAPE modelling. International Journal of Wildland Fire 20:563-577.

Kotchi SO, Barrette N, Viau AA, Jang J-G, Gond V, Mir AA. 2016. Estimation and Uncertainty Assessment of Surface Microclimate Indicators at Local Scale Using Airborne Infrared Thermography and Multispectral Imagery. Environmental and Social Applications, Dr. Pasquale Imperatore, editor. Available : http://www.intechopen.com/books/geospatial-technology-environmental-and-social-applications/estimation-and-uncertainty-assessment-of-surface-microclimate-indicators-at-local-scale-using-airbor

Kull S, Rampley G, Morken S, Metsaranta J, Neilson E, Kurz WA. 2011. Operational-scale Carbon Budget Model of the Canadian Forest Sector (CBM-CFS3) version 1.2: user's guide. Natural Resources Canada, Canadian Forest Service, Northern Forestry Center, Edmonton, AB.

Kurz WA, Apps MJ, Beukema SJ, Lekstrum T. 1995. 20th century carbon budget of Canadian forests. Tellus 47B:170-177.

Kurz WA, Apps MJ. 1999. A 70-year retrospective analysis of carbon fluxes in the Canadian forest sector. Ecological Applications 9:526-547.

Kurz WA, Stinson G, Rampley G. 2008. Could increased boreal forest ecosystem productivity offset carbon losses from increased disturbances? Philosophical Transactions of the Royal Society B 363:2261-2269.

Kurz WA, Dymond CC, White TM, Stinson G, Shaw CH, Rampley GJ, Smyth C, Simpson BN, Neilson ET, Trofymow J, Metsaranta J, Apps MJ. 2009. CBM-CFS3: A model of carbon-dynamics in forestry and land-use change implementing IPCC standards. Ecological

Modelling 220:480-504.

Kurz WA, Shaw CH, Boisvenue C, Stinson G, Metsaranta J, Leckie D, Dyk A, Smyth C, Neilson E. 2013. Carbon in Canada's boreal forest-a synthesis. Environmental Reviews 21:260-292.

Lacerte V, Larocque GR, Woods M, Parton WJ, Penner M. 2006. Calibration of the forest vegetation simulator (FVS) model for the main forest species of Ontario, Canada. Ecological Modelling 199: 336-349.

Laganière J, Paré D, Bergeron Y, Chen HYH, Brassard BW, Cavard X. 2013. Stability of Soil Carbon Stocks Varies with Forest Composition in the Canadian Boreal Biome. Ecosystems 16:852-865.

Lapointe-Garant MP, Huang JG, Gea-Izquierdo G, Raulier F, Bernier P, Berninger F. 2010. Use of tree rings to study the effect of climate change on trembling aspen in Québec. Global Change Biology 16:2039-2051.

Lal R. 2004. Soil carbon sequestration to mitigate climate change. Geoderma 123:1-22.

Lambert MC, Ung CH, Raulier F. 2005. Canadian national tree aboveground biomass equations. Canadian Journal of Forest Research 35:1996-2018.

Leduc A, Bergeron Y, Gauthier S. 2007. Relationships between prefire composition, fire impact, and postfire legacies in the boreal forest of eastern Canada. In: Butler BW, Cook W, editors. The fire environment-innovations, management, and policy. Fort Collins, CO: USDA Forest Service, pp. 187-193.

Le Goff H, Flannigan MD, Bergeron Y. 2009. Potential changes in monthly fire risk in the eastern Canadian boreal forest under future climate change. Canadian Journal of Forest Research 39:2369-2380.

Lempriѐre TC, Kurz WA, Hogg EH, Schmoll C, Rampley GJ, Yemshanov D, McKenney DW, Gilsenan R, Beatch A, Blain D, et al. 2013. Canadian boreal forests and climate change mitigation 1. Environtal Review 21:293-321.

Li C. 2002. Estimation of fire frequency and fire cycle: A computational perspective. Ecological Modelling 154:103-120.

Mäkelä A, Landsberg J, Ek AR, Burk TE, Ter-Mikaelian M, Agren GI, Oliver CD, Puttonen P. 2000. Process-based models for forest ecosystem management: current state of the art and challenges for practical implementation. Tree Physiology 20:289-298.

Manies KL, Harden JW, Neill KPO. 2005. Woody debris along an upland chronosequence in boreal Manitoba and its impact on long-term carbon storage. Candian Journal of Forest Research 482:472-482.

Mansuy N, Gauthier S, Robitaille A, Bergeron Y. 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 19:1083-1098.

Masera OR, Garza-Caligaris JF, Kanninen M, Karjalainen T, Liski J, Nabuurs G., Pussinen A, de Jong BH., Mohrenf GMJ. 2003. Modelling carbon sequestration in afforestation, agroforestry and forest management projects: the CO2FIX V.2 approach. Ecological

Modelling164:177-199.

Matthias L, Kenkel N, de Groot A, Kneeshaw D, Macdonald E, Messier C, Morin H, Ruel JC, Wang G. 2003. Differential growth and mortality of advance regeneration acroos the Canadian boreal forest. University of Alberta, Alberta, Canada, Project Reports 2003/2004.

Ministère des Ressources Naturelles du Québec.2011. Forest Inventory Norms. 2008 ed. Québec: Direction des inventaires forestiers.

MFFP : Ministère des Forets, de la Faune et des Parcs Naturelles du Québec. 2008. Forest Inventory Norms [draft]. Forest Inventory Division. Québec, Quebec, Canada.

Miquelajauregui Y, Cumming SG, Gauthier S. 2016. Modelling variable fire severity in boreal forests: effects of fire intensity and stand structure. PLoS one 11:2

Miquelajauregui Y, Cumming SG, Gauthier S. (in review). Sensitivity of boreal carbon stocks to fire return interval and seasonality of head fire intensity: a simulation study of black spruce forests.

Moon K, Duff TF, Tolhurst KG. Characterising forest wind profiles for utilisation in fire spread models. 2013. Twentieth International Congress on Modelling and Simulation. Adelaide: Australia.

Moss RH, Edmonds JA, Hibbard KA, Manning MR, Rose SK, van Vuuren DP, Carter TR, Emori S, Kainuma M, Kram T, et al. 2010. The next generation of scenarios for climate change research and assessment. Nature 463:747-56.

Mruzik L. Analysis of reducing ladder fuels which contribute to fireline intensity and fire severity in the North Murphy Project Area. 2001. Technical Fire Management Paper TFM-15-351. Duvall, Washington.

Oliver CD, Larson BC. 1996. Forest stand dynamics. New York : John Wiley & Sons, Inc, 540p.

Oris F, Asselin H, Ali AA, Finsinger W, Bergeron Y. 2014. Effect of increased fire activity on global warming in the boreal forest. Environmental Reviews 22:206-219.

Ouimet R, Camiré C, Brazeau M, Moore JD. 2008. Estimation of coarse root biomass and nutrient content for sugar maple, jack pine, and black spruce using stem diameter at breast height. Canadian Journal of Forest Research 38: 92-100.

Pan Y, Birdsey R, Fang J, Houghton R, Kauppi PE, Kurz WA, Phillips OL, Shvidenko A, Lewis SL, Canadell JG, Ciais P, Jackson RB, Pacala SW, McGuire AD, Piao S, Rautiainen A, Sitch S, Hayes D. 2011. A large and persistent carbon sink in the world´s forest. Science 333:988-993.

Parsons R, Mell WE, McCauley P. 2011. Linking 3D spatial models of fuels and fire: Effects of spatial heterogeneity on fire behavior. Ecological Modelling 222:679-91.

Peng C. 1999. Nonlinear Height-Diameter Models for Nine Boreal Forest Tree Species in Ontario. Sault Ste. Marie, ON: Ontario Forest Research Institute, For. Res. Rep.155.

Peng C. 2000. Growth and yield models for uneven-aged stands: past, present and future. Forest Ecology and Management 132:259-279.

Peng C, Liu JX, Dang QL, Apps MJ, Jiang H. 2002.TRIPLEX: a generic hybrid model for predicting forest growth and carbon and nitrogen dynamics. Ecological Modelling 153:109-130.

Pelletier G, St-Onge-J, Bordeleau P, De Rainville P, Bart F, Aubin E, et al. 2009. Classification of forest stands as fuels according to the Canadian Forest Fire Behavior Prediction (FBP) System- Third Ten-Year Quebec Forest Survey Program. Québec. Available: http://www.mern.gouv.qc.ca/english/publications/forest/fimaq/classification-forest-stand-third.pdf.

Peterson DL. 1985. Crown scorch volume and scorch height: estimates of postfire tree condition. Canadian Journal of Forest Research 15:596-598.

Pinheiro J, Bates D, DebRoy S, Sarkar D, R Core Team. 2015. nmle: Linear and Nonlinear Mixed Effects Models. R package version 3.1-127.

Pinheiro JC, Bates DM. 2000. Mixed-effects models in S and S-PLUS. New York: Springer-Verlag New York. 528p.

Preston CM, Schmidt MWI. 2006. Black (pyrogenic) carbon : a synthesis of current knowledge and uncertainties with special consideration of boreal regions. Biogeosciences 3: 397-420.

Price DT, Peng CH, Apps MJ, Halliwell DH. 1999. Simulating effects of climate change on boreal ecosystem carbon pools in central Canada. Journal of Biogeography 26:1237-1248.

Price DT, Alfaro RI, Brown KJ, Flannigan MD, Fleming RA, Hogg EH, Girardin MP, Lakusta T, Johnston M, Mckenney DW, et al. 2013. Anticipating the consequences of climate change for Canada ' s boreal forest ecosystems. Environmental Reviews 365:322-365.

Powers, EM, Marshall, JD, Zhang J, Wei L. 2013. Post-fire management regimes affect carbon sequestration and storage in a Sierra Nevada mixed conifer forest. Forest Ecology and Management 291:268-277.

Purdon M, Brais S, Bergeron Y. 2004. Initial response of understory vegetation to fire severity and salvage-logging in the southern boreal forest of Quebec. Applied Vegetation Science 7:49-60.

R Development Core Team. 2012. R: A language and environment for statistical computing.

Räisänen J, Tuomenvirta H. 2009. Interactions between boreal forests and climate change. In: Pertti Hari, Liisa Kulmala, editors. Boreal Forest and Climate Change. Springer. p. 479-528.

Régnière J, Saint-Amant R, Béchard A. 2014. BioSIM 10: user's manual. Information report LAU-X-137E. Natural Resources Canada, Canadian Forest Service, Laurentian Forestry Centre, Québec, Quebec, Canada.

Riahi K, Rao S, Krey V, Cho C, Chirkov V, Fischer G, Kindermann G, Nakicenovic N, Rafaj P. 2011. RCP 8.5-A scenario of comparatively high greenhouse gas emissions. Climate Change 109:33-57.

Rossi S, Tremblay M-J, Morin H, Levasseur V. 2009. Stand structure and dynamics of Picea mariana on the northern border of the natural closed boreal forest in Quebec, Canada.

Canadian Journal of Forest Research 39:2307-2318.

Reinhardt E, Crookston N. 2003. The Fire and Fuels Extension to the Forest Vegetation Simulator (No. RMRS-GTR-116). Ogden, UT. Department of Agriculture. Forest Service Center. Rocky Mountain Research Station.

Reinhardt E, Scott J, Gray K, Keane R. 2006. Estimating canopy fuel characteristics in five conifer stands in the western United States using tree and stand measurements. Canadian Journal of Forest Research 36: 2803-2814.

Rossi S, Tremblay M-J, Morin H, Savard G. 2009. Growth and productivity of black spruce in even- and uneven-aged stands at the limit of the closed boreal forest. Forest Ecology and Management 258:2153-2161.

Rowe J. 1972. Forest regions of Canada. Canadian Forestry Service. Ottawa, Ontario.

Running S., Gower S. 1991. FOREST-BGC, A general model of forest ecosystem processes for regional applications. II. Dynamic carbon allocation and nitrogen budgets. Tree Physiology 9:161-172.

Russell MB, Woodall CW, Amato AWD, Fraver S, Bradford JB. 2014. Technical Note: Linking climate change and downed woody debris decomposition across forests of the eastern United States. Biogeosciences 11: 6417-6425.

Ryan KC. 2002. Dynamic interactions between forest structure and fire behavior in boreal ecosystems. Silva Fennica 36:13-39.

Saucier JP, Bergeron JF, Grondin P, Robitaille A.1998. Les regions écologiques du Québec méridional.

Seedre M, Shrestha BM, Chen HYH, Colombo S, Jõgiste K. 2011. Carbon dynamics of North American boreal forest after stand replacing wildfire and clearcut logging. Journal of Forest Research 16:168-183.

Sikkink P, Keane RE. 2012. Predicting fire severity using surface fuels and moisture. Fort Collins, CO.

Simard A. 1975. Wildland fire occurrence in Canada. Environment Canada, Canadian Forestry Service. Available: http://cfs.nrcan.gc.ca/pubwarehouse/pdfs/25586.pdf.

Skowroski N, Clark K, Duveneck M, Hom J. 2011. Three-dimensional canopy fuel loading predicted using upward and downward sensing LiDAR system. Remote Sensing of Environment 115:703-14.

Smith D, Larson B, Kelty M, Ashton PM. 1997. The practice of silviculture: Applied Forest Ecology. 9th ed. New York, USA: John Wiley & Sons, Inc.

Soil Classification Working Group. 1998. The Canadian system of soil classification. Agriculture and Agri-Food Canada Publ. 1646 (revised). NRC Research Press, Ottawa, ON.

SOPFEU. 2012. Plan stratégique 2012-2015. 2012 ;1-24. Available: http://www.sopfeu.qc.ca.

Staudhammer CL, LeMay VM. 2001. Introduction and evaluation of possible indices of stand structural diversity. Canadian Journal of Forest Research 31:1105-1115.

Stinson G, Kurz WA, Smyth CE, Neilson ET, Dymond CC, Metsaranta JM, Boisvenue C, Rampley GJ, Li Q, White TM, Blain D. 2011. An inventory-based analysis of Canada´s managed forest carbon dynamics, 1990 to 2008. Global Change Biology 17: 2227-2244.

Stocks BJ. 1980. Black spruce crown fuel weights in northern Ontario. Canadian Journal of Forest Research 10:498-501.

Stocks BJ, Alexander ME, Wotton BM, Stefner CN, Flannigan MD, Taylor S., Lavoie N, Mason J., Hartley G., Maffey M., et al. 2004. Crown fire behaviour in a northern jack pine-black spruce forest. Canadian Journal of Forest Research 34:1548-1560.

Subedi N, Sharma M. 2013. Climate-diameter growth relationships of black spruce and jack pine trees in boreal Ontario, Canada. Global Change Biology 19:505-516.

Teck R, Hilt D. 1991. Individual-tree diameter growth model for the Northeastern United States.USDA Forest Service Research Paper NE-649.

Thies WG, Westlind DJ, Loewen M, Brenner G. 2006. Prediction of delayed mortality of fire-damaged ponderosa pine following prescribed fires in eastern Oregon, USA. International Journal of Wildland Fire 15:19-29.

Thompson JR, Spies T. 2009. Vegetation and weather explain variation in crown damage within a large mixed-severity wildfire. Forest Ecology and Management 258:1684-1694.

Tian H, Melillo JM, Kicklighter DW, McGuire AD, Helfrich JVK, Moore B, Vörösmarty CJ. 1998. Effect of interannual climate variability on carbon storage in Amazonian ecosystems. Nature 396:664-667.

Tremblay S, Ouimet R, Houle D. 2002. Prediction of organic carbon content in upland forest soils of Quebec, Canada. Canadian Journal of Forest Research 32: 903–914.

van Bellen S, Garneau M, Bergeron Y. 2010. Impact of climate change on forest fire severity and consequences for carbon stocks in boreal forest stands of Quebec, Canada: a synthesis. Fire Ecology 6:16-44.

Van Bogaert R, Gauthier S, Raulier F, Saucier J, Boucher D, Robitaille A, Bergeron Y. 2015. Exploring forest productivity at an early age after fire : a case study at the northern limit of commercial forests in Quebec. Canadian Journal of Forest Research 45:1-15.

Van Cleve K, Oechel W, Hom J. 1990. Response of black spruce (Picea mariana) ecosystems to soil temperature modification in interior Alaska. Canadian Journal of Forest Research 20:1530-1535.

Van Wagner CE. 1973. Height of crown scorch in forest fires. Canadian Journal of Forest Research 3:373-378.

Van Wagner CE. 1977. Conditions for the start and spread of crown fire. Canadian Journal of Forest Research 7:23-34.

Van Wagner CE. 1978. Age-class distribution and the forest fire cycle. Canadian Journal of Forest Research 8:220-227.

Van Wagner CE. 1983. Fire behaviour in northern conifer forests and shrublands. In: Wein

RW, MacLean D, editors. The role of fire in northern circumpolar ecosystems. Chichester, England: John Wiley & Sons, Inc, pp. 65-80.

Wang CK, Bond-Lamberty B, Gower ST. 2003. Carbon distribution of a well- and poorly-drained black spruce fire chronosequence. Global Change Biology 9:1066-1079.

Wang W, Peng C, Kneeshaw DD, Larocque GR, Lei X, Zhu Q, Song X, Tong Q. 2013. Modeling the effects of varied forest management regimes on carbon dynamics in jack pine stands under climate change. Canadian Journal of Forest Research 43:469-479.

Weber MG, Flannigan MD. 1997. Canadian boreal forest ecosystem structure and function in a changing climate: impact on fire regimes. Environmental Review 5:145-166.

Whelan RJ. 1995. The Ecology of Fire. 1st ed. Cambridge, United Kingdom: Cambridge University Press.

Wotton BM, Alexander ME, Taylor S. 2009. Updates and revisions to the 1992 Canadian Forest Fire Behaviour Prediction System. 1-45. Available: http://www.cfs.nrcan.gc.ca/bookstore_pdfs/31414.pdf.

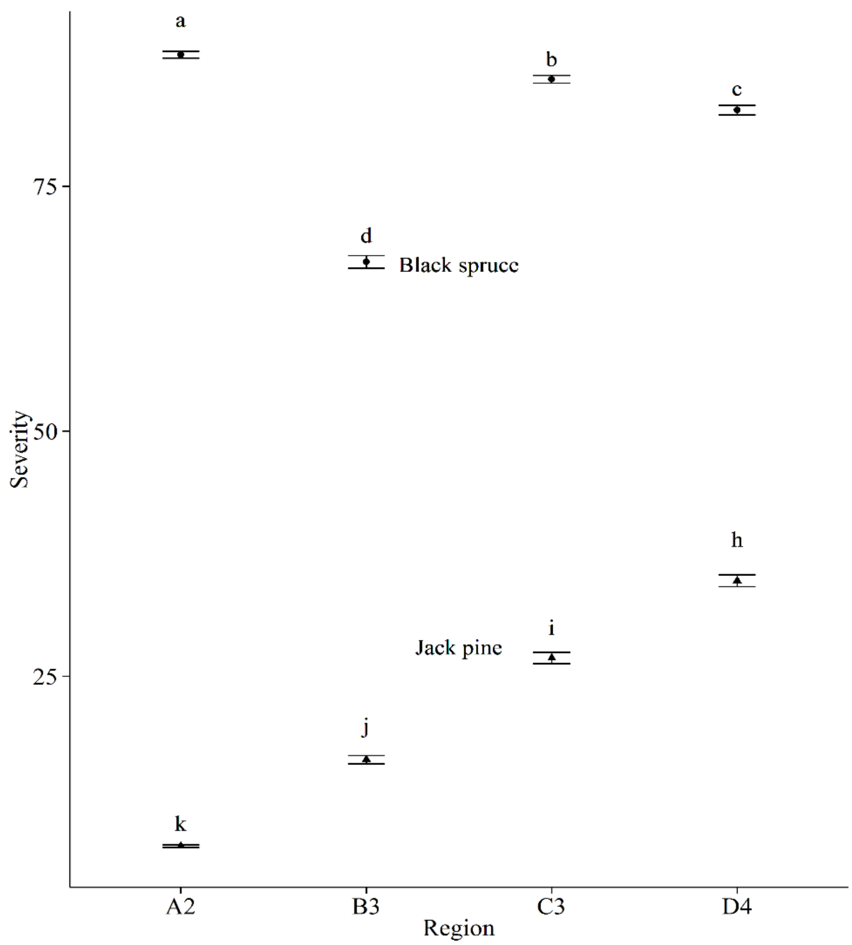
Xu W, Li W, Jiang P, Wang H, Bai E. 2014. Distinct temperature sensitivity of soil carbon decomposition in forest organic layer and mineral soil. Scientific Reports 4:6512.

Zuur AF, Ieno EN, Walker NJ, Saveliev A, Smith GM. 2009. Mixed effects models and extensions in ecology with R. New York: Springer-Verlag New York.

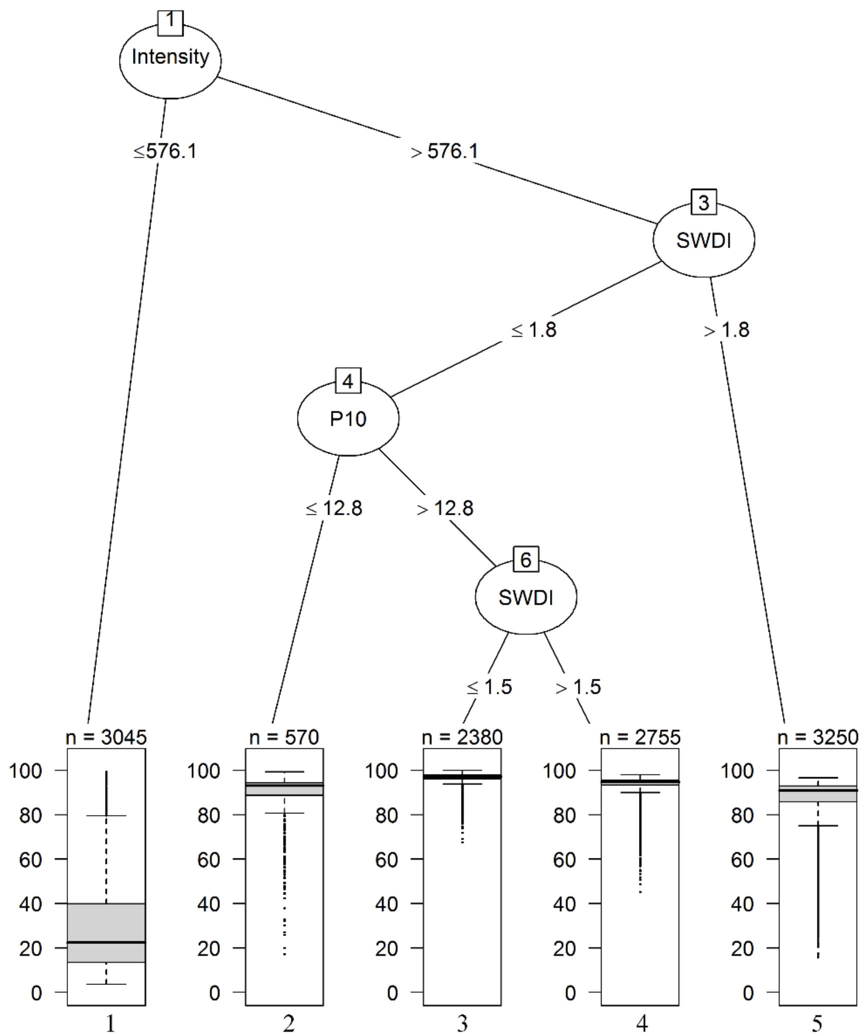
Annexes

Appendix A Supplementary material for Chapter 1

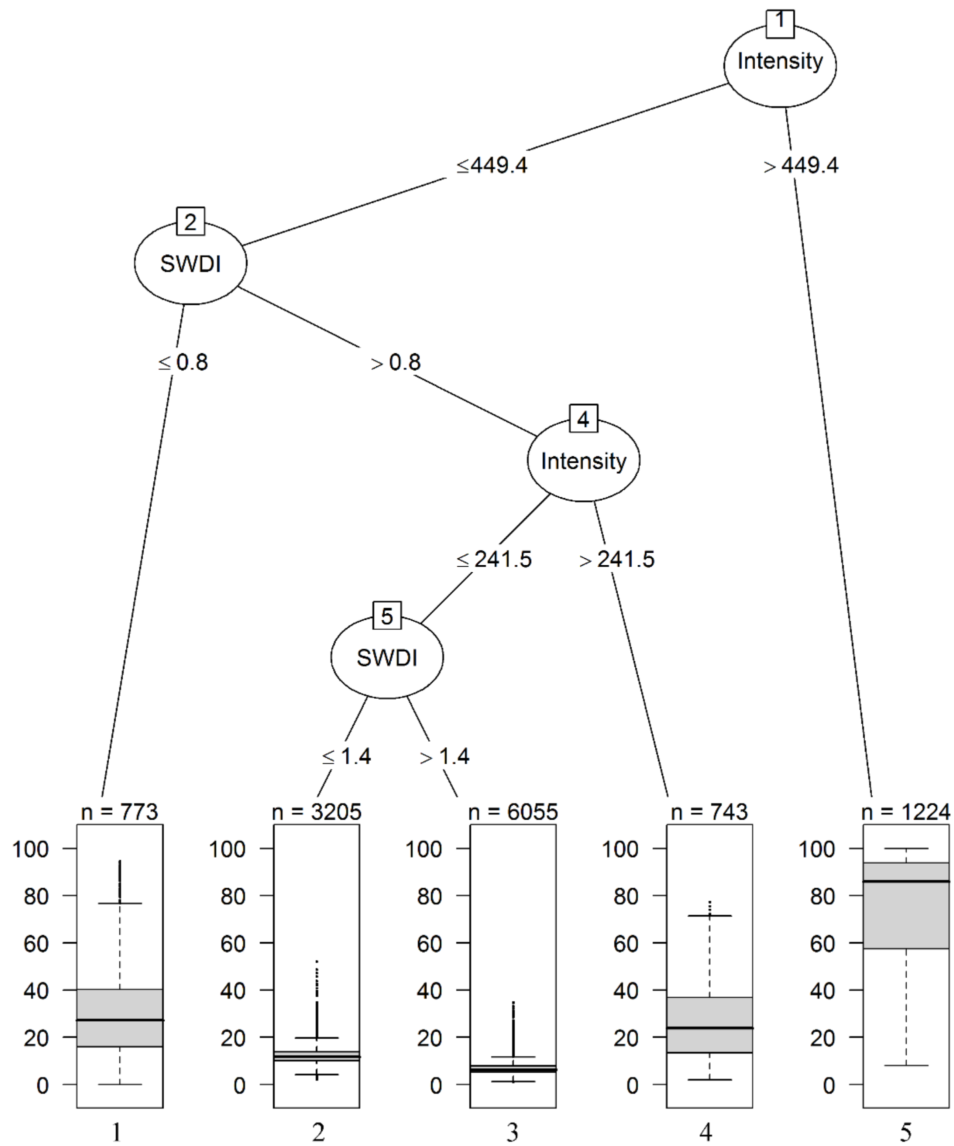
A-1 Interaction plot showing the effect of fire region and species on the mean fire severity with 95% confidence intervals. Different letters represent significant differences between the means obtained from a Tukey's multiple comparison test (α=0.05). The four fire regions defined based on the fire cycle and the fire frequency: A2 (>1100 yrs; low-medium), B3 (500-1100 yrs; medium), C3 (200-500 yrs; medium), D4 (100-200 yrs; medium-high).



A-2 Regression tree for simulated fire severity in black spruce patches, without simulating crown fire development. The first split in the tree is defined by the initial intensity which has the strongest relationship with fire severity. Box plots at terminal nodes show the distribution of the fire severity data within each branch of the tree. The number of observations within each branch is shown at the top of each boxplot. The total number of simulated fires was 12,000.

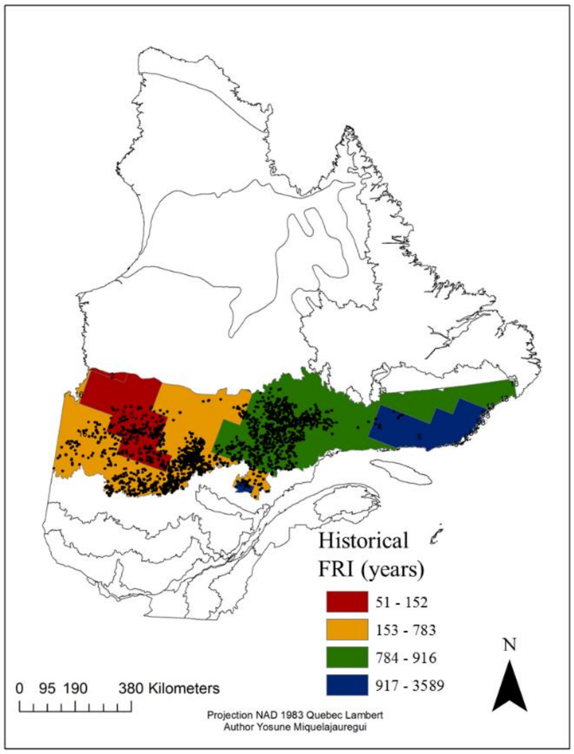


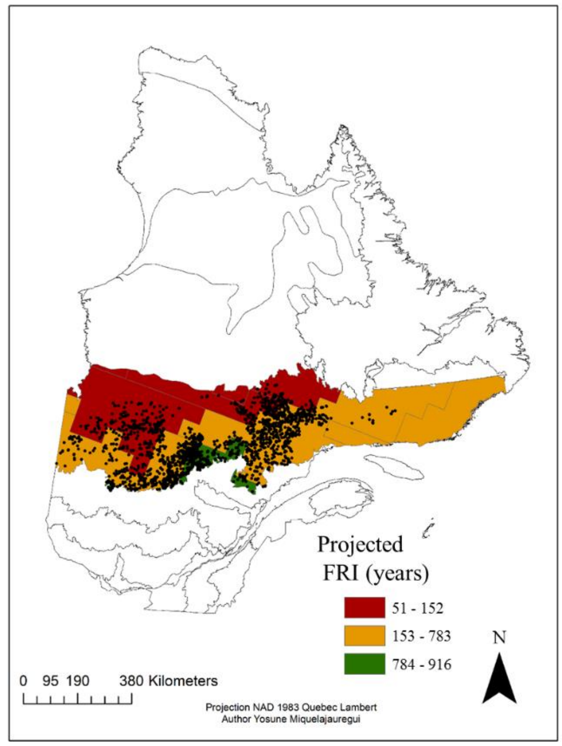
A-3 Regression tree for simulated fire severity in jack pine patches, without simulating crown fire development. The first split in the tree is defined by the initial intensity which has the strongest relationship with fire severity. Box plots at terminal nodes show the distribution of the fire severity data within each branch of the tree. The number of observations within each branch is shown at the top of each boxplot. The total number of simulated fires was 12,000.



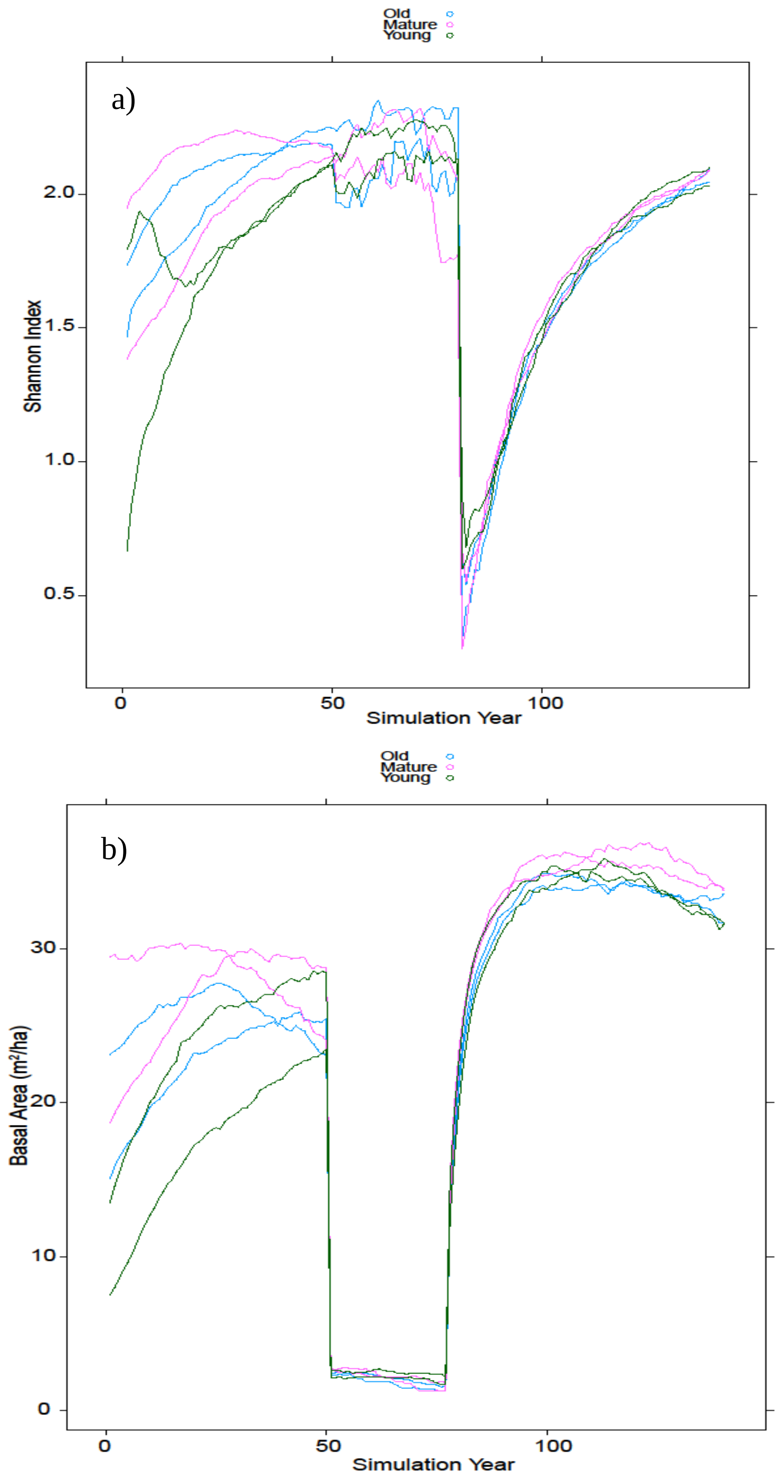
Appendix B Supplementary material for Chapter 2

B-1 Historical (1961-1990) and projected (2070-2100) fire return interval maps derived from Boulanger et al. (2013) for the black spruce feather moss domain in northern Québec, Canada.

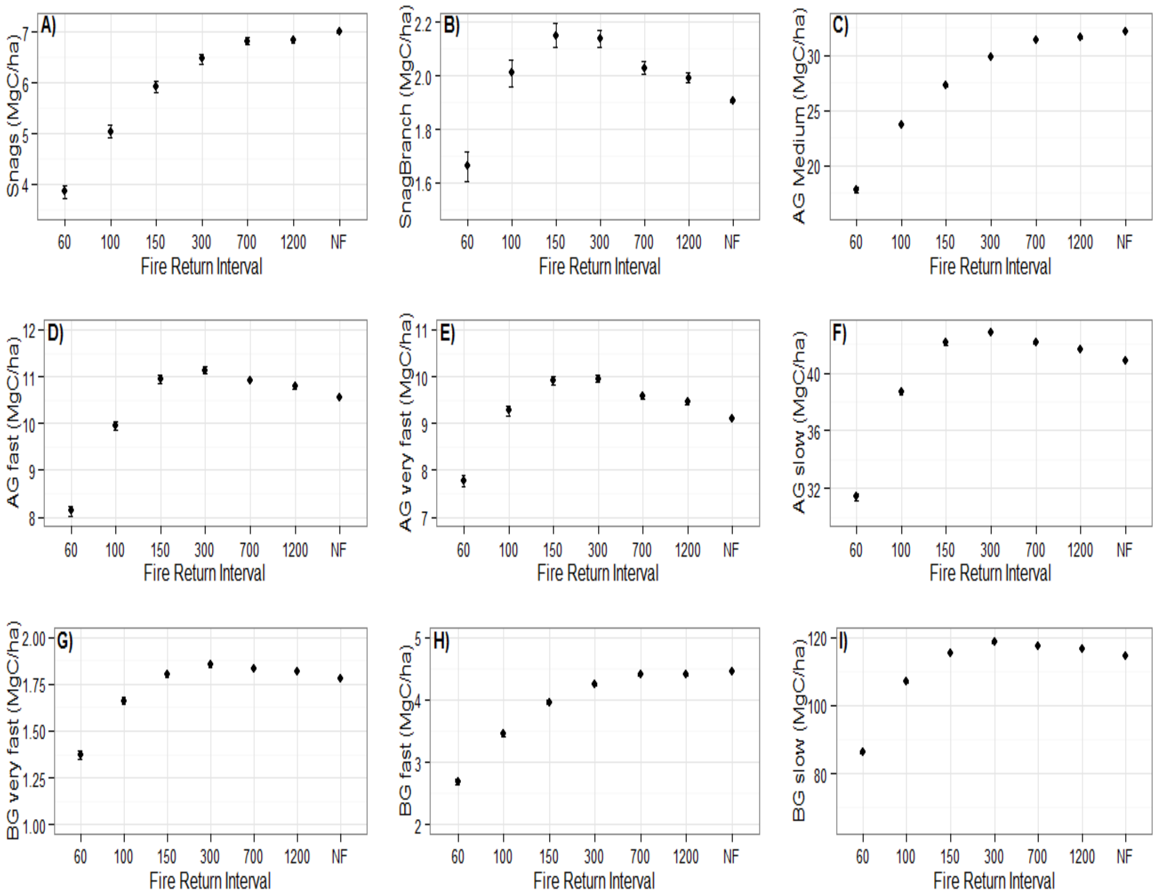




B-2. Changes in a) stand structure measured by the Shannon-Wiener diversity index and b) basal area (m^2/ha) for young (50-100 yrs), mature (100-200 yrs) and old-growth (>200 yrs) black spruce stands over a simulation period of 150 years. A stand-replacing fire event occurred at year 50.



B-3 Mean DOM C stocks (Mg C ha $^{-1}$, mean ± ci) over 1000 replicate simulation runs of 2400 years by FRI (x-axes). A) Snags, B) Snag branches, C) Aboveground Medium, D) Aboveground fast, E) Aboveground very fast, F) Aboveground slow, G) Belowground very fast, H) Belowground fast, I) Belowground slow.

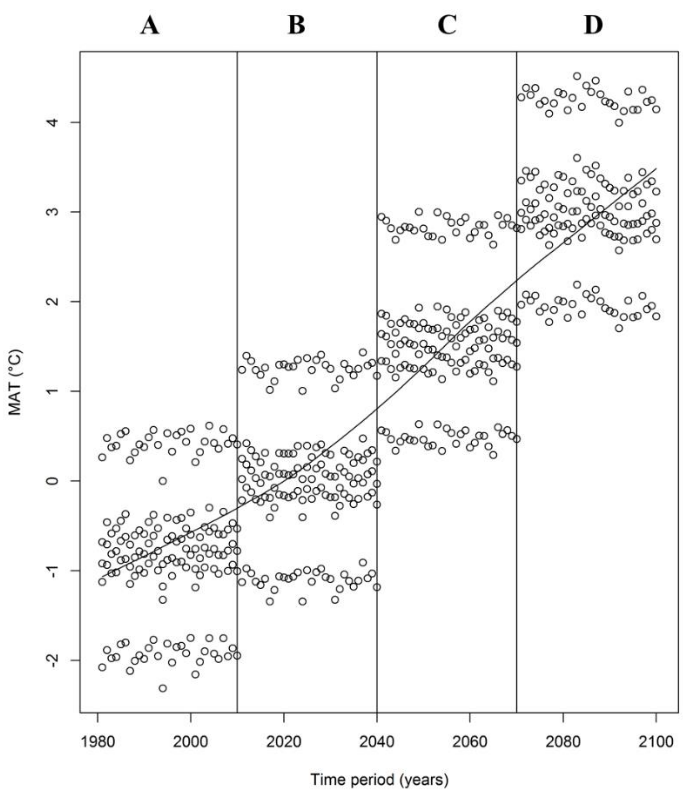


B-4 Distribution of the two structural types (uneven-sized and even-sized) in the different fire return interval and season combinations (n=14,000). Season 1: Spring; Season 2: Summer.

	Fire return interval						
Season 1	**60**	**100**	**150**	**300**	**700**	**1200**	**NF**
Uneven-sized	656	772	863	914	967	978	1000
Even-sized	344	228	137	86	33	22	0
Season 2							
Uneven-sized	624	745	828	916	968	975	1000
Even-sized	376	255	172	84	32	25	0

Appendix C Supplementary material for Chapter 3

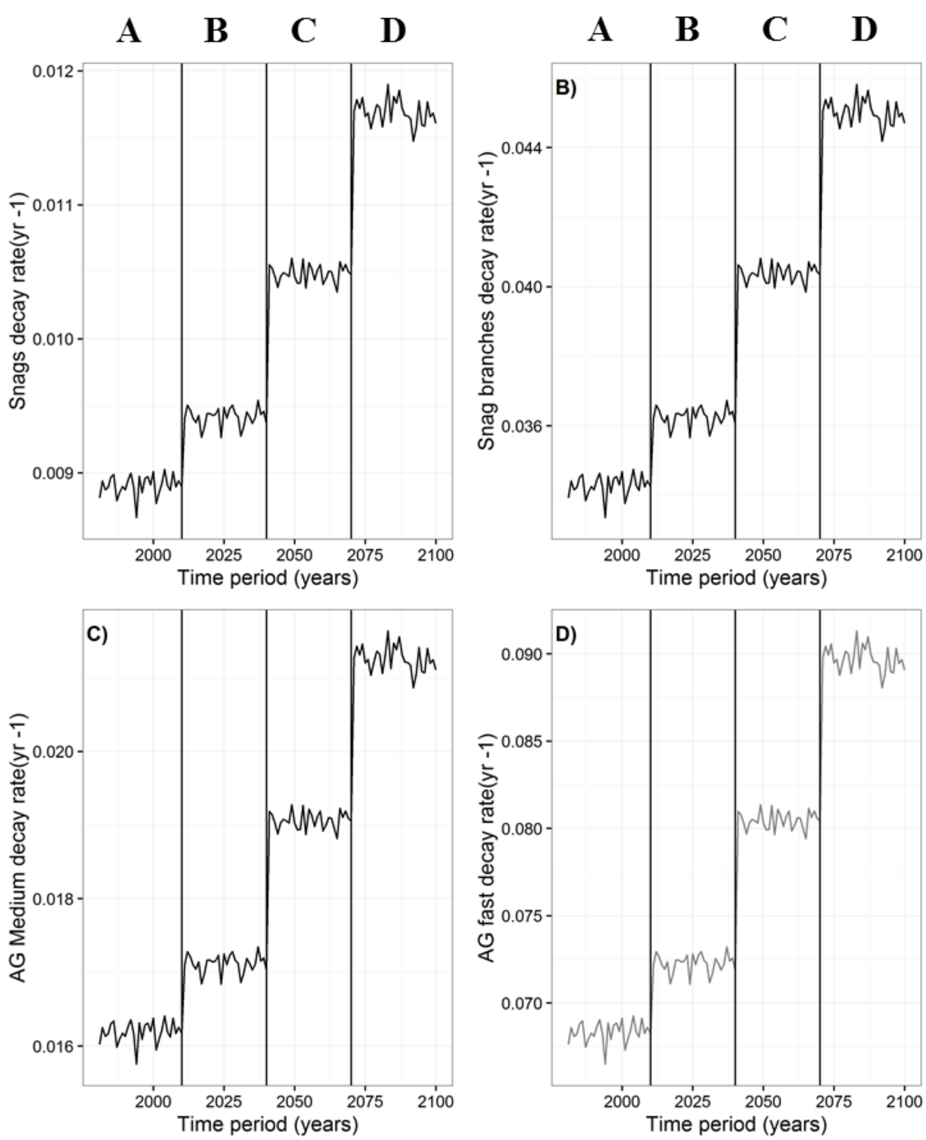
C-1 Mean annual temperature (MAT, °C) calculated over 1000 replicate simulation runs of 120 years by time period (x-axes). The vertical lines mark the beginning the end of each climatic period. Letters on the top of the plot indicate the four climatic periods evaluated: A: Historical/1980-2010, B: 2010-2040, C: 2040-2070, D: 2070-2100. Smooth fit line is also shown (black line).

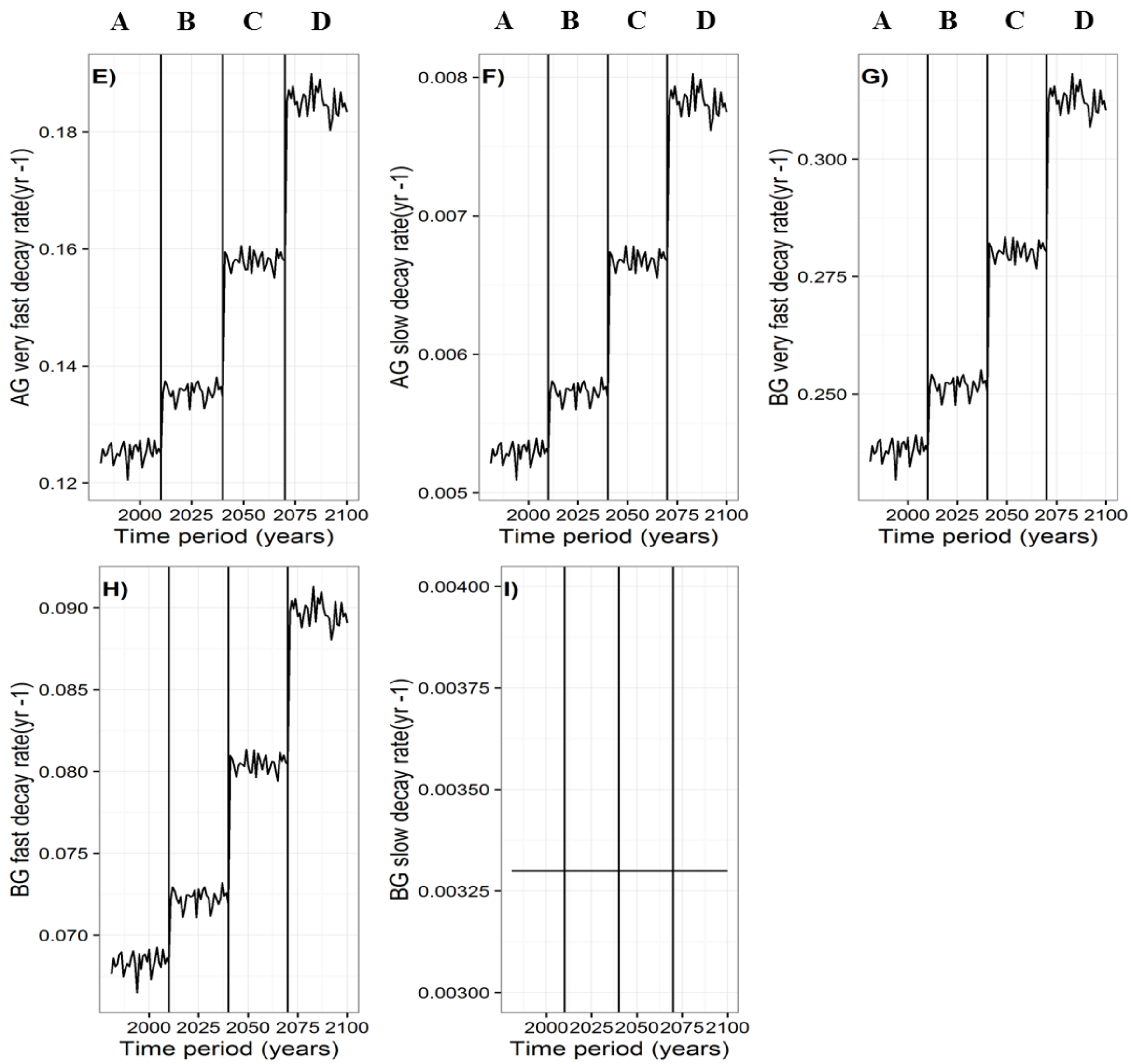


C-2 Initial DOM C stocks (Mg C ha-1) for 1: Snags, 2: Snag Branches, 3: Aboveground Medium, 4: Aboveground fast, 5: Aboveground very fast, 6: Aboveground slow, 7: Belowground very fast, 8: Belowground fast, 9: Belowground slow carbon pools growth index (m), stand structure measured by the Shannon-Wiener diversity index (H') and patch-level attributes (mean ± sd) per FRI pathway and climatic period: A: Historical, B: 2010-2040, C: 2040-2070, D: 2070-2100. The number of simulated fires for the 1000 simulations per FRI pathway and climatic period are also reported.

FRI Pathway	DOM C stocks									Growth index (m)	Basal area (m^2/ha)	Stand structure (H´)	Density (stems/ha)	No. simulated fires for the 1000 simulations			
	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**					**A**	**B**	**C**	**D**
Pathway 1	6.5	2.0	34.3	11.7	10.6	44.1	1.9	4.6	121.2	13.7	24.2±9.0	1.70±0.33	4024.9±2506.4	38	52	75	130
Pathway 2	7.1	2.1	37.5	13.0	11.9	46.5	2.1	5.3	124.9	13.9	21.1±8.9	1.65±0.31	3768.1±2491.3	28	112	138	230
Pathway 3	6.8	2.0	33.5	11.7	10.7	43.6	1.9	4.7	120.7	13.9	20.6±9.4	1.61±0.37	3966.8±3351.3	46	158	151	176
Pathway 4	6.0	2.2	29.0	11.7	11.1	43.7	2.0	4.2	117.9	13.9	18.8±9.0	1.56±0.37	3695.3±2892.4	234	228	159	347
Pathway 5	6.9	2.0	31.0	10.9	9.5	41.7	1.8	4.4	116.9	13.7	23.1±9.9	1.57±0.40	4292.8±2656.5	31	33	45	102

C-3 Average temperature-sensitive decomposition rates (% yr^{-1}) for each DOM carbon pool tracked. Averages were calculated over 1000 replicate simulation runs of 120 years. Letters on the top of the plot indicate the four climatic periods evaluated: A: Historical, B: 2010-2040, C: 2040-2070, D: 2070-2100




A B C D
E)
AG very fast decay rate(yr -1)
0.12
0.14
0.16
0.18
F)
AG slow decay rate(yr -1)
0.005
0.006
0.007
0.008
G)
BG very fast decay rate(yr -1)
0.250
0.275
0.300
H)
BG fast decay rate(yr -1)
0.070
0.075
0.080
0.085
0.090
I)
BG slow decay rate(yr -1)
0.00300
0.00325
0.00350
0.00375
0.00400
2000 2025 2050 2075 2100
Time period (years)

C-4 Relative effect of historical and projected FRI´s, without accounting for changes in temperature and precipitation effects on growth and decomposition, on mean C stocks (Mg C ha^{-1}, mean ± 95% CI) over 1000 replicate simulation runs of 120 years calculated at the end of each climatic period A: Historical/1980-2010, B: 2010-2040, C: 2040-2070, D: 2070-2100 (x-axes) and FRI pathway. A) Ecosystem C, B) Total DOM, C) Total live biomass, D) Organic layer, E) Woody debris and F) Mineral soil C stocks.