Research Article

Impact of Climate Change on Forest Fire Severity and Consequences for Carbon Stocks in Boreal Forest Stands of Quebec, Canada: a Synthesis

Simon van Bellen[1]*, Michelle Garneau[2], and Yves Bergeron[3]

[1]Chaire DÉCLIQUE UQAM-Hydro-Québec,
Institut des Sciences de l'Environnement and GEOTOP, Université du Québec à Montréal,
Succursale Centre-Ville, C.P. 8888, Montréal, Québec, H3C 3P8, Canada

[2]Chaire DÉCLIQUE UQAM-Hydro-Québec, GEOTOP and Département de Géographie,
Université du Québec à Montréal, Succursale Centre-Ville,
C.P. 8888, Montréal, Québec, H3C 3P8, Canada

[3]Chaire Industrielle CRSNG-UQAT-UQAM en Aménagement Forestier Durable,
Université du Québec en Abitibi-Témiscamingue,
445 boulevard de l'Université, Rouyn-Noranda, Québec, J9X 5E4, Canada

*Corresponding author: Tel.: 001-514-987-3000 #6680;
e-mail: van_bellen.simon@courrier.uqam.ca

ABSTRACT

The global boreal forests comprise large stocks of organic carbon that vary with climate and fire regimes. Global warming is likely to influence several aspects of fire and cause shifts in carbon sequestration patterns. Fire severity or forest floor depth of burn is one important aspect that influences both carbon emission during combustion as well as post-fire ecosystem regeneration. Numerous publications on projections of future area burned exist, whereas scenarios on twenty-first century fire severity are more scarce, and the stand-typical response to severe fire weather is rarely taken into account. This paper aims to synthesize knowledge on boreal forest carbon stocks in relation to changes in fire severity for Quebec, Canada. Besides warming, this region may be subjected to an important increase in future precipitation. Future fire severity and area burned may well increase as fire weather will be drier, especially near the end of the twenty-first century. Moreover, the fire season peak may shift towards the late summer. Intense burning will favour tree cover development while the forest floor carbon stock may become less important. As a result, total Quebec boreal carbon sequestration may diminish. The development of dynamic vegetation models may improve scenarios on twenty-first century changes in carbon sequestration driven by climate change and fire severity and frequency effects.

Keywords: boreal forest, carbon, climate change, eastern Canada, fire regime, fire severity, Fire Weather Index, forest floor

Citation: van Bellen, S., M. Garneau, and Y. Bergeron. 2010. Impact of climate change on forest fire severity and consequences for carbon stocks in boreal Quebec, Canada: a synthesis. Fire Ecology 6(3): 16-44. doi 10.4996/fireecology.0603016

INTRODUCTION

The boreal forest ecosystems (boreal forest, peatlands, and tundra) contain approximately 882 Pg of carbon (C) in living biomass, detritus, and soils (Apps *et al.* 1993), representing 49% to 64% of global forest C (Kasischke 2000, Lal 2005). Due to these important quantities, boreal ecosystems possess a potential to influence atmospheric composition by release of carbon dioxide (CO_2) and methane (CH_4) (Bonan *et al.* 1995). A 43 yr average C sequestration rate of 82 Tg ha^{-1} has been reported for boreal North America, despite net emissions in years with high fire activity (Balshi *et al.* 2007). Although forest stands occupy the largest area of the Canadian boreal region (304 × 10^6 ha), peatlands, covering 89 × 10^6 ha (Tarnocai 2006), represent 61% of the boreal C stock (Bhatti *et al.* 2003).

Boreal forest stands sequester C in biomass, forest floor, and mineral layer. Rates of sequestration are directly linked to four processes: 1) the rate of plant growth, including trees, shrubs and moss layer; 2) the rate of decomposition of organic matter; 3) permafrost formation; 4) fire frequency and severity (i.e., depth of burning) (Kasischke *et al.* 1995). These processes are influenced by climate and local landscape and soil factors in the long term, whereas other factors such as fires, insect outbreaks, diseases, droughts, and ice storms may alter C dynamics almost instantly. Wildland fire is the most important factor, due to its potential for direct C release through combustion and postfire C release resulting from enhanced decomposition. In addition, fire has an indirect effect on C budgets as it largely determines postfire stand regeneration potential (Lal 2005). Wildland fire intensity is highest in the northern boreal regions (Bergeron *et al.* 2004*b*), whereas insect outbreaks are concentrated in the southern mixedwood region (Gray 2008). Insect outbreaks may cause large forested regions to shift from C sinks to sources (Dymond *et al.* 2010).

At the stand scale, C stock distribution depends primarily on stand age and species composition (Nalder and Wein 1999, Tremblay *et al.* 2002), with the larger part of the stand C stocks typically present in the forest floor (Dixon *et al.* 1994, Gower *et al.* 1997). During fire events, forest floor C release has been estimated at 0.3 kg m^{-2} to 2.4 kg m^{-2} in central and western Canada (de Groot *et al.* 2009), to maxima of 0.6 kg m^{-2} to 5.7 kg m^{-2} per fire event in Alaskan black spruce (*Picea mariana* (Mill.) BSP) forest (Kasischke and Johnstone 2005) (Figure 1). The amount of C released by fire is typically much greater than the annual ecosystem C accumulation in absence of fire (potentially a factor 100, Figure 2), indicating the importance of fire on the boreal C stock. Mean surface fuel consumption per fire in Canada's boreal forest can be up to four times larger than crown fuel consumption (Amiro *et*

Figure 1. Recently burned boreal forest stand showing differential fire severity in the Eastmain region, Quebec (52°N, 76°W).

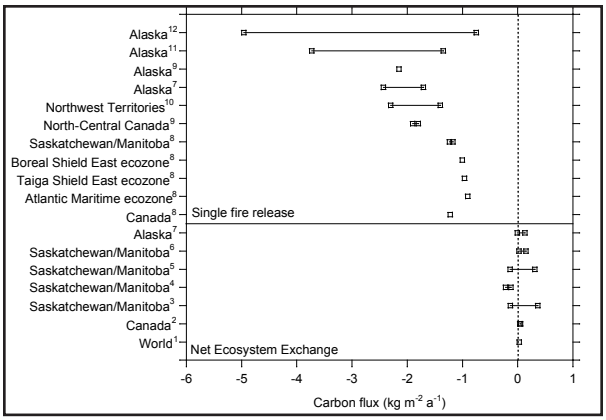

Figure 2. NEE and fire C fluxes for a number of boreal regions. [1]Pregitzer and Euskirchen (2004); [2]Kurz and Apps (1999); [3]Amiro *et al.* (2006); [4]O'Connell *et al.* (2003); [5]Bond-Lamberty *et al.* (2004); [6]Litvak *et al.* (2003); [7]French *et al.* (2003); [8]Amiro *et al.* (2001); [9]Turquety *et al.* (2007); [10]Stocks *et al.* (2004); [11]Tan *et al.* (2007); [12]Kasischke and Johnstone (2005).

al. 2001, Kasischke *et al.* 2005) and it is likely to be much more sensitive to changing climatic conditions than crown fuel consumption (Amiro *et al.* 2009). Moreover, the degree to which the forest floor is affected by burning influences secondary succession and thus C sequestration rates (Johnstone and Chapin 2006, Lecomte *et al.* 2006*a*, Johnstone *et al.* 2010). Hence, knowledge of shifts in potential forest floor consumption is essential for the evaluation of the global boreal C budget under changing climatic regimes.

Boreal forest fire occurrence is generally favoured by dry and warm meteorological conditions (Flannigan and Harrington 1988). Climate change is likely to significantly alter temperature and precipitation patterns at high latitudes (Solomon *et al.* 2007) as well as growing season length (Wotton and Flannigan 1993). The effect of climate change on fire frequency and area burned in boreal regions has been the subject of numerous publications (Bergeron and Flannigan 1995, Flannigan *et al.* 1998, Stocks *et al.* 1998, Flannigan *et al.* 2001, de Groot *et al.* 2003, Flannigan *et al.* 2005, Girardin and Mudelsee 2008, Flannigan *et al.* 2009, Krawchuk *et al.* 2009, Wotton *et al.* 2010). Most studies in Canada use the Fire Weather Index (FWI) to project either fire frequency or area burned. The FWI is composed of a number of indices that represent fuel moisture estimations based on meteorological observations (Van Wagner 1987). To obtain twenty-first century estimations, the FWI has been used in combination with general and regional circulation model (GCM and RCM) outputs. Other approaches used dynamic vegetation or C accumulation models combined with GCMs (de Groot *et al.* 2003, Balshi *et al.* 2009). Besides affecting boreal C stocks, changes in forest fire dynamics are likely to change forest management and fire protection strategies (Bergeron *et al.* 2004*a,* Flannigan *et al.* 2009).

The use of weather-based indices as the FWI in combination with GCM and RCM outputs does not take account of the effect of climate change on forest composition and age structure of the boreal biomes (Hély *et al.* 2001). The dominating scientific interest to obtain scenarios on area burned may be explained by estimations that changes in total future fuel consumption may be due to a change in area burned rather than to a change in fuel consumption density (Amiro *et al.* 2009). This paper aims to apply fire severity scenarios from Quebec to specific biomes and to estimate the effects on the boreal C stock. The proportion of Quebec boreal forest area touched by fire is 5 to 10 times lower than that of central and western Canada for the 1980-1999 period (Flannigan *et al.* 2009), primarily resulting from a more humid climate. Moreover, mean fire event C emissions for the Quebec ecozones have been estimated at around 1.0 kg m^{-2}, compared to 1.2 kg m^{-2} to 1.6 kg m^{-2} release of C from ecozones in central and western Canada (Amiro *et al.* 2001).

This paper has three main objectives: 1) summarizing the knowledge of boreal forest dynamics with respect to vegetation and forest floor C stocks; 2) identifying the influence of fire severity on boreal stand types and the con-

sequences for stand C stocks on different time scales; and 3) applying these dynamics to climate change scenarios to estimate potential changes in Quebec boreal biome C stocks for the mid- to late twenty-first century. Although peatlands in Quebec sequester important quantities of organic C (van Bellen *et al.* 2011), we focused on forests as these are more vulnerable to intense burning compared to the dominant unforested peatlands in Quebec.

QUEBEC BOREAL FOREST ECOZONES

The Quebec boreal forest covers two ecozones that are distinguished by abiotic and biotic factors (Wiken 1986). Latitudinal differences in boreal forest types are the result of postfire response; the various fire regimes being initially driven by zonal climate conditions (Payette 1992). As a result of these effects and varying with stand age, the ecozones show variations in vegetation (Table 1) and stand-typical patterns of C distribution (Table 2).

The southern Boreal Shield East covers the territory south of the fifty-second parallel and north of the Saint Lawrence River (Wiken 1986), and is characterized by closed-crown forest with both coniferous and deciduous species (Rowe 1972, Payette 1992, Saucier *et al.* 1998; Table 1). It is dominated in the south by balsam fir (*Abies balsamea* [L.] Mill.) stands with co-dominance of black spruce and white spruce (*Picea glauca* [Moench] Voss.) with paper birch (*Betula papyrifera* Marsh.) on mesic sites (Saucier *et al.* 1998). Northwards, black spruce stands with a forest floor cover of feathermoss (e.g., *Hylocomium* spp. Schimp.) are present (Saucier *et al.* 1998). Tree cover varies between 40% and 80% in mature stands. Understorey vegetation is present in the more open parts with bog Labrador tea (*Rhododendron groenlandicum* [Oeder] Kron & Judd), lowbush blueberry (*Vaccinium angustifolium* Aiton), and sheep laurel (*Kalmia angustifolia* L.) (King 1987). The mean annual temperature lies between 0 °C and -2.5 °C, and mean annual precipitation varies between 700 mm and 1100 mm (Saucier *et al.* 1998, Payette and Rochefort 2001), with the highest values in the eastern part of Quebec. Large differences in present-day (1920-1999) mean

Table 1: Importance of fuel types and mean forest floor C for the Quebec boreal ecozones (Amiro *et al.* 2009). Forest floor C stocks were calculated assuming 50% C in organic matter.

	Fraction of fuel type in each ecozone (%)						
Ecozone	**Spruce-lichen woodland**	**Boreal spruce**	**Mature jack pine**	**Immature jack pine**	**Deciduous**	**Mixedwood**	**Mean (kg C m^{-2})**
Taiga Shield East	71	28	---	---	---	---	1.72
Boreal Shield East	12	50	4	2	16	17	3.01

Table 2: Mean and range of forest floor and mineral soil organic C contents (kg m^{-2}) for various Quebec upland stand types in forest floor and mineral soil of the boreal biomes (Tremblay *et al.* 2002).

	Organic C content (kg m^{-2})					
	Deciduous	**Jack pine**	**Mixed**	**Balsam fir**	**Black spruce**	**Mean**
Forest floor	3.9 (0.8-12.8)	4.1 (0.7-11.6)	4.4 (1.3-10.6)	4.7 (1.6-11.8)	5.8 (1.0-12.3)	4.5 (0.7-12.8)
Mineral soil	6.5 (0.1-26.3)	4.4 (0.2-13.3)	5.9 (0.1-17.2)	6.6 (0.2-27.9)	6.0 (0-24.9)	6.2 (0-27.9)

fire cycles are present in this ecozone, varying from 398 yr (Bergeron *et al.* 2004*b*) to 191 yr and 521 yr in west and central Quebec (Bergeron *et al.* 2001). In the eastern part of Quebec, along the Labrador border, a fire rotation of 500 yr was ascribed to high amounts of precipitation and high peatland density functioning as fire breaks (Foster 1985). The length of the growing season lies between 145 days and 155 days (Gérardin 1980).

The northern Taiga Shield East extends roughly from the fifty-second parallel up to the tree line distribution and is dominated by open lichen woodland and a northern forest-tundra zone (Rowe 1972, Payette 1992, Saucier *et al.* 1998; Table 1). This ecozone is subdivided into lichen woodland and forest tundra based on differences in tree cover. Only the lichen woodland will be discussed here, as fires are very infrequent in the open forest-tundra, with fire cycles attaining 1460 years in northern sectors (Payette *et al.* 1989). Lichen woodland vegetation is dominated by black spruce, reindeer lichen (*Cladina* [Nyl.] Nyl.,), and cup lichen (*Cladonia* P. Browne) that dominate the forest floor (Payette 1992, Saucier *et al.* 1998). The tree cover ranges from 40% in the south to 5% at the transition to the forest-tundra. The mean annual temperature varies between -2.5 °C and -5.0 °C, with mean annual precipitation between 650 mm and 900 mm (Saucier *et al.* 1998, Payette and Rochefort 2001). The growing season covers 110 days to 125 days (Gérardin 1980). The lichen woodland is the biome that is most exposed to frequent burning, with an actual fire rotation period of approximately 100 yr in western Quebec (Payette *et al.* 1989). Due to the openness of the canopy, shrubs such as bog Labrador tea, resin birch (*Betula glandulosa* Michx.), sheep laurel, lowbush blueberry, and velvetleaf huckleberry (*Vaccinium myrtilloides* Michx.) are frequent (King 1987, Payette *et al.* 2000). Lichen generally cover the ground in stands exceeding 60 years of age, while mosses can be found under trees and in more recent burns (King 1987). In the southern part of the lichen-woodland, forming the transition to the closed-crown forest, denser black spruce stands with a preference for poorly drained soils are present (Girard *et al.* 2008). In contrast, in the northern part where longer fire cycles exist, black spruce populations remain marginal due to less frequent episodes of postfire seedling establishment and the gradual dependence on layering for reproduction. Discontinuous permafrost is limited to the northern part of the lichen woodland and becomes more important towards the forest-tundra (Allard and Seguin 1987).

FACTORS AFFECTING FOREST C STOCKS

Stand C contents are influenced by a great number of factors, e.g., climate (temperature and precipitation), stand age (Yu *et al.* 2002), past fire severity (Johnstone and Chapin 2006), prefire stand age (Johnstone 2006), dominant vegetation species, mineral substrate (Bhatti and Apps 2000), and the relative presence of overstorey, understorey, and moss layer. To estimate variability of the boreal C stock resulting from changes in climate and fire severity regimes, all of these factors need to be taken into account, except for the mineral substrate as it is not related to changes in climate.

Climate may largely control forest dynamics at the level of the various biomes, whereas the other factors affect C dynamics at the stand scale. Besides climate and change regimes, relatively stable factors such as mineral substrate and topography also influence C stocks by regulating drainage conditions. The interaction between climate and change factors results in great temporal and regional variations in C budgets within each biome. Influenced by climate gradients, C stocks decrease globally from the southern boreal biomes to the tundra (McGuire *et al.* 2002). Likewise, in Quebec, forest floor C stocks are higher in the southern Boreal Shield East ecozone than in the northern Taiga Shield East (Amiro *et al.* 2009; Table 1).

Besides spatial variations in C budgets, important temporal variations are present at the stand level. A stand C stock is the sum of organic C present in biomass, forest floor, and mineral layer. During stand development, the relative importance of these components varies by changes in environmental conditions, e.g., humidity and nutrient availability (Yu *et al.* 2002). For instance, a closed tree cover limits understorey development by providing low light conditions, whereas an important moss cover generally limits the potential for tree regeneration. Trees, shrubs, and mosses provide litter that is gradually incorporated into the forest floor, which may eventually represent the major part of the stand C stock (Nalder and Wein 1999). Floristic composition of black spruce stands has been shown to be a major factor influencing stand C sequestration rates, which correlate particularly well with bryophyte presence, especially sphagnum peat mosses (*Sphagnum* spp. L.) (Hollingsworth *et al.* 2008). Mosses actively regulate C cycling by their low thermal conductivity and high water-holding capacity, producing recalcitrant litter, and inhibiting seedling germination (Turetsky *et al.* 2010). Moreover, stands with important moss layers show higher resilience to changes in soil temperature and moisture associated with climate change (Turetsky *et al.* 2010). With increasing age, the major C stock generally moves from living biomass to the forest floor (Wardle *et al.* 1997, Lecomte *et al.* 2006*b*).

FIRE REGIME CONTROLS ON BOREAL FOREST C STOCKS

Fire type, intensity, severity, size, and frequency for a specific land unit are elements that define a fire regime (Heinselman 1981), and seasonality could be considered an important trait as well. Fire severity has been used in various senses, often indicating the degree of burning of a combination of vegetation layers (Conard *et al.* 2002, Kasischke *et al.* 2008). As we aimed to evaluate the effect on forest floor C stocks, we used the definition by Payette (1992), who considered fire severity as an indication of the proportion of the forest floor affected by fire as well as the ecological effects of fire on plant community and habitat. Fire frequency represents the number of fires per unit time in a given area, while a fire cycle is the time necessary to burn one time an area equal to the total area investigated (Payette 1992).

Fire Severity Control on Boreal Forest C Dynamics

Fire regimes have a very complex influence on boreal forest C stocks. Fire frequency and fire severity represent the most important factors of a fire regime. A low severity fire can be defined as a fire that potentially kills trees while leaving parts of the forest floor intact. High severity fires may burn the complete forest floor, leaving the mineral layer exposed (*sensu* Miyanishi and Johnson 2002). Frequently burning biomes will lose larger amounts of C and, therefore, C stocks will be limited, while severe fires will cause a relatively great C loss per event. In addition, the complexity of the vegetation reaction on differential fire severity needs to be taken into account. By influencing regeneration potential, stands that burn severely will re-establish and sequester C in a different way and at a different rate than stands that are only slightly affected by fire.

Carbon can be released to the atmosphere through burning of the biomass or smouldering of the forest floor (Johnson 1992). As crown fires are the dominant fire type in North America (Johnson 1992), the total C emission depends primarily on how much C is released from the forest floor (Amiro *et al.* 2009). The forest floor is constituted of a litter (L) layer and two duff (F, upper duff, and H, deeper duff) layers. Van Wagner (1987) assigned typical bulk densities for litter of 21 kg m^{-3}, for upper duff of 71 kg m^{-3}, and 139 kg m^{-3} for

deeper duff. The importance of fire severity is illustrated by the dominant C concentration gradient; i.e., C density increases downward into the organic soil (Kasischke *et al.* 2005). Hence, as the depth of burn increases, the loss of C to the atmosphere increases nonlinearly. The duff moisture content, duff thickness, and bulk density are major factors determining fire consumption potential (Van Wagner 1972, Miyanishi and Johnson 2002). However, potential duff consumption decreases with increasing bulk density due to its limiting effects on heat transfer during smouldering, the low levels of oxygen present in compacted fuel, and the fact that denser duff dries more slowly (Miyanishi and Johnson 2002). Differences in bulk density imply a shorter drying period for the loosely compacted organic duff and a longer one for the compacted duff (Van Wagner 1987). In forested regions with discontinuous permafrost, permanently frozen soils affect C storage in forest floor and soil as well as fire severity, especially when a thick sphagnum peat moss cover is present (Shetler *et al.* 2008, Turetsky *et al.* 2010). Permafrost aggradation typically generates an important accumulation of organic matter as poor drainage and cool conditions inhibit decomposition. As these humid, thick mats are relatively resistant to combustion, permafrost aggradation limits fire severity (Harden *et al.* 2006).

Fire Severity and Postfire Effects on C Stocks

Postfire vegetation and forest floor development are related to preceding fire severity (Viereck 1983, Nalder and Wein 1999, Kasischke and Johnstone 2005, Lecomte *et al.* 2005). Generally, a remaining organic soil limits postfire vegetation growth. Therefore, more severe burning increases the range of postfire vegetation types within the potential of the site (Johnstone and Chapin 2006). In addition, both fire severity and postfire climatic conditions influence the soil thermal and moisture regime for decades after fire, thereby influencing soil decomposition rates (Bergner *et al.* 2004, Kasischke and Johnstone 2005). Nevertheless, the influence of fire severity on tree recruitment depends on landscape characteristics, including drainage and pre-fire organic layer depth. As the length of a fire cycle can be close to the length of most boreal tree species' life spans, the first-arriving tree species can remain dominant within its stand. In boreal Canada, early successional jack pine (*Pinus banksiana* Lamb.) and black spruce typically establish within three to nine years after fire (DesRochers and Gagnon 1997, Gutsell and Johnson 2002). Jack pine as well as quaking aspen (*Populus tremuloides* Michx) establish easily on thin duff forming warm and dry forest floors under high light conditions (Chrosciewicz 1974, Comtois and Payette 1987, Bonan and Shugart 1989, Yu *et al.* 2002, Lecomte *et al.* 2005), while more shade-tolerant black spruce grows moderately well on remaining duff horizons (Johnson 1992) and on dry, rocky outcrops (Asselin *et al.* 2006). Balsam fir is a late-successional species not adapted to fire that shows greatest potential in mesic stands that develop from mixedwood stands (de Groot *et al.* 2003, Messaoud *et al.* 2007). Sites that develop after deep burning are advantageous to jack pine establishment and will develop thin forest floors with low C contents, whereas the overstorey constitutes a relatively important C stock (Figure 3). Jack pine stands are generally replaced by more tolerant species after 100 yr to 150 yr (Cayford and McRae 1983, Smirnova *et al.* 2008). When fire cycles exceed this period, replacement of a postfire cohort by a late-succesionnal stage is common. This is characteristic for the closed-crown forests of western Quebec (Bergeron *et al.* 2004*b*) where, on a centennial scale, vegetation assemblages tolerant to moist conditions (e.g., sphagnum mosses) may establish while canopy opens after death of the postfire tree cohort (Taylor *et al.* 1988, Lecomte *et al.* 2005). Sites with a moderately thick remaining forest floor are predominantly occupied by black spruce

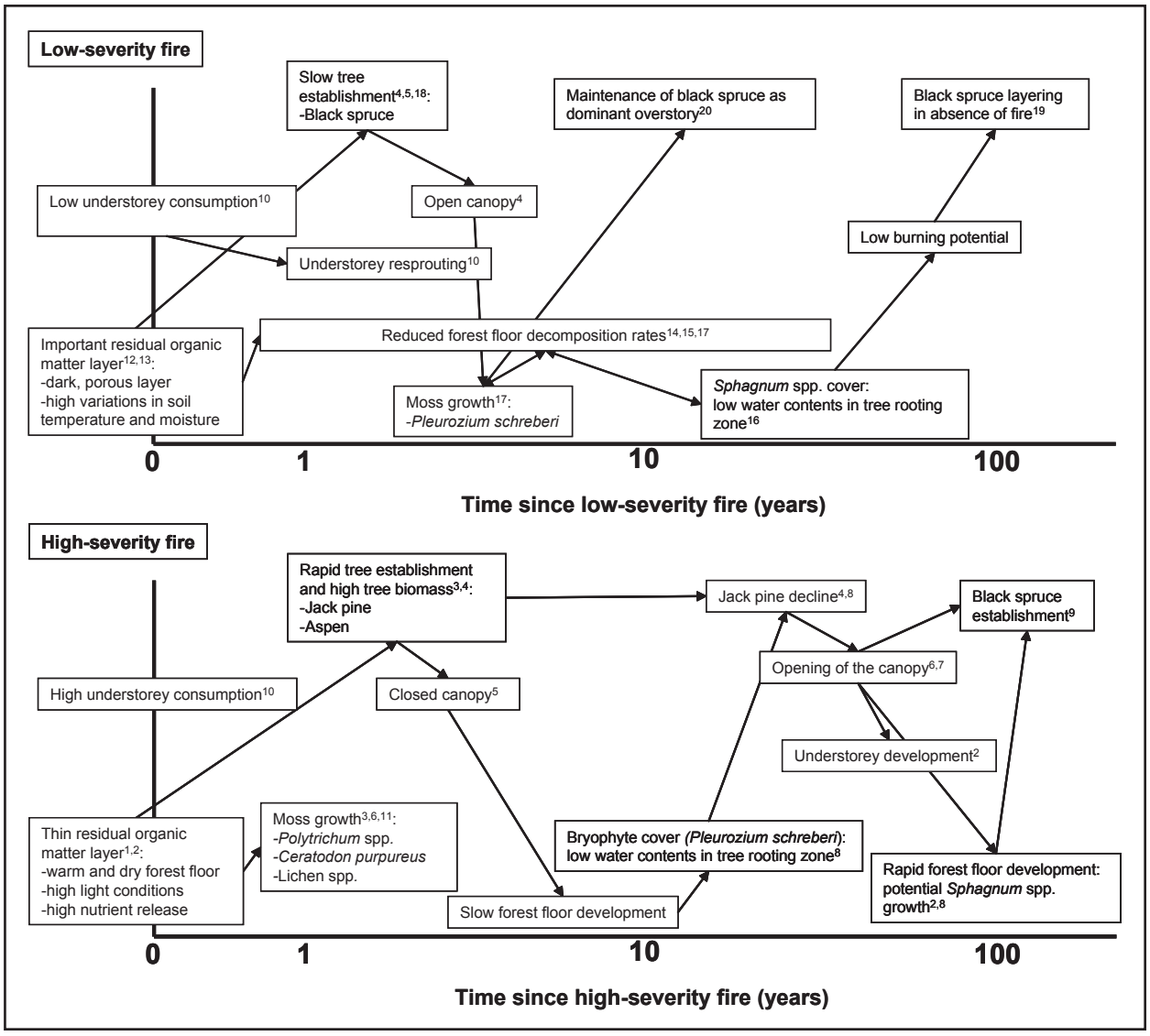

Figure 3. Scenarios of stand development patterns and processes after high-severity and low-severity fires. Numbers refer to publications: [1]Bonan and Shugart (1989), [2]Lecomte *et al.* (2005), [3]Foster (1985), [4]Lecomte *et al.* (2006*b*), [5]Johnstone and Chapin (2006), [6]Cayford and McRae (1983), [7]Smirnova *et al.* (2008), [8]Taylor *et al.* (1988), [9]Lecomte and Bergeron (2005), [10]Schimmel and Granström (1996), [11]Wang and Kemball (2005), [12]Duchesne and Sirois (1995), [13]Charron and Greene (2002), [14]Zoltai *et al.* (1998), [15]Yu *et al.* (2002), [16]Fenton *et al.* (2005), [17]Oechel and Van Cleve (1986), [18]Chrosciewicz (1974), [19]Morneau and Payette (1989),[20]Payette *et al.* (2000).

(Figure 3). The growth of deciduous trees on these sites is very limited because of their inability to establish on organic soils (Johnstone and Chapin 2006). If rhizomes remain alive in the organic soil layer, the understorey may resprout. Due to the resulting relatively open canopy, the forest floor can develop rapidly. In stands where sphagnum mosses are able to establish, forest floor decomposition rates will remain low and an open canopy may be maintained (Fenton *et al.* 2005). Thus, relatively large amounts of C will be stored within the forest floor compared to the tree layer. If fires remain absent for a long period, black spruce can persist by layering, at least in moderately drained forest floors (Paquin *et al.* 1999). In addition, patches with sphagnum moss rarely burn, thereby forming an effective shield

against subsequent fires once dominant, as well as a positive factor for long-term C sequestration (Shetler *et al.* 2008).

Fire severity influences the local C stock on long time scales by providing advantages to some vegetation types while limiting others. Fire frequency should be taken into account as it determines the maximum period of vegetation development and thus C accumulation pattern resulting from the severity of the last fire. Lecomte *et al.* (2006*b*) demonstrated that forest floor thickness and standing tree biomass values of an old (>250 years) stand resulting from a severe fire can be similar to that of younger (<150 years) stands established after a low-severity fire. More generally, stand age has highly significant effects on both vegetation biomass and forest floor C contents (Wang *et al.* 2003). Thus, fire severity may be an important factor in determining long-term C dynamics in boreal forests only if local fire frequencies are sufficiently high to prevent a stand from developing an identical postfire vegetation structure after both high- and low-severity fires. However, large-scale distribution of the Quebec boreal biomes is at least partly the result of variations in fire regimes, including both fire severity and fire frequency as important components. Payette (1992) stated that the lichen woodland is a stable ecosystem with characteristic vegetation that can exist as small patches within the closed-crown boreal forest under the same fire regimes and climate conditions. This, and the fact that most species that establish immediately after fire can remain dominant for 250 years in the absence of fire in various biomes (Morneau and Payette 1989, Sirois and Payette 1991), show that it is important to acknowledge the influence of fire severity, even when fire cycles are long.

Fire severity is not tightly linked to fire frequency as fire frequencies are primarily determined by climate conditions (Flannigan *et al.* 2001), while climate only affects fire severity in an indirect way. As fire severity typically varies both between and within stands, small-scale factors such as moss cover type, forest floor bulk density and moisture content, and thickness of the duff layer may be more important (Miyanishi and Johnson 2002, Greene *et al.* 2007, Shetler *et al.* 2008). Thus, a site that burns very infrequently can burn deeply into the duff layer if this layer has very low moisture content. For all that, stand burning frequency negatively affects the depth of the remaining forest floor after fire. The influence of frequency on postfire community composition may be even stronger than other environmental factors such as soil texture, elevation, or insolation (Johnstone 2006). Sites that burn infrequently, e.g., as found in the Quebec closed-crown forest, often possess relatively high quantities of coarse woody debris and thick, humid forest floors and that prevent deep burning (Foster 1985, Johnstone 2006). On the other hand, the link between fire severity and fire frequency is perturbed by climate conditions (i.e., temperature and precipitation), postfire vegetation species, and mineral soil type. These factors determine the potential pathways of postfire vegetation establishment, so fire severity and frequency need to be regarded separately when considering C dynamics.

INFLUENCE OF STAND AGE, CLIMATE, AND FIRE SEVERITY ON BOREAL C STOCKS

To estimate the effect of changes in fire severity on the total C storage in the boreal forest, there is a need to quantify C stocks for the components (plant biomass and forest floor) that constitute the boreal forest ecosystem. As one of the objectives of the study was to estimate long-term changes in boreal C stock, the typical C stock for each stand type needed to be linked to the potential shifts in stand characteristics.

Stand Age Effects on Boreal C Stocks

Generally, tree biomass C increases with time for various tree species (Gower *et al.*

1997, Nalder and Wein 1999, Yu *et al.* 2002, Lecomte *et al.* 2006*b*) until a decline in tree production occurs due to a poor regeneration potential after postfire stand break-up (Lecomte *et al.* 2006*b*). The onset of tree C accumulation rate slowdown depends on the initial growth rates (Gower *et al.* 1997) and the previous fire severity (Lecomte *et al.* 2006*b*). The effect of stand break-up on the stand C budget is complex. Snags may initially decompose at very low rates, remaining standing for 20 years after fire, while fallen logs may decompose very slowly as they become part of the humid forest floor (Nalder and Wein 1999). However, important decay of coarse woody debris has been shown to be a major factor affecting stand C budgets (Mkhabela *et al.* 2009). In jack pine stands, C contents of moss and lichen show strong linear increases with time in stands up to 150 years (Nalder and Wein 1999). In addition, forest floor C contents are highly correlated with stand age (Paré *et al.* 1993, Nalder and Wein 1999, O'Neill *et al.* 2006). Coarse woody debris is high immediately after stand establishment, but its importance diminishes quickly with time (Yu *et al.* 2002). However, woody debris can increase again when stands break up or when self-thinning occurs, as in aspen and pine stands. Lecomte *et al.* (2006*b*) showed that even 700 yr old stands potentially still accumulate total biomass by increasing forest floor C, while tree biomass C remains relatively constant in black spruce-feathermoss stands of northwestern Quebec. Gower *et al.* (1997) found two mature black spruce stands (115 to 155 years) containing 44.6 kg m^{-2} to 247.9 kg m^{-2} of total ecosystem C, while young (25 yr to 65 yr) jack pine stands showed values of 5.1 kg m^{-2} to 7.6 kg m^{-2}. However, it is uncertain if the latter findings can be attributed solely to variations in stand age, because other factors such as anterior fire severity and dominant species vary as well. Wardle *et al.* (2003) indicated that the absence of fire causes a decrease in decomposition rates that acts before the decline in ecosystem productivity on millenium-scales on lake islands in boreal Sweden. Yet it may be difficult to extrapolate these trends to a global scale, as boreal fire frequencies are much higher in North America.

Climate and Soil Effects on Boreal C Stocks

Temperature and precipitation are the most important direct climatic variables influencing C accumulation patterns, whereas permafrost as a function of climate conditions has an effect on soil C sequestration as well. Comparing these variables, high temperatures causing high litter production rates may be of greater importance than high precipitation values maintaining low decomposition rates, as suggested by high C accumulation rates in relatively warm forest floors in quaking aspen stands (Nalder and Wein 1999, Yu *et al.* 2002). However, Simmons *et al.* (1996) and Gower *et al.* (1997) found higher C stocks in stands in a cooler climate in Maine and in Saskatchewan and Manitoba respectively, while other factors remained relatively constant. These differences in forest floor C content along climatic gradients may be explained by species-specific differential growth and decomposition response to varying climates.

Wang *et al.* (2003) studied C distribution chronosequences of wet and dry black spruce stands in northern Manitoba, Canada. Comparing stands under similar climatic conditions, dry sites show greater vegetation biomass (including overstorey, understorey, and ground cover biomass) than wet sites. Nonetheless, understorey and bryophyte biomass, as well as the forest floor C pool, are greater in wet stands. Considering total postfire biomass development, dry sites accumulate C at higher rates and peak at a higher level than wet sites (Wang *et al.* 2003). An inversed pattern was found in quaking aspen stands in the same region. Mean annual temperature was highly positively correlated while precipitation was negatively correlated with forest floor C (Nalder and Wein 1999), suggesting that warm and

dry regions that produce high amounts of litter may be advantageous to forest floor C in stands dominated by quaking aspen. Thus, the reaction of C allocation to climate may depend on dominant vegetation species.

Fire Severity and Species Effects on Boreal C Stocks

Species effects on C contents in the boreal forest are highly influenced by past fire severity as fire severity has a strong effect on postfire vegetation re-establishment. Forest floor C was found to be higher in quaking aspen than in jack pine stands (Nalder and Wein 1999) but black spruce-feathermoss stand forest floor C contents generally exceed those of quaking aspen stands (Yu *et al.* 2002). Jack pine stands often establish after a severe fire that removes all organic material from the forest floor. Although Nalder and Wein (1999) did not measure for past fire severity, the assumed species effect on stand C stocks might be caused by differential fire severity, given the strong link between fire severity and postfire tree species establishment. This is strengthened by the fact that the studied stands were from the same climatic region. High fire severity causes a high initial C accumulation in the overstorey but an earlier break-up of the tree canopy (Lecomte *et al.* 2006b). This break-up may cause a decline in long-term litterfall and a decrease in forest floor accumulation. A bryophyte layer that covers the forest floor positively influences C accumulation. In addition, bryophyte covers benefit from large amounts of overstorey and shrub C, as dense tree covers or shrub layers cause shading conditions favouring feathermoss (e.g., [Schreber's big red stem moss (*Pleurozium schreberi* {Brid.} Mitt.]), after which *Sphagnum* spp. can establish (Figure 3). Nalder and Wein (1999) found a highly positive link between tree and forest floor C, which was explained by the higher litterfall from developed overstorey.

Do stands that establish after a low-severity fire generally incorporate higher amounts of C than those developed after high-severity fire if other factors (e.g., climate) are constant? An increase in ecosystem C after a low-severity fire is possible if the impact of thicker forest floors on stand C sequestration compensates for the consequent lower values in tree biomass C. Considering the high C contents in sphagnum moss, forest floors, or peat accumulation compared to black spruce stand tree biomass (Gower *et al.* 1997), this seems indeed probable. This is supported by additional forest floor C data. Wirth (2005) found an average around 2.0 kg m^{-2} of tree biomass C and 5.0 kg m^{-2} of organic layer C for a variety of stand types in central Canada; while, for the same region, Bhatti and Apps (2000) reported mean values of around 4.5 kg m^{-2} and 3.7 kg m^{-2}, respectively. Other studies obtained young jack pine stand tree C contents of 1.2 kg m^{-2} and 0.8 kg m^{-2} with corresponding forest floor C contents of 1.8 kg m^{-2} and 4.0 kg m^{-2} (Gower *et al.* 1997). Old jack pine stands showed overstorey C contents ranging from 3.1 kg m^{-2} to 2.3 kg m^{-2}, while forest floor C contents were 1.5 kg m^{-2} and 1.2 kg m^{-2}, respectively. The total stand C contents from Nalder and Wein (1999) were 4.0 kg m^{-2} for jack pine trees and 1.3 kg m^{-2} for corresponding forest floors; mean quaking aspen tree C contents were 5.5 kg m^{-2} while the forest floor contained 2.8 kg m^{-2}. The fact that paludification is a potential process in forests on fine-textured soils that lack fire for a long period (Fenton *et al.* 2005) justifies the comparison of potential forest floor C stocks with peat C contents. Peat accumulations of 2.3 m thickness typically constitute a C stock of 133 kg m^{-2} (Gorham 1991), indicating the potential for large total boreal stand C stores once a thick sphagnum cover is present (Shetler *et al.* 2008, Turetsky *et al.* 2010).

In short, old stands that developed after shallow burning and that possess thick forest floors with a bryophyte cover and an overstorey typically characterized by black spruce (Van Cleve *et al.* 1983) contain large amounts of C. In contrast, young stands that are char-

acterized by a jack pine cover resulting from severe burning and a shallow forest floor contain less ecosystem C.

THE USE OF FWI IN PROJECTING FIRE SEVERITY

The FWI index is based on both the moisture content of the different forest floor horizons, and fire behaviour indices such as rate of spread, weight of fuel consumed, and fire intensity (Van Wagner 1987). Although plant death and fire spreading rates depend to a great extent on the intensity of the fire, the FWI cannot directly be used in estimating the fire severity, i.e., the depth of burning into the forest floor, because fire severity is related to some specific characteristics of the forest floor such as density and thickness (Miyanishi and Johnson 2002). The FWI includes the fine fuel moisture code (FFMC) for litter and fine fuel moisture contents, the duff moisture code (DMC) for the upper duff layer, and the drought code (DC) for the more compact lower duff. High temperatures or low precipitation generally cause an increase in fire danger, reflected by high code values. The FFMC, DMC, and DC have different drying rates, showing a predictable response to drying and wetting (Miyanishi and Johnson 2002; Table 3). The DMC and DC indirectly reflect the potential for deep smouldering.

Linking FWI Components to Forest Floor Moisture Contents

The FWI has been developed to represent the moisture content of forest floors in a mature, closed-canopy pine stand (Van Wagner 1987, Wotton and Beverly 2007). Nevertheless, the relation between moisture code values and forest floor moisture content is nonlinear, varying with stand type, stand density, and season (Wotton and Beverly 2007, Wotton 2009). The FFMC and DC calibration curves have been constructed to link FWI values to litter and deep duff moisture contents, respectively, for various biome characteristics (Lawson and Dalrymple [1996] for DC values; Wotton and Beverly [2007] for FFMC values). However, the DC calibration curves from Lawson and Dalrymple (1996) are limited to forest types rare or absent in Quebec (e.g., coastal British Colombia cedar-hemlock forests). Wotton and Beverly (2007) provided calibration curves for a variety of stand densities and forest types as well as seasons (Figure 4). The FFMC has been shown to represent particularly well fire occurrence, whereas the DMC and DC better indicate fire sustainability (Van Wagner 1987, Wotton *et al.* 2010). The FFMC calibration curves show large differences in litter moisture contents, especially when FFMC values are low. Under uniform FFMC conditions, mixedwood stands, found at the southern edge of the Quebec closed-crown forest, have high litter moisture contents compared to open-canopy lichen woodlands. At the wet side of the range of weather conditions (e.g., a FFMC of 75; Wotton and Beverly 2007), the litter moisture content varies from 55.6% (dense spruce stands) to 26.9% (open spruce stands), resulting from varying stand density.

The variability in moisture contents has implications for the expected fire severity in the various stand types in the boreal forest. A

Table 3. FWI code characteristics.

Code	Timelag (days)	Water capacity (mm)	Nominal fuel depth (cm)	Nominal fuel load (kg m^{-2})
FFMC	⅔	0.6	1.2	0.25
DMC	12	15	7	5
DC	52	100	18	25

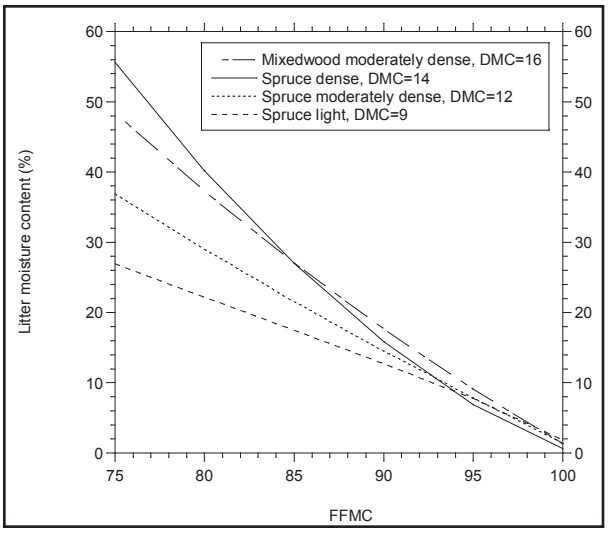

Figure 4. FFMC to observed litter moisture content calibration curves for Quebec mixedwood and spruce stands of various densities (equations from Wotton and Beverly 2007). The FFMC range corresponds to potential fire spread values. The DMC varies between stand types according to July normals.

decrease in the mean FFMC (indicating more frequent wet conditions) would have a greater impact on dense mixedwood stands, as these stands will retain litter moisture for a relatively long time. In contrast, open pine and spruce stands during spring, when understorey is poorly developed, show only a very slight increase in the litter moisture contents with diminishing FFMC, indicating that these stands cannot retain high moisture amounts even under humid conditions. In addition, variable humidity of the underlying duff layer likely mediates the nonlinear relation between moisture contents and FFMC values (Wotton and Beverly 2007). This implies that, under a changing climate regime, the fire severity regime would remain relatively stable in open pine and spruce forests compared to the more sensitive dense mixedwood forests.

The FFMC in Quebec generally diminishes during the fire season, with higher starting values but a larger decrease in the southern boreal forest as compared to the northern part of Quebec (Amiro *et al.* 2004) (Figure 5). Thus, depending on the drying rates of the specific soil types, spring forest floor moisture is generally low but increases during the summer. The DMC values fluctuate strongly during the fire season, implying a great sensitivity to weather conditions, with general highest values, in May (southern Quebec) and June (northern Quebec) (Amiro *et al.* 2004). Finally, the deep duff layer moisture content (represented by the DC) varies only slightly with weather but has a more or less continuous decreasing trend during the fire season with the lowest moisture contents in August (McAlpine 1990, Miyanishi and Johnson 2002, Amiro *et al.* 2004, Girardin *et al.* 2004). This indicates a high probability of deep burning later in the fire season

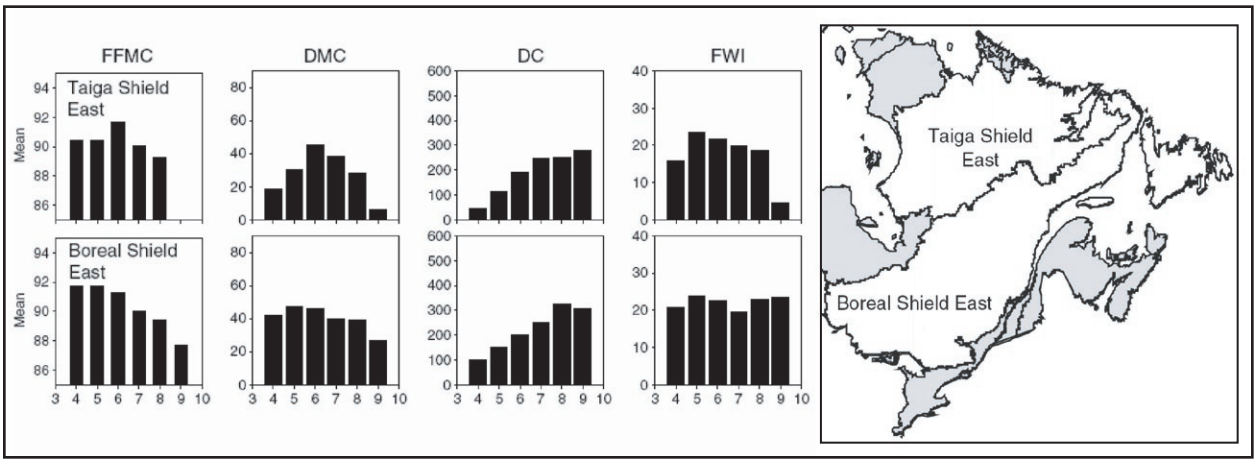

Figure 5. Mean monthly values of the FWI components and the FWI (3 = March, 10 = October) (Amiro *et al.* 2004) in the two eastern Canadian ecozones, redrawn from Amiro *et al.* (2009).

(Amiro *et al.* 2004, Amiro *et al.* 2009). In addition, deep duff is highly influenced by local drainage as precipitation may not be able to percolate downwards (de Groot *et al.* 2009). Van Wagner (1987) and Lawson and Dalrymple (1996) also reported the importance of the autumn moisture contents on the next spring's DC, depending on winter temperature and precipitation as well as on site characteristics.

The differences in forest floor drying patterns have important implications for spatial and temporal patterns of severe fire occurrence. First, stands that have shallow forest floors (e.g., pine stands) have high drying rates of both litter and duff and will therefore be susceptible to deep burning early in the fire season when both litter and duff moisture contents are low. In these stands, the potential for high-severity fires is spread relatively uniformly during the fire season as it takes only a couple of days without precipitation to create circumstances prone to high-severity fire. In contrast, stands with thick forest floors (e.g., spruce stands), and thus a thick duff layer, dry substantially only at the end of the fire season, so deep burning is temporally limited to this period. Summer precipitation is likely to be less important than snowmelt for the deep duff moisture contents, but drying rates of litter in thick forest floors may be difficult to estimate. Data from Wotton and Beverly (2007) show a slightly higher litter moisture content in black spruce stands compared to equally dense pine stands under equal FFMC and DMC. Duff moisture variation is also found within stands as duff generally contains less water if positioned under tree crowns compared to duff in gaps. Miyanishi and Johnson (2002) explained this as the result of the interception of precipitation and the lower amounts of dew formed under trees. This is reflected by the findings that duff consumption by fire often shows a patchy distribution, with the largest removal around tree bases that were alive at the time of fire. Nevertheless, Greene *et al.* (2007) attributed this pattern to a lower heat loss to evaporating water adjacent to tree boles. Inversely, low moisture amounts in litter were found in stands with an open canopy, and this effect is stronger under humid conditions (Wotton and Beverly 2007). The differences between the contrasting relative positions of humid litter and humid duff within a stand may cause different forest floor consumption patterns within and between stands.

Tree Layer versus Forest Floor Sensitivity: the Effect on Forest Floor Moisture

In a changing climate, spatial and temporal temperature and precipitation patterns, as well as the occurrence and severity of fire, are changing. It is important to evaluate to what extent different vegetation patterns can exist under the influence of changing climate circumstances. Jasinski and Payette (2005) concluded that vegetation patterns are primarily determined by the fire history, and that edaphic conditions are not necessarily a determinant factor as different forest types can exist under the same climatic and environmental conditions. This is supported by the findings that changing vegetation zones on a small scale do not seem to be limited to specific edaphic conditions (Payette *et al.* 2000). The effect of a changing climate will most probably cause a latitudinal shift in biome distribution linked to changing fire regimes. In identifying the effect of changes in climatic conditions on fire severity, it is critical to estimate the change in forest type and vegetation composition and structure, as these mediate the climatic influence on forest floor moisture contents (Girardin and Mudelsee 2008). In other words, the specific moisture codes may be substantially higher (implicating drier forest floor layers) in a changing climate, but if the importance of each forest component (e.g., overstorey, understorey, and forest floor) changes, litter moisture contents may well become higher, thereby decreasing local potential fire severity (Wotton and Beverly 2007). Yet a change in forest

structure cannot be projected without taking into account future fire severity. This is elaborated in an example where we regard fire severity and climate as two variables that are linked only to the FFMC. Although the FFMC is supposed to represent litter moisture content and is not linked to duff layers, it was shown to be the principal variable explaining forest floor consumption in upland spruce-lichen woodlands (de Groot *et al.* 2009). In the hypothetical case of a substantial warming without any change in precipitation, mean FFMC values will increase as the weather conditions will dry out the litter layer. Increasing code values generally indicate a higher potential (expressed as either intensity or frequency) for litter burning. At the same time, the increase in temperature causes an increase in tree regeneration potential or tree production (Bergeron 1998), which corresponds to the large-scale boreal forest tree production pattern on the latitudinal gradient if fire regime effects are kept out of consideration. As a result, potential tree stand density increases. From this point, two effects are possible (Figure 6): 1) if the increase in tree density due to the warming is more important than the increase in mean FFMC, the litter moisture content will increase, causing a decrease in potential fire severity; and 2) if the increase in FFMC is more important than the increase in tree density due to the warming, the litter moisture content will decrease, causing an increase in potential fire severity.

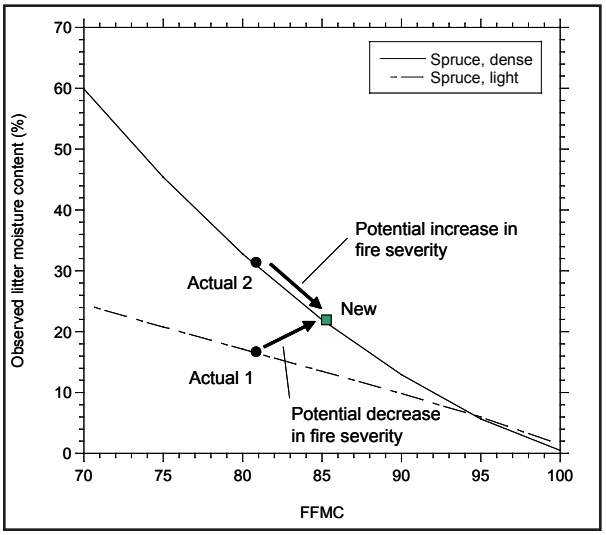

Figure 6. FFMC—Observed litter moisture calibration diagram for dense and open spruce stands (Wotton and Beverly 2007).

In situation 1, the decrease in fire severity will have its proper effect on tree density. One could hypothesize that, in the long term, the decrease in fire severity will lead to thicker forest floors and an opening of the forest canopy, which would eventually result in a decrease in observed duff moisture contents if climate (and thus the mean FFMC) remains stable. In situation 2, an increase in fire severity can result in increased tree productivity with more abundant closed canopies. While climate and FFMC remain stable, the litter layer will become more humid. Situation 1 may be typical for an ecosystem where tree growth is currently strongly limited by temperature, as in the northern forest-tundra (Payette 1992, Lloyd *et al.* 2005). Situation 2 may be found in the southern boreal forest, where tree reproduction is already high and canopy closure is close to complete. These examples show that, on a large scale, a change in climate and FWI can eventually lead to a typical fire severity status with a stable vegetation pattern, but the pathways and stable configuration may vary per ecosystem.

CHANGES IN FIRE SEVERITY AND CLIMATE IN QUEBEC BOREAL FORESTS

We compared data from recent publications to derive twenty-first century temperature and precipitation projections for three regions in Quebec (Tables 4 and 5). The 50 °N latitude corresponds to the Boreal Shield East; 53 °N and 56 °N represent Taiga Shield East latitudes. Fire regime changes for the two Quebec boreal ecozones are shown in Table 6.

Table 4. Mean temperature change (%) at variable latitudes according to climate scenarios.

Publication	Reference and projection period	Summer temperature (°C)			Winter temperature (°C)		
		50°N, 74°W	53°N, 74°W	56°N, 74°W	50°N, 74°W	53°N, 74°W	56°N, 74°W
Price *et al*. (2001)	1961-1990 to 2041-2070	+2.5	+3.2	+3.2	+3.1	+4.0	+6.0
Plummer *et al*. (2006)	1971-1990 to 2041-2060	+2.4	+2.6	+2.7	+2.5	+4.0	+5.5
IPCC (2007)	1980-1999 to 2080-2099	+3.5	+3.3	+3.2	+6.0	+6.8	+7.5

Table 5. Mean precipitation change (%) at variable latitudes according to climate scenarios.

Publication	Reference and projection period	Summer precipitation (%)			Winter precipitation (%)		
		50°N, 74°W	53°N, 74°W	56°N, 74°W	50°N, 74°W	53°N, 74°W	56°N, 74°W
Price *et al*.(2001)	1961-1990 to 2041-2070	+2	+13	+15	+1	+13	+12
Plummer *et al*. (2006)	1971-1990 to 2041-2060	+7	+10	+12	+4	+15	+25
IPCC (2007)	1980-1999 to 2080-2099	+2	+7	+10	+26	+32	+38

Table 6. Fire regime scenarios for the Quebec boreal ecozones.

Publication	Ecozone	Period	
		2040-2060	2080-2100
Flannigan *et al.* (2001)	Taiga Shield East	~15 % decrease in area burned	No data
	Boreal Shield East	~50 % increase in area burned (south) to ~10 % decrease in area burned (north)	No data
Flannigan *et al.* (2005)	Taiga Shield	No data	111 % to 112 % increase in area burned
	Boreal Shield East	No data	64 % to 73 % increase in area burned
Amiro *et al.* (2009)	Taiga Shield East	4 % increase in mean forest floor fuel consumption (kg m^{-2})	13 % increase mean forest floor fuel consumption (kg m^{-2})
	Boreal Shield East	5 % increase in mean forest floor fuel consumption (kg m^{-2})	13 % increase in mean forest floor fuel consumption (kg m^{-2})
Le Goff *et al.* (2009)	Boreal Shield East (Waswanipi area)	4 % increase in annual area burned; 22 % decrease in fire risk in May. Increase in fire risk in June (4 %) - August (25 %) [a]	7 % increase in annual area burned; 20 % decrease in fire risk in May. Increase in fire risk in June (10 %) - August (109 %) [a]

[a] Scenarios for 2030-2060 and 2070-2100.

Changes in the Boreal Shield East Ecozone

The boreal forest dynamics of the southern part of this ecozone are mediated by factors that are independent of climate regime. The presence of lakes and a pronounced topography that influence potential fire size, as well as the abundance of deciduous species that lowers potential fire severity, has been shown to be positively correlated with balsam fir presence in western Quebec (Bergeron *et al.* 2004*b*). In the northern closed-crown forest, balsam fir stands may establish where quaking aspen and paper birch dominate the postfire stand (Messaoud *et al.* 2007), e.g., after a high-severity fire that removes all or most of the organic soil (Bourgeau-Chavez *et al.* 2000), or on outcrops with shallow tills (Bergeron 1998). In contrast, balsam fir is limited where black spruce dominates because of generally lower temperatures and frequent presence of humid and thick forest floors (Harper *et al.* 2003, Messaoud *et al.* 2007). On the stand scale, forest floor moisture contents in closed black spruce-balsam fir stands are relatively high (Hare 1950). High amounts of deep duff moisture in spring cause a low potential for severe burning, while in the late summer, potential fire severity increases due to continuous drying of the deep duff.

The twenty-first century climate change may well affect the Boreal Shield East biomes (Table 4 and 5). Around 2050, mean summer temperatures may have risen by 2.5 °C, whereas a 3.5 °C increase is possible at the end of the century. Mean winter temperature increases may be even more drastic. However, scenarios show that winter precipitation will increase 1% to 26% for mid- and late twenty-first century, respectively. Summer precipitation could increase as well (2% to 7%), but a long-term tendency is less clear.

Mean forest floor fuel consumption may increase with 5% to 13% for 2040-2060 and 2080-2100, respectively (Amiro *et al.* 2009). The mixedwood forest floor consumption model (de Groot *et al.* 2009) that is based on both experimental burning and wildfire data is particularly useful for the southern Boreal Shield East ecozone typified by thick forest floors. The optimal model for mixed stands is especially sensitive to the pre-burn forest floor fuel load, showing a positive relationship between forest floor consumption and fuel load. Hence, as a warmer and wetter climate may cause a more efficient accumulation of organic matter, more severe burning may have a partially limiting effect on long-term forest floor thickness and C stock. The model for dense spruce stands is less reliable as no single variable in the FWI appeared significant affecting fuel consumption.

Flannigan *et al.* (2001) projected high spatial variability in the area burned in the 2040-2060 scenario for this ecozone, with high increases in the south but slight decreases in the northern part, whereas Flannigan *et al.* (2005) obtained scenarios that showed a 63% to 72% increase in future area burned for 2080-2100 for the entire ecozone. Using the same GCM scenarios, a small (<10%) increase in lightning fire occurrence was projected for 2030 for the entire ecozone, but increases of 10% to 25% and 25% to 50% were expected around 2090 for the southern and the northern Boreal Shield East ecozone, respectively (Wotton *et al.* 2010). Le Goff *et al.* (2009) found slight increases for a smaller area within the ecozone for both 2030-2060 and 2070-2100. Moreover, a shift in dominant fire risk towards the late summer was projected for this region.

The combination of an increase in mean forest floor consumption and a shifting dominant fire risk towards the late summer indicates that fire will become more severe, especially at the end of the twenty-first century. Due to the closed canopy, the litter layers of the Boreal Shield East forests retain moisture better than litter layers of open stands, especially when FWI code values are low. Nevertheless, closed-canopy forest floors are more sensitive to fluctuations in meteorological conditions

than those of open forests, as visible by the slope of the calibration diagram (Figure 4). Therefore, the relative importance of tree biomass, understorey, and forest floor may be much less stable than in the open Taiga Shield East biomes. Higher summer temperatures may increase production rates (Bergeron 1998) and the overstorey may remain dominant. In addition, more frequent and severe burning may be advantageous to dense tree covers that may shift to more dominant deciduous species that resprout from the mineral layer, e.g., quaking aspen (de Groot *et al.* 2003), while understorey development may be limited and a forest floor cover of feathermoss is favoured relative to *Sphagnum* spp. (Johnstone 2006, Turetsky *et al.* 2010). Driven by climate and fire, some parts of the southern boreal forest and mixedwood region may show a negative C balance during the twenty-first century (Balshi *et al.* 2009), although values depend strongly on the climate scenario and the intensity of the CO_2 fertilization effect.

Changes in the Taiga Shield East Ecozone

The status of the lichen woodland zone in the postfire regeneration process has been subject of debate (e.g., Maikawa and Kershaw 1976, Payette and Morneau 1993, Payette *et al.* 2000). Maikawa and Kershaw (1976) mentioned that in the absence of fire, the lichen woodland will close and the lichen cover will be replaced by moss. Payette and Morneau (1993) stated that the lichen woodland can be regarded as a stable ecosystem that maintains its structure for thousands of years in regions near the treeline that remain exceptionally undisturbed. Payette (1992) and Payette *et al.* (2000) added that lichen woodlands can persevere in the southern and central part of the boreal forest by a combination of climate conditions and dry and mesic soils favouring high fire frequencies. Finally, Jasinski and Payette (2005) acknowledged higher fire frequencies typical in sites with microclimatic conditions due to local orographic variations combined with frequent spruce budworm (*Choristoneura fumiferana* Clem.) outbreaks, influencing stable lichen woodland patches in closed-crown forests as well. In this biome, lichen woodland can establish after severe fire if the normally dominant balsam fir is impeded to return by seeding from nearby unburned sites (Jasinski and Payette 2005). In addition, lichen will be able to colonize sites where pre-fire shrub populations are eliminated due to severe burning of the rhizomes, thus impeding shrub growth from sprouts (Rowe 1983, Viereck 1983, Payette 1992, Schimmel and Granström 1996). In estimating the effect of a decrease in fire severity and frequency on the lichen woodland biome, it is important to consider the possible long-term pathways of lichen woodland development in the absence of fire.

Scenarios predict that mean summer temperatures will increase around 3 °C during the twenty-first century, with the highest rate of warming in the first half of the century (Table 4). Winter temperature increases may be more pronounced from 4.0 °C to 7.5 °C. Precipitation projections seem less equivocal, as increases in summer precipitation (10 % to 15 %) may be highest in the mid-twenty-first century, whereas increases in winter precipitation may be drastic (32 % to 38 %), especially around 2090 (Table 5).

The projected mean forest floor fuel consumption is close to that of the Boreal Shield East, increasing 4 % to 13 % for 2040-2060 and 2080-2100, respectively (Amiro *et al.* 2009). Forest floor consumption is positively related to FFMC in spruce-lichen woodlands (de Groot *et al.* 2009). The importance of the litter moisture content for forest floor consumption implies that deep burning may occur during the entire fire season, as FFMC is high at the start and diminishes only slightly in this ecozone (Amiro *et al.* 2004).

Scenarios of future area burned differ dramatically depending on the period of projection. Flannigan *et al.* (2001) found important

decreases in parts of the lichen woodland for 2040-2060, whereas Flannigan *et al.* (2005) indicated more than twice the amount of area burned for 2080-2100 relative to the 1 × CO_2 scenario. These differences are the result of the use of monthly data in Flannigan *et al.* (2001), while Flannigan *et al.* (2005) used daily data. In addition, the latter scenario was based on the entire Taiga Shield ecozone, including parts of northern Ontario, Manitoba, Saskatchewan, a portion of southern Nunavut, and the south-central area of the Northwest Territories that are under the influence of different climate regimes. Wotton *et al.* (2010) projected increases in lightning fire occurrence of <10% and 10% to 25% for 2030 and 2090, respectively.

Comparing climate data to the fire regime scenarios, we may conclude that warming will be likely to compensate for the increase in precipitation. Therefore, effective precipitation should diminish, resulting in the greater area burned and a higher forest floor consumption. The relative changes in mean forest floor fuel consumption are comparable to those of the closed-crown forest. However, the sensitivity of the lichen woodland to changes in effective precipitation may be different. The open nature of the lichen woodland with its lichen ground cover is typified by high drying rates. Thus, higher precipitation and higher summer temperatures might therefore cause only a minor increase in fire severity compared to the reference periods (Wotton and Beverly 2007). In contrast with the closed-crown forest, forest floor moisture contents may show less variation during the season and slightly higher values for the duff layer (Amiro *et al.* 2004). Future climate may become much warmer with increases in precipitation so that, if not for the increase in fire activity for this region, parts of the actual lichen woodland could resemble black spruce-feathermoss forests in the near future. On the other hand, fire regimes are likely to become more severe, which would actually accentuate the contrast between the lichen woodlands and closed-crown forests. Future severe burning in combination with higher temperatures may cause an increase in tree cover as general forest floor thickness diminishes and, consequently, a higher representation of deciduous species that establish rapidly after fire on shallow forest floors such as quaking aspen and balsam poplar (*Populus balsamifera* L) (Comtois and Payette 1987, de Groot *et al.* 2003, Greene *et al.* 2007). Although forest fire activity will negatively affect C stocks in the Taiga Shield East ecozone, Balshi *et al.* (2009) projected a relatively stable C sink functioning during the twenty-first century due to a positive climatic effect. However, as twenty-first century scenarios of changes in Quebec boreal biome distribution resulting from changes in temperature and precipitation are absent for both the Boreal Shield East and the Taiga Shield East ecozones, the respective contribution of fire and climate on changes in stand C distribution remains largely uncertain.

CONCLUSION

Global warming in the boreal ecosystems is likely to have important effects on fire regimes. Specifically, the Quebec boreal region will experience a general increase in both temperature and precipitation (Price *et al.* 2001, Plummer *et al.* 2006, Solomon *et al.* 2007). Climate scenarios have been used as input for the FWI that allows one to project aspects of fire regimes such as fire frequency, area burned, and fire severity for the twenty-first century. As the increase in temperature will generally compensate the increase in precipitation, fire frequencies and fire severity may well increase. Moreover, the fire season peak might shift to the late summer when forests are generally prone to deep burning (Le Goff *et al.* 2009). Besides changes in fire regime, climate may also be a direct agent in changes in the boreal forest. The relative importance of fire regimes and climate as a factor in global forest dynamics is difficult to estimate.

Boreal C sequestration is a function of a number of factors including stand age, climate, fire severity, and species. Numerous interactions exist between these factors, yet some patterns can be discerned. Boreal C stocks generally increase with increasing stand age. Fire severity and species effects are closely linked, as vegetation establishment after fire is highly dependent on fire severity. Generally, low fire severity is advantageous to forest floor development, thereby limiting tree regeneration, whereas high fire severity induces an inverse tendency. Finally, the influence of climate is less clear. High temperatures may be linked to high litter production rates and thus influence forest floor build-up. On the other hand, decomposition rates also increase with warmer forest floors. High amounts of precipitation may induce low forest floor decomposition rates, resulting in net accumulation as long as forest floor development does not limit tree growth and thus litter production.

Linking the increase in general fire severity in boreal Quebec to possible C sequestration tendencies, we may observe a decrease in the boreal C stock during the twenty-first century. Nonetheless, the studied climate and fire regime projections remain uncertain about the magnitude of changes. As present data on stand C distributions in boreal Quebec is limited, additional research on this subject may be necessary. In addition, the influence of changes in temperature, precipitation, permafrost dynamics, and insect and disease outbreaks should be taken into account for a complete image. The future development of dynamic vegetation models that include climate-driven fire severity and frequency effects that take into account fire-vegetation interaction may improve estimates on boreal stand C stocks during the twenty-first century.

ACKNOWLEDGEMENTS

Funding was provided by Hydro-Quebec Production through the EM-1 Project Reservoirs' net greenhouse gas emissions research project (2005-2009). Thanks to P.J.H. Richard and W. Hoek for helpful comments on an earlier version of this paper.

LITERATURE CITED

Allard, M., and M.K. Seguin. 1987. Le pergélisol au Québec nordique: bilan et perspectives. Géographie physique et Quaternaire 41: 12 [In French.]

Amiro, B.D., A.G. Barr, T.A. Black, H. Iwashita, N. Kljun, J.H. McCaughey, K. Morgenstern, S. Murayama, Z. Nesic, A.L. Orchansky, and N. Saigusa. 2006. Carbon, energy and water fluxes at mature and disturbed forest sites, Saskatchewan, Canada. Agricultural and Forest Meteorology 136: 237-251. doi: 10.1016/j.agrformet.2004.11.012

Amiro, B.D., A. Cantin, M.D. Flannigan, and W.J. de Groot. 2009. Future emissions from Canadian boreal forest fires. Canadian Journal of Forest Research 39: 383-395. doi: 10.1139/X08-154

Amiro, B.D., K.A. Logan, B.M. Wotton, M.D. Flannigan, J.B. Todd, B.J. Stocks, and D.L. Martell. 2004. Fire weather index system components for large fires in the Canadian boreal forest. International Journal of Wildland Fire 13: 391-400. doi: 10.1071/WF03066

Amiro, B.D., J.B. Todd, B.M. Wotton, K.A. Logan, M.D. Flannigan, B.J. Stocks, J.A. Mason, D.L. Martell, and K.G. Hirsch. 2001. Direct carbon emissions from Canadian forest fires, 1959-1999. Canadian Journal of Forest Research 31: 512-525. doi: 10.1139/cjfr-31-3-512

Apps, M.J., W.A. Kurz, R.J. Luxmoore, L.O. Nilsson, R.A. Sedjo, R. Schmidt, L.G. Simpson, and T.S. Vinson. 1993. Boreal forests and tundra. Water, Air, & Soil Pollution 70: 39-53. doi: 10.1007/BF01104987

Asselin, H., A. Belleau, and Y. Bergeron. 2006. Factors responsible for the co-occurrence of forested and unforested rock outcrops in the boreal forest. Landscape Ecology 21: 271-280. doi: 10.1007/s10980-005-1393-1

Balshi, M.S., A.D. McGuire, P. Duffy, M. Flannigan, D.W. Kicklighter, and J. Melillo. 2009. Vulnerability of carbon storage in North American boreal forests to wildfires during the 21st century. Global Change Biology 15: 1491-1510. doi: 10.1111/j.1365-2486.2009.01877.x

Balshi, M.S., A.D. McGuire, Q. Zhuang, J.M. Melillo, D.W. Kicklighter, E. Kasischke, C. Wirth, M. Flannigan, J. Harden, J.S. Clein, T.J. Burnside, J. McAllister, W.A. Kurz, M. Apps, and A. Shvidenko. 2007. The role of historical fire disturbance in the carbon dynamics of the pan-boreal region: a process-based analysis. Journal of Geophysical Research 112: doi: 10.1029/2006JG000380

Bergeron, Y. 1998. Les conséquences des changements climatiques sur la fréquence des feux et la composition forestière au sud-ouest de la forêt boréale québécoise. Géographie physique et Quaternaire 52: 167-174. [In French.]

Bergeron, Y., M. Flannigan, S. Gauthier, A. Leduc, and P. Lefort. 2004*a*. 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., and M.D. Flannigan. 1995. Predicting the effects of climate change on fire frequency in the southeastern Canadian boreal forest. Water, Air, & Soil Pollution 82: 437-444. doi: 10.1007/BF01182853

Bergeron, Y., S. Gauthier, M. Flannigan, and V. Kafka. 2004*b*. Fire regimes at the transition between mixedwood and coniferous boreal forest in northwestern Quebec. Ecology 85: 1916-1932. doi: 10.1890/02-0716

Bergeron, Y., S. Gauthier, V. Kafka, P. Lefort, and D. Lesieur. 2001. Natural fire frequency for the eastern Canadian boreal forest: consequences for sustainable forestry. Canadian Journal of Forest Research 31: 384-391. doi: 10.1139/cjfr-31-3-384

Bergner, B., J. Johnstone, and K.K. Treseder. 2004. Experimental warming and burn severity alter soil CO_2 flux and soil functional groups in a recently burned boreal forest. Global Change Biology 10: 1996-2004. doi: 10.1111/j.1365-2486.2004.00868.x

Bhatti, J.S., and M.J. Apps. 2000. Carbon and nitrogen storage in upland boreal forests. Pages 79-89 in: R. Lal, J.M. Kimble, H. Eswarn, and B.A. Stewart, editors. Global climate change and cold ecosystems. CRC Lewis Publishers, Boca Raton, Florida, USA.

Bhatti, J.S., G.C. van Kooten, M.J. Apps, L.D. Laird, I.D. Campbell, C. Campbell, M.R. Turetsky, Z. Yu, and E. Banfield. 2003. Carbon balance and climate change in boreal forests. Pages 799-855 in: P.J. Burton, C. Messier, D.W. Smith, and W.L. Adamowicz, editors. Towards sustainable management of the boreal forest. NRC Research Press, Ottawa, Ontario, Canada.

Bonan, G.B., F.S. Chapin, and S.L. Thompson. 1995. Boreal forest and tundra ecosystems as components of the climate system. Climatic Change 29: 145-167. doi: 10.1007/BF01094014

Bonan, G.B., and H.H. Shugart. 1989. Environmental factors and ecological processes in boreal forests. Annual Review of Ecology and Systematics 20: 1-28. doi: 10.1146/annurev.es.20.110189.000245

Bond-Lamberty, B., C. Wang, and S.T. Gower. 2004. Net primary production and net ecosystem production of a boreal black spruce wildfire chronosequence. Global Change Biology 10: 473-487. doi: 10.1111/j.1529-8817.2003.0742.x

Bourgeau-Chavez, L.L., M.E. Alexander, B.J. Stocks, and E.S. Kasischke. 2000. Distribution of forest ecosystems and the role of fire in the boreal region. Pages 111-131 in: E.S. Kasischke and B.J. Stocks, editors. Fire, climate change and carbon cycling in the boreal forest. Springer-Verlag, New York, New York, USA.

Cayford, J.H., and D.J. McRae. 1983. The ecological role of fire in jack pine forests. Pages 183-199 in: R.W. Wein and D.A. MacLean, editors. The role of fire in northern circumpolar ecosystems. John Wiley & Sons, New York, New York, USA.

Charron, I., and D.F. Greene. 2002. Post-wildfire seedbeds and tree establishment in the southern mixedwood boreal forest. Canadian Journal of Forest Research 32: 1607-1615. doi: 10.1139/x02-085

Chrosciewicz, Z. 1974. Evaluation of fire-produced seedbeds for jack pine regeneration in central Ontario. Canadian Journal of Forest Research 4: 455-457. doi: 10.1139/x74-067

Comtois, P., and S. Payette. 1987. Le développement spatial et floristique des populations clonales de peupliers baumier (*Populus balsamifera* L.) au Nouveau-Québec. Géographie physique et Quaternaire 41: 65-78. [In French].

Conard, S.G., A.I. Sukhinin, B.J. Stocks, D.R. Cahoon, E.P. Davidenko, and G.A. Ivanova. 2002. Determining effects of area burned and fire severity on carbon cycling and emissions in Siberia. Climatic Change 55: 197-211. doi: 10.1023/A:1020207710195

de Groot, W.J., P.M. Bothwell, D.H. Carlsson, and K.A. Logan. 2003. Simulating the effects of future fire regimes on western Canadian boreal forests. Journal of Vegetation Science 14: 355-364. doi: 10.1658/1100-9233(2003)014[0355:STEOFF]2.0.CO;2

de Groot, W.J., J.M. Pritchard, and T.J. Lynham. 2009. Forest floor fuel consumption and carbon emissions in Canadian boreal forest fires. Canadian Journal of Forest Research 39: 367-382. doi: 10.1139/X08-192

DesRochers, A., and R. Gagnon. 1997. Is ring count at ground level a good estimation of black spruce age? Canadian Journal of Forest Research 27: 1263-1267.

Dixon, R.K., A.M. Solomon, S. Brown, R.A. Houghton, M.C. Trexier, and J. Wisniewski. 1994. Carbon pools and flux of global forest ecosystems. Science 263: 185-190. doi: 10.1126/science.263.5144.185

Duchesne, S., and L. Sirois. 1995. Phase initiale de régénération après feu des populations coniférienes subarctiques. Canadian Journal of Forest Research 25: 307-318. [In French.] doi: 10.1139/x95-035

Dymond, C.C., E.T. Neilson, G. Stinson, K. Porter, D.A. MacLean, D.R. Gray, M. Campagna, and W.A. Kurz. 2010. Future spruce budworm outbreak may create a carbon source in eastern Canadian forests. Ecosystems 13: 917-931. doi: 10.1007/s10021-010-9364-z

Fenton, N., N. Lecomte, S. Légaré, and Y. Bergeron. 2005. Paludification in black spruce (*Picea mariana*) forests of eastern Canada: potential factors and management implications. Forest Ecology and Management 213: 151-159. doi: 10.1016/j.foreco.2005.03.017

Flannigan, M., I. Campbell, M. Wotton, C. Carcaillet, P. Richard, and Y. Bergeron. 2001. Future fire in Canada's boreal forest: paleoecology results and general circulation model—regional climate model simulations. Canadian Journal of Forest Research 31: 854-864. doi: 10.1139/cjfr-31-5-854

Flannigan, M., K. Logan, B. Amiro, W. Skinner, and B. Stocks. 2005. Future area burned in Canada. Climatic Change 72: 1-16. doi: 10.1007/s10584-005-5935-y

Flannigan, M., B. Stocks, M. Turetsky, and M. Wotton. 2009. Impacts of climate change on fire activity and fire management in the circumboreal forest. Global Change Biology 15: 549-560. doi: 10.1111/j.1365-2486.2008.01660.x

Flannigan, M.D., Y. Bergeron, O. Engelmark, and B.M. Wotton. 1998. Future wildfire in circumboreal forests in relation to global warming. Journal of Vegetation Science 9: 469-476. doi: 10.2307/3237261

Flannigan, M.D., and J.B. Harrington. 1988. A study of the relation of meteorological variables to monthly provincial area burned by wildfire in Canada (1953-80). Journal of Applied Meteorology 27: 441-452. doi: 10.1175/1520-0450(1988)027<0441:ASOTRO>2.0.CO;2

Foster, D.R. 1985. Vegetation development following fire in *Picea mariana* (black spruce)-Pleurozium forests of south-eastern Labrador, Canada. Journal of Ecology 73: 517-534. doi: 10.2307/2260491

French, N.H.F., E.S. Kasischke, and D.G. Williams. 2003. Variability in the emission of carbon-based trace gases from wildfire in the Alaskan boreal forest. Journal of Geophysical Research 107: doi: 10.1029/2001JD000480

Gérardin, V. 1980. L'inventaire du capital-nature du territoire de la Baie-James: les régions écologiques et la végétation des sols minéraux. Tome 1: méthodologie et description. Environnement Canada, Ste-Foy, Quebec. [In French.]

Girard, F., S. Payette, and R. Gagnon. 2008. Rapid expansion of lichen woodlands within the closed-crown boreal forest zone over the last 50 years caused by stand disturbances in eastern Canada. Journal of Biogeography 35: 529-537. doi: 10.1111/j.1365-2699.2007.01816.x

Girardin, M.P., and M. Mudelsee. 2008. Past and future changes in Canadian boreal wildfire activity. Ecological Applications 18: 391-406. doi: 10.1890/07-0747.1

Girardin, M.P., J. Tardif, M.D. Flannigan, B.M. Wotton, and Y. Bergeron. 2004. Trends and periodicities in the Canadian Drought Code and their relationships with atmospheric circulation for the southern Canadian boreal forest. Canadian Journal of Forest Research 34: 103-119. doi: 10.1139/x03-195

Gorham, E. 1991. Northern peatlands: role in the carbon cycle and probable responses to climatic warming. Ecological Applications 1: 182-195. doi: 10.2307/1941811

Gower, S.T., J.G. Vogel, J.M. Norman, C.J. Kucharik, S.J. Steele, and T.K. Stowe. 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 102: 29029-29041. doi: 10.1029/97JD02317

Gray, D. 2008. The relationship between climate and outbreak characteristics of the spruce budworm in eastern Canada. Climatic Change 87: 361-383. doi: 10.1007/s10584-007-9317-5

Greene, D.F., S.E. MacDonald, S. Haeussler, S. Domenicano, J. Noël, K. Jayen, I. Charron, S. Gauthier, S. Hunt, E.T. Gielau, Y. Bergeron, and L. Swift. 2007. The reduction of organic-layer depth by wildfire in the North American boreal forest and its effect on tree recruitment by seed. Canadian Journal of Forest Research 37: 1012-1023. doi: 10.1139/X06-245

Gutsell, S.L., and E.A. Johnson. 2002. Accurately ageing trees and examining their height-growth rates: implications for interpreting forest dynamics. Journal of Ecology 90: 153-166. doi: 10.1046/j.0022-0477.2001.00646.x

Harden, J.W., K.L. Manies, M.R. Turetsky, and J.C. Neff. 2006. Effects of wildfire and permafrost on soil organic matter and soil climate in interior Alaska. Global Change Biology 12: 2391-2403. doi: 10.1111/j.1365-2486.2006.01255.x

Hare, F.K. 1950. Climate and zonal divisions of the boreal forest formation in eastern Canada. Geographical Review 40: 615-635. doi: 10.2307/211106

Harper, K., C. Boudreault, L. DeGrandpré, P. Drapeau, S. Gauthier, and Y. Bergeron. 2003. Structure, composition, and diversity of old-growth black spruce boreal forest of the Clay Belt region in Quebec and Ontario. Environmental Reviews 11: S79-S98. doi: 10.1139/a03-013

Heinselman, M.L. 1981. Fire and succession in the conifer forests of northern North America. Pages 374-405 in: D.C. West, H.H. Shugart, and D.B. Botkin, editors. Forest succession: concepts and application. Springer-Verlag, New York, New York, USA.

Hély, C., M. Flannigan, Y. Bergeron, and D. McRae. 2001. Role of vegetation and weather on fire behavior in the Canadian mixedwood boreal forest using two fire behavior prediction systems. Canadian Journal of Forest Research 31: 430-441. doi: 10.1139/cjfr-31-3-430

Hollingsworth, T., E. Schuur, F. Chapin, and M. Walker. 2008. Plant community composition as a predictor of regional soil carbon storage in Alaskan boreal black spruce ecosystems. Ecosystems 11: 629-642. doi: 10.1007/s10021-008-9147-y

Jasinski, J.P.P., and S. Payette. 2005. The creation of alternative stable states in the southern boreal forest, Québec, Canada. Ecological Monographs 75: 561-583. doi: 10.1890/04-1621

Johnson, E.A. 1992. Fire and vegetation dynamics: studies from the North American boreal forest. Cambridge University Press, United Kingdom. doi: 10.1017/CBO9780511623516

Johnstone, J., and F. Chapin. 2006. Effects of soil burn severity on post-fire tree recruitment in boreal forest. Ecosystems 9: 14-31. doi: 10.1007/s10021-004-0042-x

Johnstone, J.F. 2006. Response of boreal plant communities to variations in previous fire-free interval. International Journal of Wildland Fire 15: 497-508. doi: 10.1071/WF06012

Johnstone, J.F., T.N. Hollingsworth, F.S. Chapin, and M.C. Mack. 2010. Changes in fire regime break the legacy lock on successional trajectories in Alaskan boreal forest. Global Change Biology 16: 1281-1295. doi: 10.1111/j.1365-2486.2009.02051.x

Kasischke, E. 2000. Boreal ecosystems in the global carbon cycle. Pages 19-30 in: E.S. Kasischke, and B.J. Stocks, editors. Fire, climate change and carbon cycling in the boreal forest. Springer-Verlag, New York, New York, USA.

Kasischke, E.S., N.L. Christensen, Jr., and B.J. Stocks. 1995. Fire, global warming, and the carbon balance of boreal forests. Ecological Applications 5: 437-451. doi: 10.2307/1942034

Kasischke, E.S., E.J. Hyer, P.C. Novelli, L.P. Bruhwiler, N.H.F. French, A.I. Sukhinin, J.H. Hewson, and B.J. Stocks. 2005. Influences of boreal fire emissions on Northern Hemisphere atmospheric carbon and carbon monoxide. Global Biogeochemical Cycles 19: doi: 10.1029/2004GB002300

Kasischke, E.S., and J.F. Johnstone. 2005. Variation in postfire organic layer thickness in a black spruce forest complex in interior Alaska and its effects on soil temperature and moisture. Canadian Journal of Forest Research 35: 2164-2177. doi: 10.1139/x05-159

Kasischke, E.S., M.R. Turetsky, R.D. Ottmar, N.H.F. French, E.E. Hoy, and E.S. Kane. 2008. Evaluation of the composite burn index for assessing fire severity in Alaskan black spruce forests. International Journal of Wildland Fire 17: 515-526. doi: 10.1071/WF08002

King, G.A. 1987. Deglaciation and vegetation history of western Labrador and adjacent Quebec. Dissertation, University of Minnesota, Minneapolis, USA.

Krawchuk, M.A., S.G. Cumming, and M.D. Flannigan. 2009. Predicted changes in fire weather suggest increases in lightning fire initiation and future area burned in the mixedwood boreal forest. Climatic Change 92: 83-97. doi: 10.1007/s10584-008-9460-7

Kurz, W.A., and M.J. Apps. 1999. A 70-year retrospective analysis of carbon fluxes in the Canadian forest sector. Ecological Applications 9: 526-547. doi: 10.1890/1051-0761(1999)009[0526:AYRAOC]2.0.CO;2

Lal, R. 2005. Forest soils and carbon sequestration. Forest Ecology and Management 220: 242-258. doi: 10.1016/j.foreco.2005.08.015

Lawson, B.D., and G.N. Dalrymple. 1996. Ground-truthing the Drought Code: field verification of over-winter recharge of forest floor moisture. Natural Resources Canada, Canadian Forest Service, Pacific Forestry Centre, Victoria, British Columbia, Canada.

Le Goff, H., M.D. Flannigan, and Y. Bergeron. 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. doi: 10.1139/X09-153

Lecomte, N., and Y. Bergeron. 2005. Successional pathways on different surficial deposits in the coniferous boreal forest of the Quebec Clay Belt. Canadian Journal of Forest Research 35: 1984-1995. doi: 10.1139/x05-114

Lecomte, N., M. Simard, and Y. Bergeron. 2006*a*. Effects of fire severity and initial tree composition on stand structural development in the coniferous boreal forest of northwestern Québec, Canada. Ecoscience 13: 152-163. doi: 10.2980/i1195-6860-13-2-152.1

Lecomte, N., M. Simard, Y. Bergeron, A. Larouche, H. Asnong, and P.J.H. Richard. 2005. Effects of fire severity and initial tree composition on understorey vegetation dynamics in a boreal landscape inferred from chronosequence and paleoecological data. Journal of Vegetation Science 16: 665-674. doi: 10.1111/j.1654-1103.2005.tb02409.x

Lecomte, N., M. Simard, N. Fenton, and Y. Bergeron. 2006*b*. Fire severity and long-term ecosystem biomass dynamics in coniferous boreal forests of eastern Canada. Ecosystems 9: 1215-1230. doi: 10.1007/s10021-004-0168-x

Litvak, M., S. Miller, S.C. Wofsy, and M. Goulden. 2003. Effect of stand age on whole ecosystem CO_2 exchange in the Canadian boreal forest. Journal of Geophysical Research 108: doi: 10.1029/2001JD000854

Lloyd, A.H., A.E. Wilson, C.L. Fastie, and R.M. Landis. 2005. Population dynamics of black spruce and white spruce near the arctic tree line in the southern Brooks Range, Alaska. Canadian Journal of Forest Research 35: 2073-2081. doi: 10.1139/x05-119

Maikawa, E., and K.A. Kershaw. 1976. Studies on lichen-dominated systems. XIX. The post-fire recovery sequence of black spruce-lichen woodland in the Abitau Lake Region, N.W.T. Canadian Journal of Botany 54: 2679-2687. doi: 10.1139/b76-288

McAlpine, R.S. 1990. Seasonal trends in the Drought Code component of the Canadian Forest Fire Weather Index System. Forestry Canada, Petawawa National Forestry Institute, Chalk River, Ontario, Canada.

McGuire, A.D., C. Wirth, M. Apps, J. Beringer, J. Clein, H. Epstein, D.W. Kicklighter, J. Bhatti, F.S. Chapin, B. de Groot, D. Efremov, W. Eugster, M. Fukuda, T. Gower, L. Hinzman, B. Huntley, G.J. Jia, E. Kasischke, J. Melillo, V. Romanovsky, A. Shvidenko, E. Vaganov, and D. Walker. 2002. Environmental variation, vegetation distribution, carbon dynamics and water/energy exchange at high latitudes. Journal of Vegetation Science 13: 301-314. doi: 10.1111/j.1654-1103.2002.tb02055.x

Messaoud, Y., Y. Bergeron, and A. Leduc. 2007. Ecological factors explaining the location of the boundary between the mixedwood and coniferous bioclimatic zones in the boreal biome of eastern North America. Global Ecology and Biogeography 16: 90-102. doi: 10.1111/j.1466-8238.2006.00277.x

Miyanishi, K., and E.A. Johnson. 2002. Process and patterns of duff consumption in the mixedwood boreal forest. Canadian Journal of Forest Research 32: 1285-1295. doi: 10.1139/x02-051

Mkhabela, M.S., B.D. Amiro, A.G. Barr, T.A. Black, I. Hawthorne, J. Kidston, J.H. McCaughey, A.L. Orchansky, Z. Nesic, A. Sass, A. Shashkov, and T. Zha. 2009. Comparison of carbon dynamics and water use efficiency following fire and harvesting in Canadian boreal forests. Agricultural and Forest Meteorology 149: 783-794. doi: 10.1016/j.agrformet.2008.10.025

Morneau, C., and S. Payette. 1989. Postfire lichen-spruce woodland recovery at the limit of the boreal forest in northern Québec. Canadian Journal of Botany 67: 2770-2782. doi: 10.1139/b89-357

Nalder, I.A., and R.W. Wein. 1999. Long-term forest floor carbon dynamics after fire in upland boreal forests of western Canada. Global Biogeochemical Cycles 13: 951-968. doi: 10.1029/1999GB900056

O'Connell, K.E.B., S.T. Gower, and J.M. Norman. 2003. Comparison of Net Primary Production and light-use dynamics of two boreal black spruce forest communities. Ecosystems 6: 236-247. doi: 10.1007/s10021-002-0201-x

O'Neill, K., D. Richter, and E. Kasischke. 2006. Succession-driven changes in soil respiration following fire in black spruce stands of interior Alaska. Biogeochemistry 80: 1-20. doi: 10.1007/s10533-005-5964-7

Oechel, W.C., and K. Van Cleve. 1986. The role of bryophytes in nutrient cycling in the taiga. Pages 121-137 in: K. Van Cleve, F.S. Chapin, P.W. Flanagan, L.A. Viereck, and C.T. Dyrness, editors. Forest ecosystems in the Alaskan taiga: a synthesis of structure and function. Springer-Verlag, New York, New York, USA.

Paquin, R., H.A. Margolis, R. Doucet, and M.R. Coyea. 1999. Comparison of growth and physiology of layers and naturally established seedlings of black spruce in a boreal cutover in Quebec. Canadian Journal of Forest Research 29: 1-8. doi: 10.1139/cjfr-29-1-1

Paré, D., Y. Bergeron, and C. Camiré. 1993. Changes in the forest floor of Canadian southern boreal forest after disturbance. Journal of Vegetation Science 4: 811-818. doi: 10.2307/3235619

Payette, S. 1992. Fire as a controlling process in the North American boreal forest. Pages 144-169 in: H.H. Shugart, R. Leemans, and G.B. Bonan, editors. A systems analysis of the global boreal forest. Cambridge University Press, United Kingdom. doi: 10.1017/CBO9780511565489.006

Payette, S., N. Bhiry, A. Delwaide, and M. Simard. 2000. Origin of the lichen woodland at its southern range limit in eastern Canada: the catastrophic impact of insect defoliators and fire on the spruce–moss forest. Canadian Journal of Forest Research 30: 288-305. doi: 10.1139/cjfr-30-2-288

Payette, S., and C. Morneau. 1993. Holocene relict woodlands at the eastern Canadian treeline. Quaternary Research 39: 84-89. doi: 10.1006/qres.1993.1010

Payette, S., C. Morneau, L. Sirois, and M. Desponts. 1989. Recent fire history of the northern Quebec biomes. Ecology 70: 656-673. doi: 10.2307/1940217

Payette, S., and L. Rochefort. 2001. Écologie des tourbières du Québec-Labrador. Les Presses de l'Université Laval, Ste-Foy, Quebec, Canada. [In French.]

Plummer, D.A., D. Caya, A. Frigon, H. Côté, M. Giguère, D. Paquin, S. Biner, R. Harvey, and R. de Elia. 2006. Climate and climate change over North America as simulated by the Canadian RCM. Journal of Climate 19: 3112-3132. doi: 10.1175/JCLI3769.1

Pregitzer, K.S., and E.S. Euskirchen. 2004. Carbon cycling and storage in world forests: biome patterns related to forest age. Global Change Biology 10: 2052-2077. doi: 10.1111/j.1365-2486.2004.00866.x

Price, D.T., D.W. McKenney, D. Caya, and H. Côté. 2001. Transient climate change scenarios for high resolution assessment of impacts on Canada's forest ecosystems. CICS, Victoria, British Columbia, Canada.

Rowe, J.S. 1972. The forest regions of Canada. Fisheries and Environment Canada, Canadian Forest Service, Ottawa.

Rowe, J.S. 1983. Concepts of fire effects on plant individual and species. Pages 134-154 in: R.W. Wein and D.A. MacLean, editors. The role of fire in northern circumpolar ecosystems. John Wiley & Sons, New York, New York, USA.

Saucier, J.-P., J.-F. Bergeron, P. Grondin, and A. Robitaille. 1998. Les régions écologiques du Québec méridional (3e version): un des éléments du système hiérarchique de classification écologique du territoire mis au point par le ministère des Ressources naturelles du Québec. L'Aubelle 124: 1-12. [In French.]

Schimmel, J., and A. Granström. 1996. Fire severity and vegetation response in the boreal Swedish forest. Ecology 77: 1436-1450. doi: 10.2307/2265541

Shetler, G., M.R. Turetsky, E. Kane, and E. Kasischke. 2008. Sphagnum mosses control ground-layer fuel consumption during fire in Alaskan black spruce forests: implications for long-term carbon storage. Canadian Journal of Forest Research 38: 2328-2336. doi: 10.1139/X08-057

Simmons, J.A., I.J. Fernandez, R.D. Briggs, and M.T. Delaney. 1996. Forest floor carbon pools and fluxes along a regional climate gradient in Maine, USA. Forest Ecology and Management 84: 81-95. doi: 10.1016/0378-1127(96)03739-5

Sirois, L., and S. Payette. 1991. Reduced postfire tree regeneration along a boreal forest-forest-tundra transect in northern Quebec. Ecology 72: 619-627. doi: 10.2307/2937202

Smirnova, E., Y. Bergeron, and S. Brais. 2008. Influence of fire intensity on structure and composition of jack pine stands in the boreal forest of Quebec: live trees, understory vegetation and dead wood dynamics. Forest Ecology and Management 255: 2916-2927. doi: 10.1016/j.foreco.2008.01.071

Solomon, S., D. Qin, M. Manning, Z. Chen, M. Marquis, K.B. Averyt, M. Tignor, and H.L. Miller. 2007. Climate change 2007: the physical science basis. Intergovernmental Panel on Climate Change Working Group I Assessment Report. Cambridge University Press, United Kingdom.

Stocks, B.J., M.E. Alexander, B.M. Wotton, C.N. Stefner, M.D. Flannigan, S.W. Taylor, N. Lavoie, J.A. Mason, G.R. Hartley, M.E. Maffey, G.N. Dalrymple, T.W. Blake, M.G. Cruz, and R.A. Lanoville. 2004. Crown fire behaviour in a northern jack pine-black spruce forest. Canadian Journal of Forest Research 34: 1548-1560. doi: 10.1139/x04-054

Stocks, B.J., M.A. Fosberg, T.J. Lynham, L. Mearns, B.M. Wotton, Q. Yang, J.Z. Jin, K. Lawrence, G.R. Hartley, J.A. Mason, and D.W. McKenney. 1998. Climate change and forest fire potential in Russian and Canadian boreal forests. Climatic Change 38: 1-13. doi: 10.1023/A:1005306001055

Tan, Z., L. Tieszen, Z. Zhu, S. Liu, and S. Howard. 2007. An estimate of carbon emissions from 2004 wildfires across Alaskan Yukon River Basin. Carbon Balance and Management 2: doi: 10.1186/1750-0680-2-12

Tarnocai, C. 2006. The effect of climate change on carbon in Canadian peatlands. Global and Planetary Change 53: 222-232. doi: 10.1016/j.gloplacha.2006.03.012

Taylor, S.J., T.J. Carleton, and R. Adams. 1988. Understorey vegetation change in a *Picea mariana* chronosequence. Plant Ecology 73: 63-72. doi: 10.1007/BF00031853

Tremblay, S., R. Ouimet, and D. Houle. 2002. Prediction of organic carbon content in upland forest soils of Quebec, Canada. Canadian Journal of Forest Research 32: 903-914. doi: 10.1139/x02-023

Turetsky, M.R., M.C. Mack, T.N. Hollingsworth, and J.W. Harden. 2010. The role of mosses in ecosystem succession and function in Alaska's boreal forest. Canadian Journal of Forest Research 40: 1237-1264. doi: 10.1139/X10-072

Turquety, S., J.A. Logan, D.J. Jacob, R.C. Hudman, F.Y. Leung, C.L. Heald, R.M. Yantosca, S. Wu, L.K. Emmons, D.P. Edwards, and G.W. Sachse. 2007. Inventory of boreal fire emissions for North America in 2004: importance of peat burning and pyroconvective injection. Journal of Geophysical Research 112: doi: 10.1029/2006JD007281

van Bellen, S., P.-L. Dallaire, M. Garneau, and Y. Bergeron. 2011. Quantifying spatial and temporal Holocene carbon accumulation in ombrotrophic peatlands of the Eastmain region, Quebec, Canada. Global Biogeochemical Cycles.

Van Cleve, K., L. Oliver, R. Schlentner, L.A. Viereck, and C.T. Dyrness. 1983. Productivity and nutrient cycling in taiga forest ecosystems. Canadian Journal of Forest Research 13: 747-766. doi: 10.1139/x83-105

Van Wagner, C.E. 1972. Duff consumption by fire in eastern pine stands. Canadian Journal of Forest Research 2: 34-39. doi: 10.1139/x72-006

Van Wagner, C.E. 1987. The development and structure of the Canadian Forest Fire Weather Index System. Canadian Forest Service, Petawawa National Forestry Institute, Chalk River, Ontario.

Viereck, L.A. 1983. The effects of fire in black spruce ecosystems of Alaska and northern Canada. Pages 201-220 in: R.W. Wein and D.A. MacLean, editors. The role of fire in northern circumpolar ecosystems. John Wiley & Sons, New York, New York, USA.

Wang, C., B. Bond-Lamberty, and S.T. Gower. 2003. Carbon distribution of a well- and poorly-drained black spruce fire chronosequence. Global Change Biology 9: 1066-1079. doi: 10.1046/j.1365-2486.2003.00645.x

Wang, G.G., and K.J. Kemball. 2005. Effects of fire severity on early development of understory vegetation. Canadian Journal of Forest Research 35: 254-262. doi: 10.1139/x04-177

Wardle, D.A., G. Hornberg, O. Zackrisson, M. Kalela-Brundin, and D.A. Coomes. 2003. Long-term effects of wildfire on ecosystem properties across an island area gradient. Science 300: 972-975. doi: 10.1126/science.1082709

Wardle, D.A., O. Zackrisson, G. Hornberg, and C. Gallet. 1997. The influence of island area on ecosystem properties. Science 277: 1296-1299. doi: 10.1126/science.277.5330.1296

Wiken, E.B. 1986. Terrestrial ecozones of Canada. Environment Canada, Gatineau, Quebec.

Wirth, C. 2005. Fire regime and tree diversity in boreal forests: implication for the carbon cycle. Pages 309-344 in: M. Scherer-Lorenzen, C. Körner, and E.-D. Schulze, editors. Forest diversity and function. Temperate and boreal systems. Springer-Verlag, New York, New York, USA.

Wotton, B.M. 2009. Interpreting and using outputs from the Canadian Forest Fire Danger Rating System in research applications. Environmental and Ecological Statistics 16: 107-131. doi: 10.1007/s10651-007-0084-2

Wotton, B.M., and J.L. Beverly. 2007. Stand-specific litter moisture content calibrations for the Canadian Fine Fuel Moisture Code. International Journal of Wildland Fire 16: 463-472. doi: 10.1071/WF06087

Wotton, B.M., and M.D. Flannigan. 1993. Length of the fire season in a changing climate. Forestry Chronicle 69: 187-192.

Wotton, B.M., C.A. Nock, and M.D. Flannigan. 2010. Forest fire occurrence and climate change in Canada. International Journal of Wildland Fire 19: 253-271. doi: 10.1071/WF09002

Yu, Z., M.J. Apps, and J.S. Bhatti. 2002. Implications of floristic and environmental variation for carbon cycle dynamics in boreal forest ecosystems of central Canada. Journal of Vegetation Science 13: 327-340. doi: 10.1111/j.1654-1103.2002.tb02057.x

Zoltai, S.C., L.A. Morrissey, G.P. Livingston, and W.J. de Groot. 1998. Effects of fires on carbon cycling in North American boreal peatlands. Environmental Reviews 6: 13-24. doi: 10.1139/er-6-1-13