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Shifting zonal patterns of the southern boreal forest in eastern Canada associated with changing fire regime during the Holocene

Guillaume de Lafontaine*, Serge Payette

NSERC Northern Research Chair, Centre d'études nordiques, Département de Biologie, Université Laval, 1045 av. de la Médecine, Québec (QC), Canada, G1V 0A6

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A B S T R A C T

This research aims at uncovering the stand-scale Holocene fire history of balsam fir forest stands from two bioclimatic zones of the boreal forest and assessing the existence of a sub-continental shift in past fire activity that could have triggered a change in the Holocene zonal pattern. In eastern Canada, the extant closed-crown boreal forest corresponds to two ecological regions separated along 49°N, the northern black spruce zone and the southern balsam fir zone. We sampled balsam fir stands from the southern fir zone ($n = 7$) and among the northernmost patches of fir forest located far beyond the fir zone boundary, into the spruce zone ($n = 6$). Macrofossil analysis of charcoal in mineral soils was used to reconstruct both the stand-scale and regional Holocene fire histories. Data were interpreted in the context of published palaeoecological evidence. Stands of the balsam fir zone were submitted to recurrent fire disturbances between *c.* 9000 and 5000 cal. yr B.P. Local fire histories suggested that four sites within the fir zone escaped fire during the Holocene. Such fire protected sites allowed the continuous maintenance of the balsam fir forest in the southern boreal landscape. Stands of the spruce zone have been affected by recurrent fires from 5000 cal. yr B.P. to present. Local fire histories indicated that no site escaped fire in this zone. Published palaeoecological data suggested that balsam fir migrated to its current northern limit sometime between 7300 and 6200 cal. yr B.P. A change of the fire regime 5000 years ago caused the regional decline of an historical northern balsam fir forest and its replacement by black spruce forest. The consequence was a sub-continental reshuffling of the fir and spruce zones within the closed-crown boreal forest. The macrofossil analysis of charcoal in mineral soils was instrumental to the reconstruction of stand-scale Holocene fire history at sites where no other *in situ* fire proxies were available.

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1. Introduction

The circumboreal biome is subdivided into three extensive vegetation zones from south to north: the closed-crown forest, the open forest and the forest-tundra, respectively (Hare and Ritchie, 1972). These vegetation zones represent different plant communities as a function of climate (Larsen, 1980). Davis (1981) suggested climate change prevailing during the late Wisconsinan–early Holocene (*c.* 25,000–6500 cal. yr B.P.) as the ultimate cause for the post-glacial spread of tree species. However, rate of tree migration and geographic range of tree species were not always in equilibrium with climate as the post-glacial spread of species relied on propagules availability and establishment capacity of seedlings competing with other species already occupying favourable sites (Davis, 1981).

Heinselman (1981) outlined the instrumental role played by wildfires in structuring forest communities in the boreal biome. Consequently, Payette (1992) developed a model which states that the structure of vegetation zones, distribution of forest communities and presence/absence of tree species in different areas of the boreal landscape during the Holocene was a direct consequence of fire disturbance. The geographic range of a species has two major components, the distribution boundaries and the relative abundance of individuals within the range (Lomolino et al., 2006). The current range boundaries of a boreal tree species would correspond to its maximum Holocene expansion, driven by climate, whereas regional abundance within its range would be associated with prevailing disturbance regime (Payette, 1993).

The divergent community model of Payette (1992) suggests that more than a single 'climax' community type (alternative stable

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* Corresponding author. Present address: INRA, UMR BIOGECO 1202, 69 Route d'Arcachon, 33610, Cestas, France. Tel.: +33 5 57 12 28 25; fax: +33 5 57 12 28 81.
E-mail addresses: gdelafon@pierroton.inra.fr, guillaume.de-lafontaine.1@ulaval.ca (G. de Lafontaine).

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states) can theoretically exist on a given site (May, 1977; Scheffer et al., 2001). The shift from one community type to another may be due to regeneration failure during secondary succession after a disturbance or a series of compounded disturbances (Paine et al., 1998; Payette et al., 2000). At the sub-continental scale, such community transformations over the landscape may affect the geographic range of species and modify the zonal patterns of dominant vegetation assemblages. Empirical examples of the model were recently assessed in different vegetation zones of the boreal forest in eastern North America. Forest opening of the forest-tundra zone was caused by increased fire activity over the landscape starting *c.* 3200 cal. yr B.P. (Asselin and Payette, 2005). Lichen woodland patches located in moist, fire protected depressions are the remains of a forest cover more extensive prior to the change of the fire regime (Payette et al., 2001). The southernmost lichen woodland stands are located within the closed-crown forest zone and originate from post-fire regeneration failures beginning *c.* 1400 cal. yr B.P. (Jasinski and Payette, 2005). Here forest opening, triggered by wildfire activity, is currently ongoing all over the closed-crown forest zone at a faster pace over the last 100 years (Girard et al., 2008, 2009). Correspondingly, the northernmost closed-crown forest patches within the adjacent open forest zone are old-growth stands which escaped fire over the last centuries up to several millennia (Pollock and Payette, 2010). Such marginal stands are remnants of a once more extensive closed-crown forest zone which expanded further north prior to its transformation into lichen woodland zone caused by wildfire (Pollock and Payette, 2010). These empirical examples from the northern boreal landscape describe a general biogeographical pattern consistent with the divergent community model. Each vegetation zone is characterized by a dominant forest type (e.g. the open forest zone is characterized by lichen woodland). The relative abundance of each forest type throughout the landscape may be described by a normal distribution according to the latitude (Payette, 1992; Timoney et al., 1993). The greatest relative abundance (the mode of the latitudinal normal distribution) of a given forest type lies in the geographical centre of its corresponding vegetation zone and declines towards the northern and southern boundaries of the zone. The disjunct northernmost stands (northern tail of the normal distribution) are residual stands which have escaped the current fire regime (Payette, 1992; Payette et al., 2001) whereas the southernmost stands (southern tail of the normal distribution) originate from recent forest transformations caused by the disturbance (fire) regime (Payette et al., 2000).

In eastern North America, the closed-crown forest corresponds to two ecological regions roughly divided at 49°N (Lafond, 1964; Grandtner, 1966; Fig. 1). South of 49°N, the moist balsam fir (*Abies balsamea* (L.) Mill.) forest zone (fir zone, thereafter) is a mixed forest dominated by balsam fir along with white spruce (*Picea glauca* (Moench) Voss.) and white birch (*Betula papyrifera* Marsh.) as companion species. North of 49°N, the black spruce (*Picea mariana* (Mill.) B.S.P.) forest zone (spruce zone, thereafter) is dominated by extensive tracts of closed-crown black spruce forest interspaced with monospecific stands of jack pine (*Pinus banksiana* Lamb.). Of all the widespread North American boreal tree species, white spruce and especially balsam fir are the least adapted to fire, whereas jack pine and black spruce are fire-adapted species (Rowe and Scotter, 1973), suggesting fire as a major force accounting for the distinctiveness of the fir zone and spruce zone.

The northernmost patches of fir forest are located beyond the fir zone boundary, into the spruce zone up to the southern edge of the open forest zone (Fig. 1). These disjunct stands are distributed in the moist subalpine belt of three high-elevated plateaus (*c.* 1000 m above sea level [a.s.l.]) in central Québec, *c.* 300–500 km north of the fir zone. Under the hypothesis that the fir zone conforms to the divergent community model, subalpine balsam fir stands isolated in a matrix of lowland black spruce forests could be the remnants of a past northern expansion of the fir zone. The regional decline of such extensive northern fir forests in the lowlands and their replacement by extant spruce forests could be a consequence of a change in the fire regime favouring fire-prone species (black spruce and jack pine) over fire intolerant species (balsam fir and white spruce). Indeed, stands of the spruce and the fir zones are currently characterized by two distinct fire regimes, with a greater fire activity in the spruce zone compared to that of the fir zone (de Lafontaine and Payette, 2010). However, a direct comparison of the long term (i.e. Holocene) fire histories between the two zones has never been done.

We hypothesize that a period of low fire activity prevailed in the past to allow the northern expansion of fire intolerant plant assemblages (i.e. balsam fir forest flora). This expansion probably occurred sometime in the past prior to the establishment and development of the current fire regime favouring black spruce forests in the northern closed-crown forest (de Lafontaine and Payette, 2010). The first objective of this investigation is to uncover the local (i.e. stand scale) Holocene fire history of extant, old-growth balsam fir stands located in the fir zone and the spruce zone. The second objective is to assess the existence of a sub-continental

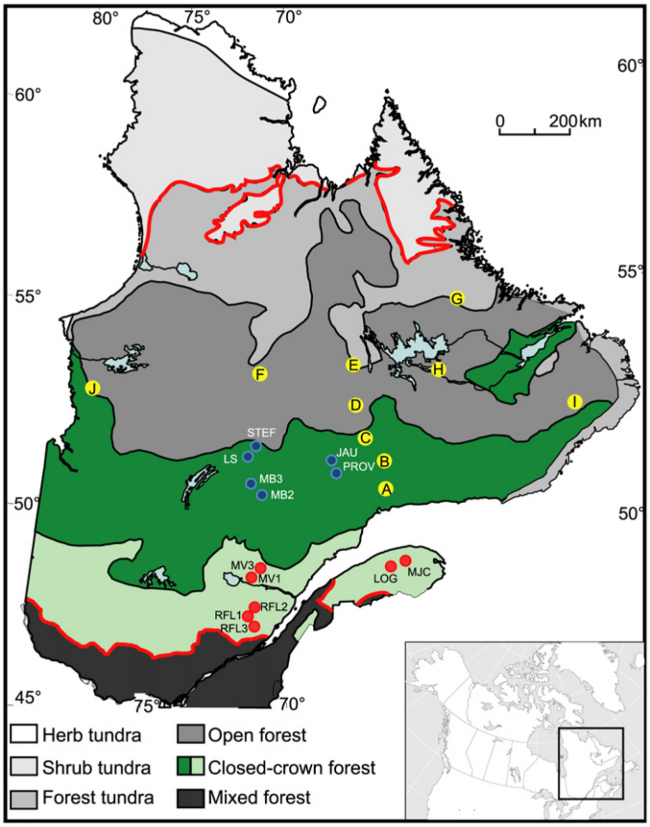

Fig. 1. Location of sampled sites. The main bioclimatic zones of Québec are represented; the zones corresponding to the boreal biome are between the two red lines. Note that the closed-crown forest is roughly subdivided along 49°N in two ecological regions represented by different shades of green; paler green represents the balsam fir zone whereas darker green represents the black spruce zone. Red dots ($n = 7$) show study sites in the balsam fir zone and blue dots ($n = 6$) study sites within the black spruce zone. Yellow circles indicate the sampling location of the published palaeoecological data discussed in the present study (A–E: King (1986); F: Richard et al. (1982); G: Lamb (1985); H: Morrison (1970); I: Lamb (1980); Engstrom and Hansen (1985); J: Arsenault and Sirois (2004)). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article).

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