Fire frequency and vegetation dynamics for the south-central boreal forest of Quebec, Canada

Daniel Lesieur, Sylvie Gauthier, and Yves Bergeron

Abstract: Fire history and forest dynamics were reconstructed for a 3800-km^2 territory located in the south-central boreal forest of Quebec. Fire cycle was characterized using a random sampling strategy combined with archival data on fires that had occurred since 1923 on private land owned by Smurfit-Stone. Bioclimatic subdomain, land use, surficial deposit, and mean distance from a firebreak did not affect the fire cycle. Fire cycles have been longer since the end of the Little Ice Age (~1850). Warming after the Little Ice Age seems to have triggered a change in fire frequency. Forest dynamics were characterized by transition matrices for changes in dominant canopy composition from 344 permanent sampling plots. These permanent plots were sampled approximately every 15 years over the preceding 40 years. We observed two distinct patterns of replacement: (*i*) deciduous and mixed stands were replaced by balsam fir (*Abies balsamifera* (L.) Mill.) (and, to a lesser extent, by black spruce (*Picea mariana* (Mill.) BSP)) and (*ii*) jack pine (*Pinus banksiana* Lamb.) was replaced by black spruce. Analyses confirm that species replacement occurs in the eastern boreal forest of Canada when the fire-return interval is long enough and that the substrate plays an important role along with other disturbances, such as insect outbreaks. Our results also suggest that the proportion of old-growth forests (>100 years old) in the landscape should increase as a result of the lengthening of the fire cycle. More and more stands are likely to experience species replacement. From the standpoint of sustainable forest management, this perspective calls into question the widespread use of clear-cutting in the boreal forest. Regional context must be taken into account in forest management if the conservation of biodiversity and ecosystem integrity are serious objectives. Economically and ecologically sound silvicultural scenarios that emulate natural processes are discussed.

Résumé : L'histoire des feux et de la dynamique forestière a été reconstruite pour le territoire privé de Smurfit-Stone (3800 km^2) situé dans le centre-sud de la forêt boréale du Québec. Le cycle des feux a été caractérisé à l'aide d'un échantillonnage aléatoire du territoire ainsi qu'avec les données d'archives de la compagnie pour les feux survenus depuis 1923. Les résultats suggèrent que le cycle des feux ne varie pas en fonction des sous-domaines bioclimatiques, des régions sous exploitation forestière, des dépôts de surface ainsi que de la distance moyenne à un coupe feu. Le cycle des feux est toutefois plus long depuis la fin du petit âge glaciaire (~1850). La dynamique forestière a été caractérisée en développant des matrices de transition de la composition de la canopée à partir de 344 placettes échantillons permanentes. Celles-ci ont été échantillonnées environ à tous les 15 ans au cours des 40 dernières années. Deux patrons de remplacements ont été observés : (*i*) les peuplements feuillus et mixtes sont remplacés par les peuplements dominés par le sapin baumier (*Abies balsamifera* (L.) Mill.) (et, dans une moindre mesure, par les peuplements d'épinette noire (*Picea mariana* (Mill.) BSP)) et (*ii*) les peuplements de pin gris (*Pinus banksiana* Lamb.) sont remplacés par les peuplements d'épinette noire. Les matrices de transition ont permis de confirmer que le remplacement des espèces en forêt boréale est possible lorsque le temps entre deux perturbations est suffisamment long et que les dépôts de surface ainsi que les perturbations secondaires comme les épidémies d'insectes jouent également un rôle important dans la dynamique. Nos résultats indiquent également que la proportion de forêts agées de plus de 100 ans occupe une place importante dans le paysage et que cette proportion devrait augmenter conséquemment à l'allongement du cycle des feux depuis la fin du petit âge glaciaire. Du point de vue de la gestion durable des forêts, nos résultats remettent en question, pour la forêt boréale, l'emploi généralisé de la coupe totale sur de courtes révolutions. La fréquence des feux à l'échelle régionale et ses conséquences sur la diversité de la mosaïque forestière naturelle devraient être considérées dans les plans d'aménagement si le maintien de la diversité biologique et de l'intégrité des écosystèmes constitue un objectif à atteindre. Des scénarios économiquement et écologiquement viables sont discutés.

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Introduction

The fire regime in the Canadian boreal forest has been characterized by large crown fires burning at short intervals (Johnson 1992; Heinselman 1973). Many studies (Bergeron 1991; Engelmark et al. 1994; Larsen 1997; Weir et al. 1999; Bergeron et al. 2001) have shown that the fire cycle can vary from one region to another. Moreover, these studies have independently reported decreases in fire frequency in different parts of the boreal forest since the end of the Little Ice Age (~1850). In eastern Canada, a change in the distribution of precipitation is believed to be the cause of the reduction in fire frequency (Bergeron and Archambault 1993).

In addition to climate, other factors are believed to play important roles in controlling the fire regime at a regional scale (Gauthier et al. 1996; Turner and Romme 1994; Johnson 1992; Fryer and Johnson 1988; Cogbill 1985; Foster 1983). For example, a high proportion of deciduous trees in the landscape may limit the spread of fires (Hély et al. 2001). Waterbodies are also reported to be highly effective natural barriers to the spread of fires (Larsen 1997; Bergeron 1991; Foster 1983; Hemstrom and Franklin 1982). Similarly, fragmentation caused by logging operations and road development may keep fires from spreading, thus altering the fire regime and resulting in a lengthening of the fire cycle. Improved access and deployment for land-based firefighting teams is also reported to alter the fire regime (Weber and Stocks 1998). Although some studies suggest that fire suppression has caused a lengthening of the fire cycle (Tande 1979; Wein and Moore 1979; Barrett et al. 1991), many authors (Johnson 1992; Master 1990; Bergeron 1991; Larsen 1997) consider that fire suppression has had a minimal influence, especially prior to the use of water bomber tankers around 1970 in Quebec (Bergeron 1991; Langlois 1994; Lefort 1998).

Many studies have suggested that high fire frequency limits species replacement in the canopy and that succession, therefore, tends to be cyclical (Dix and Swan 1971; Gagnon 1989; Johnson 1992). However, some investigators, using the chronosequence approach, have suggested that species replacement occurs when the fire-return interval is sufficiently long (Day 1972; Cogbill 1985; Bergeron and Dubuc 1989; DeGrandpré et al. 1993; Frelich and Reich 1995; Bergeron 2000; Gauthier et al. 2000). The longer the interval between two disturbance events, the more likely it is for the forest to reach an advanced stage of succession (Day 1972; DeGrandpré et al. 1993; Gauthier et al. 2000). Van Cleve and Viereck (1981) and Bergeron and Charron (1994) pointed out that the dominance of shade-intolerant species in the overstory following a disturbance is due mainly to differential growth rates rather than to the delayed arrival of tolerant species.

Considering the importance of fire frequency in relation to forest dynamics, improved knowledge of the disturbance regime and of natural succession would permit predictions of the composition and age structure of forests that should characterize the natural landscape (Leduc et al. 1995; Gauthier et al. 1996). This would allow the development of new forest management approaches that emulate natural processes (Attiwill 1994; Bergeron and Harvey 1997; Bergeron et al. 1999*a*, 1999*b*).

The south-central boreal forest of Quebec has been extensively managed throughout the last century. Unlike many other regions of the boreal forest, few studies have been conducted in this region. To improve our knowledge and understanding for this part of the boreal forest, we reconstructed fire-history and vegetation dynamics. Our objectives were (*i*) to determine whether differences in forest composition and physiography cause spatial variation in the fire cycle and (*ii*) to determine successional patterns following fire in the study area. In contrast with previous studies, succession was reconstructed from data collected at the same sites through time. This makes it possible to confirm or refute the existence of species replacement over time in the boreal forest.

Study area

The study area is located in the Upper Mauricie region (74°52′55″–73°45′15″W and 47°57′13″–49°08′22″N) near Gouin Reservoir, Quebec (Fig. 1). It covers an area of 3844 km^2 and is part of the Gouin sector of the broad boreal forest region (Rowe 1972). The area covers two subzones for forestry operations, the southern region and the northern region, which have areas of 1484 and 2360 km^2, respectively. Large-scale timber harvesting began during the 1940s in the southern region and in the late 1970s in the northern region. The territory is primarily occupied by the Western Balsam Fir – White Birch bioclimatic subdomain (76%) but also contains the Western Black Spruce – Moss subzone (24%) (Saucier et al. 1998). Balsam fir (*Abies balsamifera* (L.) Mill.) (Sirois 1997), white birch (*Betula papyrifera* Marsh.), trembling aspen (*Populus tremuloides* Michx.), black spruce (*Picea mariana* (Mill.) BSP), white spruce (*Picea glauca* (Moench) Voss), and jack pine (*Pinus banksiana* Lamb.) are the most abundant tree species (Grondin et al. 1996). Both subdomains are composed of the same species but in different proportions, with more black spruce and less balsam fir in the Western Black Spruce – Moss (Grondin et al. 1996). Unconsolidated deposits consist mainly of the glacial and glaciofluvial type throughout the region (Table 1), interspersed with rocky and organic deposits and, less commonly, aeolian, fluvial, and lacustrine deposits (see also Robitaille and Saucier 1998).

The nearest weather station located at Gouin Dam (74°06′W, 48°21′N) (Fig. 1) was in operation from 1914 to 1981. The annual mean temperature and precipitation were 0.8°C and 948.4 mm, respectively, and there were means of 2104.1 degree-days/year above 0°C and 93 frost-free days per year (Environnment Canada 1982*a*, 1982*b*, 1982*c*). The prevailing wind direction for the region is westward.

Methods

Fire-history reconstruction

To characterize the fire cycle, we used data on burned areas (>2 ha) since 1923 within the study area from the archives of Smurfit-Stone (formally Cartons St.-Laurent and C.I.P.). Smurfit-Stone also has a network of about 800 permanent transects established since 1959 in the study area. Transect locations were determined by Smurfit-Stone using a random systematic sampling design (D. Thibault, personal communication). Each transect has three permanent plots of

Fig. 1. Location of the study area within eastern Canada showing the northern (1) and southern (2) regions.

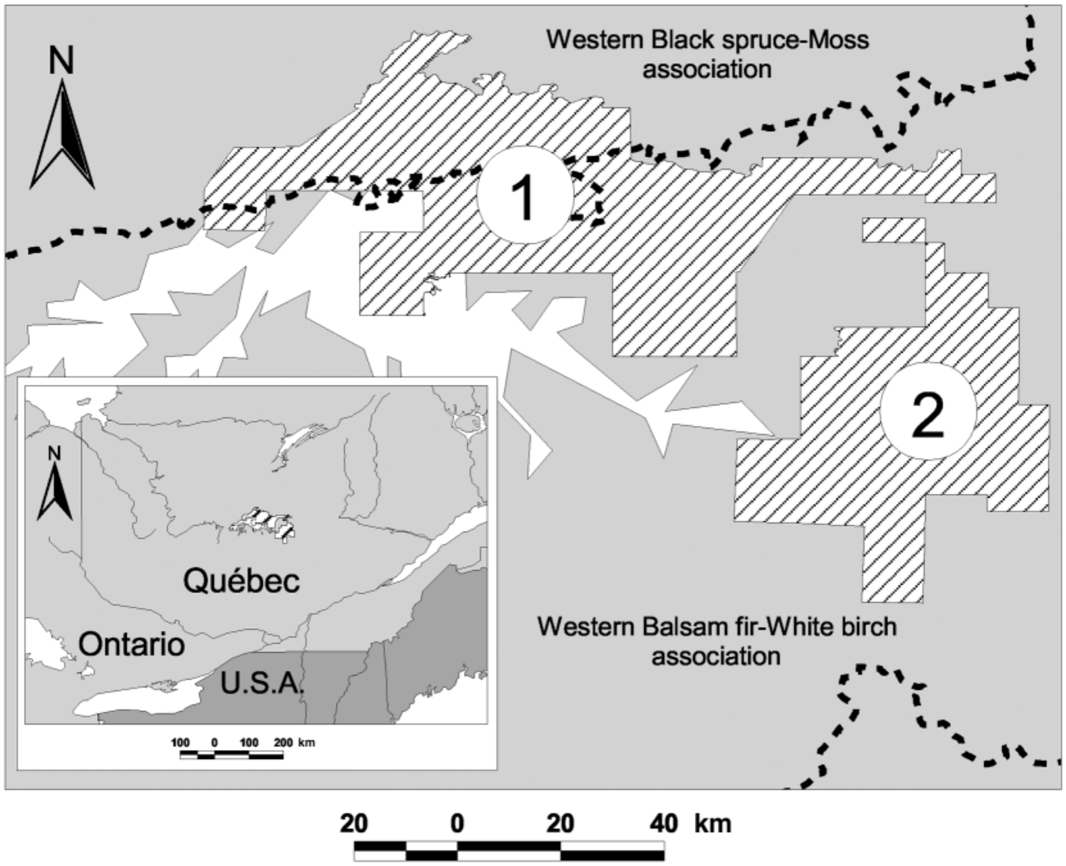


Table 1. Area covered by different surficial deposit types in the study area.

Surficial deposits	North (ha)	South (ha)	Total (ha)
Glacial	144 405 (73%)	108 123 (78%)	252 528 (75%)
Glaciofluvial	36 279 (18%)	18 209 (13%)	54 488 (16%)
Organic	8 870 (4%)	966 (<1%)	9 836 (3%)
Rock outcrops	9 135 (5%)	10 210 (7%)	19 345 (6%)
Others	142 (<1%)	1 040 (<1%)	1 182 (<1%)

Note: Values in parentheses are percentages of the total area made up by each deposit type. Area data are from Smurfit-Stone Inc. GIS database (1 : 50 000).

400 m^2, spaced about 400 m apart. In conjunction with the Smurfit-Stone inventories conducted in 1997 and 1998, 157 of the 800 transects were randomly selected to characterize the fire cycle. The archive date was determined for transects situated in mapped fire zones (43% of transects). For the remaining transects, dendrochronological analysis was used to determine the date of the last fire (Arno and Sneck 1977).

Sample collection and analysis

Five trees in each permanent plot were sampled using an increment borer or a chainsaw. Two increment cores or a disk were taken at the basis of each tree. Trees were selected subjectively; jack pine was selected first since this species presence generally corresponds to post-fire recruitment (Eyre 1938). In addition, cross sections were taken with a chainsaw from any dead or fire-scarred tree encountered. Soils were also sampled for the presence of charcoal at the surface of the mineral soil as evidence of past forest fire activity (Cogbill 1985). Physiographic characteristics (e.g., soil type) for each plot were assessed (ministère des Ressources naturelles du Québec 1994).

The age of the sanded cross sections was determined by standard dendrochronological analysis by examining at least two radii on each disk (Arno and Sneck 1977). Masters chronology was developed for white birch, black spruce, and jack pine to cross-date the sampled dead trees (Yamaguchi 1991). Cross dating was done by hand and validated using COFECHA© (Holmes 1999).

For samples with fire scars, the year of the fire was accurately determined by computing the number of annual growth rings between the year of sampling and the scar year (Arno and Sneck 1977). Trees without scars provided a fairly accurate approximation of the time since last fire if at least three of five samples from a given permanent plot had

Table 2. Classification of canopy composition.

Stand types	Code	Description*
Deciduous	Dec	Deciduous >75%
Mixedwood	Mix	Coniferous 50–75%
Jack pine	Jp	Jack pine >50% and coniferous >75%
Black spruce – jack pine	BsJp	Black spruce – jack pine >50% and coniferous >75%
Black spruce	Bs	Black spruce >50% and coniferous >75%
Balsam fir	Bf	Balsam fir >50% and coniferous >75%

*Based on basal area.

an establishment date within 10 years for jack pine or 20 years for other species (black spruce, white spruce, white birch, trembling aspen). The fire year for a transect was estimated using the age of the oldest tree in the overstory cohort (Bergeron and Dubuc 1989). When the samples did not permit a determination of the time since last fire, the age of the oldest tree was used as the minimum time since last fire, and the date was considered censored, which was taken into account in subsequent analyses. Land use region, bioclimatic subdomain, surfical deposit, and mean distance to a firebreak were determined for each transect. The latter is the mean of the distances to firebreaks (lake, river, stream, and bog) measured along each of the eight cardinal directions on 1 : 50 000 scale topographic maps. The distance to the western firebreak was also measured as it is the dominant wind direction.

Statistical analysis

In our study area, many factors (both spatial and temporal) may be responsible for a change in fire cycle. For instance, fire cycle could differ between the southern and northern regions for several reasons. First, logging began at different times. Second, the composition of the fuel materials in the Western Black Spruce – Moss bioclimatic subdomain may be more conducive to the spread of fires than the fuel composition in the Western Balsam Fir – White Birch bioclimatic subdomain (Hély et al. 2000, 2001); changes in composition at the scale of bioclimatic subdomain could engender changes in the length of the fire cycle. Third, fire cycle may differ with the type of surficial deposit; although it is generally assumed that this occurs, no studies have sought to verify this directly (however, see Bergeron 1991). Lastly, firebreaks appear to have an influence on fire spread (Larsen 1997). In terms of temporal changes, several studies have reported a change in fire cycle since the end of the Little Ice Age. Moreover, the study area may have been subject to a change in fire cycle owing to colonization, logging, or the start of fire suppression (Johnson et al. 1998; Lefort 1998; Weir et al. 1999). We therefore try to assess if the fire cycle remained constant as a function of these factors.

Given the low number of transects per surficial deposit, the data were grouped by broad type (glacial, glaciofluvial, and bedrock). We also divided the distribution temporally into two predetermined periods before and after 1850. This break point was selected, because the periods of climate warming recorded since the end of the Little Ice Age have often been reported as events that triggered changes in the length of natural fire cycles (Johnson et al. 1990; Bergeron 1991; Bergeron and Archambault 1993; Larsen 1997; Weir et al. 1999; Bergeron et al. 2001).

Several methods exist to estimate the fire cycle (the time required to burn an area equivalent to the study area). The mean stand age, the inverse of the mean annual burned area or a maximum likelihood survival analysis estimation (Johnson and Gutsell 1994) are three methods we used to evaluate the fire cycle in the study area. The inverse of the mean of annual area burned was used to assess the global fire cycle for the entire area, based on the total area burned between 1923 and 1998. Moreover, for the same time period we estimated the fire cycle using the maximum likelihood survival analysis using either the truncated time since fire map or the time since fire distribution derived from the random sample plots. Maximum likelihood survival analyses were also used to evaluate whether the fire cycle was constant as a function of land use, vegetation association, surficial deposits, mean water distance, and climatic period. The analysis (PROC LIFEREG; SAS Institute Inc. 1990) allowed to test whether the age-class distribution fit a negative exponential or a Weibull distribution and can be used to verify the effect of the preceding factors. In addition, this procedure permits censored data (minimum time since last fire) to be taken into account while estimating the fire cycle. Only 16% of the data were classified as "censored". To our knowledge, few studies have taken censored data into account in determining fire cycles.

Vegetation dynamics: transition matrices

To investigate vegetation dynamics, we used 344 plots that met the following conditions: there was no disturbance from logging, the time since last fire was known, there were at least two inventory years of data (between 1959 and 1997), and total basal area exceeded 5 m^2/ha in the first inventory. The lower limit of 5 m^2/ha was required for a plot to receive the designation of "forest land".

For each inventory year, every plot was assigned to a stand type according to the classification system used in the second decennial inventory conducted by the Quebec Department of Natural Resources. Since there were few plots in some stands type, stand types were grouped into six broad classes (Table 2). Since different surficial deposits lead to different vegetation composition (Gauthier et al. 2000), plots were grouped according to the two broad classes of surficial deposit found in the region (glacial and glaciofluvial) to better assess species replacement in the canopy.

In the sample plots, the time elapsed between the first and the last measurements rarely exceeded 20 years, which is a relatively short time period to observe a change designation from one canopy composition class to another. Therefore,

Table 3. Fire cycle estimates for different time periods from different analyses.

Method	Time period investigated	Estimated fire cycle (years)*
Stand mean age	Global	127
1/annual mean area burned	1923–1998	136±29
Survival analysis (SAS) with burned area map	1923–1998	150 (143–157)
Survival analysis (SAS) with random permanent plots network	1923–1998	147 (116–187)
Survival analysis (SAS) with random permanent plots network	Before 1850	82 (61–111)
Survival analysis (SAS) with random permanent plots network	After 1850	176 (143–216)
Annual mean area burned.	After 1940	376±80

*Values are means ± SEs or 95% CI in parentheses.

we extended the time period covered by the study by modelling species basal area change in each plot over a 30-year period after the last inventory. In other words, the modelling exercise, while increasing the study time period, also increased the probability to observe a designation change. To do this, for each species we computed the annual change in basal area (ACB) using the following equation:

$$\mathrm{ACB} = \frac{\mathrm{BA}_2 - \mathrm{BA}_1}{t_2 - t_1}$$

where BA_2 is the total basal area of a given species in the last inventory, BA_1 is the total basal area of the same species in the first inventory, and $t_2 - t_1$ is the time period between the first and last inventories in years. The ACB were compiled for each species for each plot and for all trees >9 cm at diameter at breast height (DBH), multiplied by the desired time period (30 years), and then added to the basal area values obtained in the last inventory. Therefore, the ACB is a measure that includes natural mortality, mortality due to insect outbreak, growth, and recruitment for the plot.

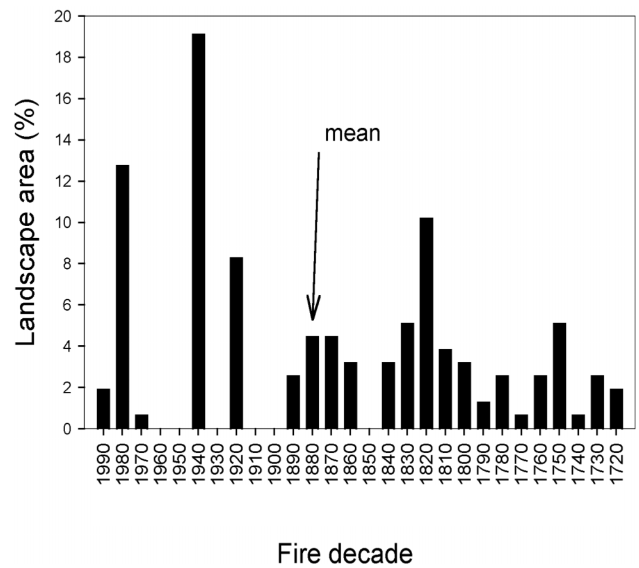
Afterwards, the plot was once again assigned to one of the six canopy composition classes. The final transition matrix allowed us to determine (*i*) the percentage of plots that had undergone a designation change during the study period and the patterns of change, (*ii*) the canopy composition that would be obtained by simulating a period of 30 years beyond the last inventory, and (*iii*) the level of agreement between the observed and modelled patterns.

Results

Fire map and records summary

The annual burned area between 1923 and 1998 was 2599 ± 11 983 ha (mean ± SD), 0.7% of the entire area. The area burned (with fire >2 ha) within the 10 fire years (1923, 1941, 1944, 1963, 1977, 1983, 1986, 1993, 1995, and 1998) varied enormously with a mean of 17 963 and an SD of 27 810 ha of forest. Figure 2 shows that about half of the landscape is characterized by stands that originated from major fire events during four decades (1980, 1940, 1920, and 1820). Provided that no logging had occurred, less than half (43%) of the study area would be composed of stands younger than 100 years, and the percentage of regenerating stands (<30 years) would be about 15%.

Fig. 2. Forest stand age distribution for the study area.



Fire-cycle estimates

Based on the fire record (1923–1998) the estimated fire cycle was 136 ± 29 years (Table 3). The fire cycle was slightly greater when estimated by the traditional likelihood method using burned areas from the time since last fire map truncated at the year 1923 (see Johnson and Gutsell 1994), or when the fire cycle was computed using a random distribution of sampling points likewise truncated at the year 1923 (Table 3). The fire cycle for the colonized period (>1940) was also assessed using burned mapped area and it was estimated at 376 ± 80 years (Table 3).

The mean time since the last fire is 127 years (Table 3). The global age-class distribution (Fig. 2) clearly does not follow a negative exponential distribution (inverse J). As indicated in Table 4, the time since last fire distribution for the entire territory does not fit a negative exponential and, therefore, appears to have a mixed distribution (Table 4), a situation that may be caused by a spatial and (or) temporal change in fire frequency (Johnson and Gutsell 1994). Therefore, we checked whether the mixed distribution was due to a mixture of landscapes that had distinct fire cycles. The fire cycle did not differ significantly between the northern and southern regions during the entire period despite the fact that they were logged during different periods (Table 4, Fig. 3). A comparison of the regions during the industrial era alone

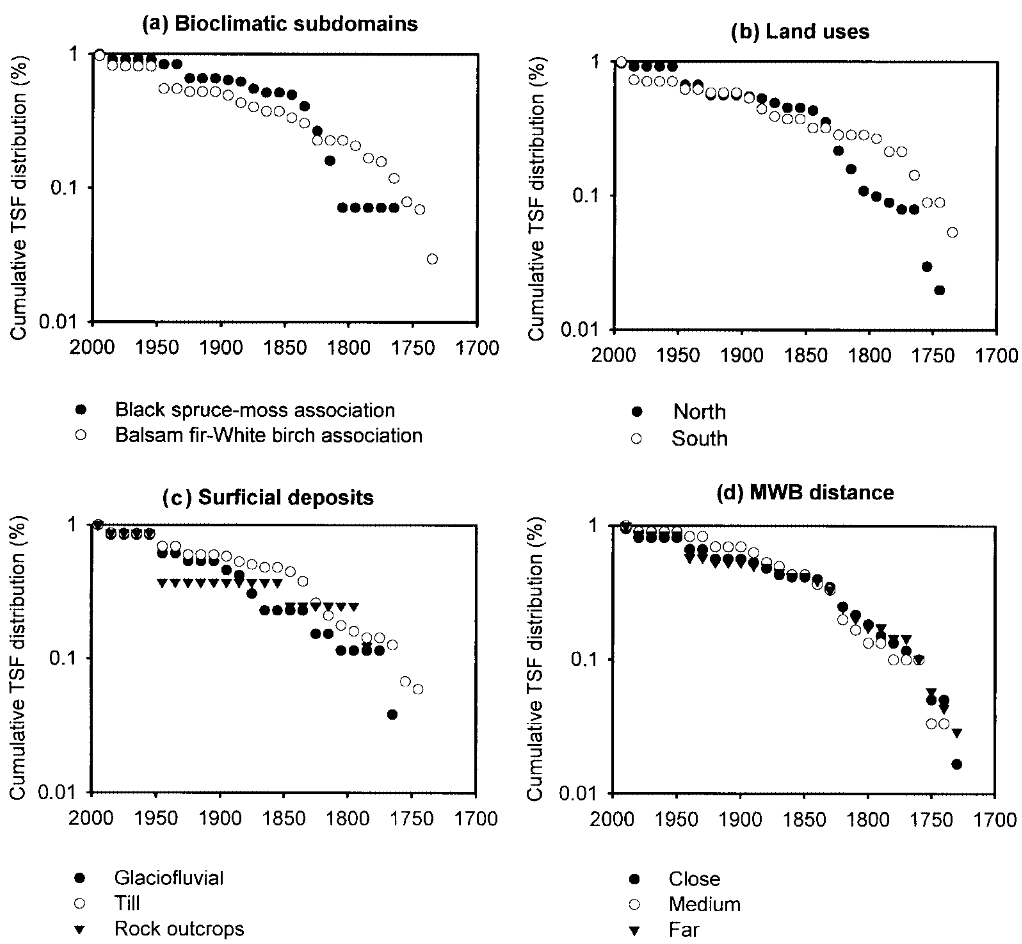
Table 4. Survival analysis and Lagrange probability results.

Time since fire distribution	Survival analysis ($p > \chi^2$)	Lagrange coefficient ($p > \chi^2$)
Total	—	0.0001
Land uses (north–south)	0.7906	0.0001
Land uses (north–south) industrial period (>1940)	0.2707	0.0001
Vegetation association (Black Spruce – Moss or Balsam Fir – White Birch)	0.9835	0.0001
Vegetation association with mapped burn area*	0.5010	0.0001
Surficial deposits (glacial, glaciofluvial, or rock outcrops)	0.1705	0.0001
Surficial deposits with mapped burn area*	0.2673	0.6894
Mean waterbreak distance (near, medium, or far)	0.8276	0.0001
Mean waterbreak distance (near, medium, or far) with respect to dominant wind direction (west)	0.4245	0.0001
Period (before 1850 or after 1850)	0.0001	0.0530

Note: Since distributions did not show a constant hazard of burning, fire cycles were computed for periods (before and after 1850) of relatively constant fire frequency only.

*The data on fires prior to 1963 were not used owing to their imprecise contour.

Fig. 3. Semilog cumulative time since fire distributions for the following comparisons: (*a*) subdomain subzones; (*b*) land uses; (*c*) surficial deposits; and (*d*) mean water break (MWB) distances. Note that computation of fire cycle with the maximum likelihood survival analysis were based on the observed age-class distributions and not on the reverse cumulative distribution. The cumulative time since fire is only used for presentation purposes.



(since 1940) yielded similar results (Table 4). From an ecological standpoint, the fire cycles also did not differ significantly by vegetation subdomain or broad class of surficial deposits (Table 4, Fig. 3). The conclusions are similar using the traditional method (based on the actual burned areas truncated at year 1963). The data on fires prior to 1963 were not used owing to their imprecise contours. Distance to firebreaks (streams, bogs, rivers, and lakes) did not have a significant effect on the time since last fire (Table 4, Fig. 3). When lakes alone or when distance with regard to dominant wind direction (west) were considered, there was still no difference (Table 4).

When considering the effects of the time periods, the survival analysis revealed a significant difference in fire cycle before and after 1850 (Table 4). In addition, the fire cycle for the two periods fits a negative exponential, suggesting a constant hazard of burning during both periods. The fire cycle for the period preceding the end of the Little Ice Age was shorter compared with the subsequent period (Table 3).

Vegetation dynamics

Transition on glacial deposits

Forest dynamics were very diverse on glacial deposits during the period studied. In the first inventory, about one-quarter of the plots (74 of 294) were dominated by stands with a large proportion of shade-intolerant deciduous trees (deciduous and mixed stands), less than 10% were dominated (Jp) or codominated by jack pine and black spruce (BsJp), 30% were stands dominated by black spruce, and more than one-third of the plots were dominated or codominated by balsam fir (Table 5). Mean time since last fire at the first inventory (Table 5) suggest patterns of replacement from deciduous to balsam fir forest types or from jack pine to black spruce forest types. Those trends were confirmed by the transition matrices (see below).

Among the plots dominated by deciduous trees, 55% remained into the deciduous class, whereas 40% changed into mixedwood forest and balsam fir dominated stands, and 5% became black spruce stands. For the predicted stands 30 years after the last inventory, the transition rate increased from 45 to ~60%, mostly because of further stands becoming dominated by balsam fir. In all cases, there was a trend of increasing conifer abundance, consisting mainly of balsam fir. The number of plots dominated by deciduous trees in the last inventory increased slightly over the first inventory: the new deciduous stands were derived primarily from mixed and balsam fir stands.

Nearly half of the mixedwood plots (46%) changed during the monitoring period. The highest rate of transition was toward balsam fir, followed by black spruce and deciduous stands. Following the modelling period, the transition rate rose to 75% with more than half of this total (54%) changing into balsam fir stands. Of the plots that did not undergo a transition, 71% nonetheless showed an increase in the basal area of spruce and (or) balsam fir (results not shown). About half of the new mixedwood stands originated from deciduous stands, which is consistent with chronosequence studies, and the other half from balsam fir stands. Only very small proportions were derived from black spruce dominated stands.

In balsam fir dominated plots, 80% did not undergo a transition, 8% changed toward stands with a greater abundance of black spruce, and 12% developed into stands dominated or codominated by deciduous trees. Extending the transition period caused a decrease in the proportion of balsam fir stands in the landscape and doubled the transition rate toward deciduous and black spruce stands. In some cases, the stands lost their designation as forested land, because the basal areas fell to under 5 m^2/ha. The new balsam fir stands developed mainly from deciduous and mixed stands, especially for the modelled period.

For the jack pine plots, canopy composition changed for only one-quarter of the plots, with most of these undergoing a transition to black spruce assemblages. The transition rate from Jp to BsJp tripled for the modelled period. None of the plots gave rise to jack pine stands, except for one black spruce stand in the modelled period. The mean time since last fire in the first inventory did not differ significantly from the other assemblages, whereas in the last inventory the time since last fire was significantly longer for plots that had undergone a transition (F = 5.64, p > 0.0368, df = 12).

There was a transition for more than half of the plots codominated by jack pine and black spruce; the majority of which changed to black spruce dominated stands. The transition rate rose to 75% for the modelling period, also mostly towards black spruce stands. BsJp stands originated almost exclusively from Jp stands.

As for balsam fir stands, black spruce stands also underwent very few transitions during the investigated period. The highest transition rate was toward balsam fir stands. When the study period was extended through simulation, the transition rate increased, primarily toward balsam fir. A few plots lost their designation as forested land, given the high rate of tree mortality encountered in some stands. Very few stands developed into black spruce stands; although for the simulated period, there was a slight increase in the number of mixedwood and balsam fir stands that changed into black spruce stands. Overall, the transition rate after an additional period of 30 years for plots on glacial deposits was 48%. The transition rate increased for every stand type.

Transition on glaciofluvial deposits

In contrast with glacial deposits, there appears to be very little diversity in species and forest dynamics for stands growing on glaciofluvial deposits, since all of the plots were dominated by conifer species (Table 6). Furthermore, more than half of the plots were dominated by black spruce in the first inventory. The mean time since last fire in the first inventory was significantly shorter for plots dominated by jack pine compared with black spruce. During the modelled period the transition rate increased by 18%. The BsJp plots had the largest increase in the transition rate, followed by black spruce and jack pine plots.

Sixty percent of the jack pine dominated plots underwent a transition during the study period, all of them toward BsJp stands. The mean time since last fire in the first inventory was significantly longer for plots where a transition occurred compared with those that had no transition (F = 10.51, p > 0.0101, df = 10). Following the modelled period, black spruce dominance increased in the stands; one plot even changed to a black spruce community. Balsam fir (>9 cm DBH) was not found in any of the jack pine plots.

Although there was no transition to other stand types during the investigated period, all of the BsJp plots showed an increase in the proportion of black spruce. Although this increase was not sufficient to result in a change in stand type, most of these stands were reclassified as black spruce stands

Table 5. Stand transitions on glacial deposits.

First*	Time first–last[†]	TSF[‡]	Dec. %row[§]	Dec. %col[¶]	Mix. %row	Mix. %col	Bf %row	Bf %col	Jp %row	Jp %col	BsJp %row	BsJp %col	Bs %row	Bs %col	Non-forested %row	Non-forested %col	Total frequency
Last inventory																	
Dec.	14.96±1.65	63±6*ab*	55	46	27	14	13	3	—	—	—	—	5	1	—	—	22
Mix.	16.56±1.46	88±6*ac*	8	15	54	65	29	12	—	—	—	—	9	6	—	—	52
Bf	16.28±0.93	91±3*c*	5	23	7	16	80	75	—	—	—	—	8	10	—	—	111
Jp	17.85±2.66	40±4*b*	8	4	—	—	—	—	77	100	15	33	—	—	—	—	13
BsJp	17.88±4.16	75±13*abcd*	12	4	—	—	12	1	—	—	38	50	38	3	—	—	8
Bs	20.41±1.14	108±4*d*	2	8	2	5	13	9	—	—	1	17	82	80	—	—	88
Total frequency	17.60±0.59		26		43		119		10		6		90		—		294
Predicted stands																	
Dec.			41	27	9	8	41	8	—	—	—	—	9	2	—	—	22
Mix.			15	24	25	52	41	28	—	—	—	—	15	9	4	10	52
Bf			11	37	6	28	56	57	—	—	—	—	17	21	10	52	111
Jp			—	—	8	4	—	—	46	86	46	75	—	—	—	—	13
BsJp			—	—	—	—	12	1	—	—	25	25	38	3	25	10	8
Bs			5	12	2	8	17	14	1	14	—	—	68	65	7	28	88
Total frequency			33		25		108		7		8		92		21		294

*Dec., deciduous; Mix., mixedwood; Bf, balsam fir; Jp, jack pine; BsJp, black spruce – jack pine; Bs, black spruce.
[†]Time first–last, time between first and last inventory (mean ± SE).
[‡]TSF, time since fire; values with different letters are significantly different at $p < 0.05$.
[§]% row, percentage of the plots in the forest type in the first inventory that have changes to the stand type at the last inventory.
[¶]% col, percentage of the plots in the forest type in the last inventory originating from the stand type in the first inventory.

Table 6. Stand transitions on glaciofluvial deposits.

First inventory*	Time first–last†	TSF‡	Jp %row§	Jp %col¶	BsJp %row	BsJp %col	Bs %row	Bs %col	Bf %row	Bf %col	Non-forested %row	Non-forested %col	Total frequency
Last inventory													
Jp	24.80±3.61	55±12*a*	40	100	60	60	—	—	—	—	—	—	10
BsJp	17.25±5.61	86±26*bc*	—	—	100	40	—	—	—	—	—	—	4
Bs	17.94±1.48	103±5*c*	—	—	—	—	100	100	—	—	—	—	32
Bf	10.25±0.95	93±11*bc*	—	—	—	—	—	—	100	100	—	—	4
Total frequency	18.64±1.34		4		10		32		4		—		50
Predicted stands													
Jp			30	100	60	100	10	3	—	—	—	—	10
BsJp			—	—	—	—	75	9	—	—	25	100	4
Bs			—	—	—	—	88	88	12	50	—	—	32
Bf			—	—	—	—	—	—	100	50	—	—	4
Total frequency			3		6		32		8		1		50

*Bf, balsam fir; Jp, jack pine; BsJp, black spruce – jack pine; Bs, black spruce.
†Time first–last, time between first and last inventory (mean ± SE).
‡TSF, time since fire; values with different letters are significantly different at $p < 0.05$.
§% row, percentage of the plots in the forest type in the first inventory that have changed to the stand type at the last inventory.
¶% col, percentage of the plots in the forest type in the last inventory originating from the sand type in the first inventory.

when modelling was used to extend the period. All of the new BsJp plots derived from former jack pine stands, accounting for 60% of the BsJp stands in the landscape. For the modelled period, the corresponding rate was 100%. As with the jack pine dominated plots, balsam fir (>9 cm DBH) is absent.

No transition took place in the black spruce plots during the study period, but for the modelled period, 12% of the black spruce plots were reclassified as balsam fir stands. Also, during the modelled period, new black spruce stands originated solely from jack pine (25%) and BsJp (75%) stands. These results therefore suggest that a change in dominance occurred from jack pine to black spruce. This replacement pattern is similar to that seen on glacial deposits and in chronosequence studies.

The balsam fir plots were not well represented on glaciofluvial deposits, and they did not undergo a transition during the study period or the modelled period. However, the percentage of balsam fir dominated stands doubled during the modelled period on glaciofluvial deposits in the landscape. All of these new balsam fir stands originated from black spruce stands.

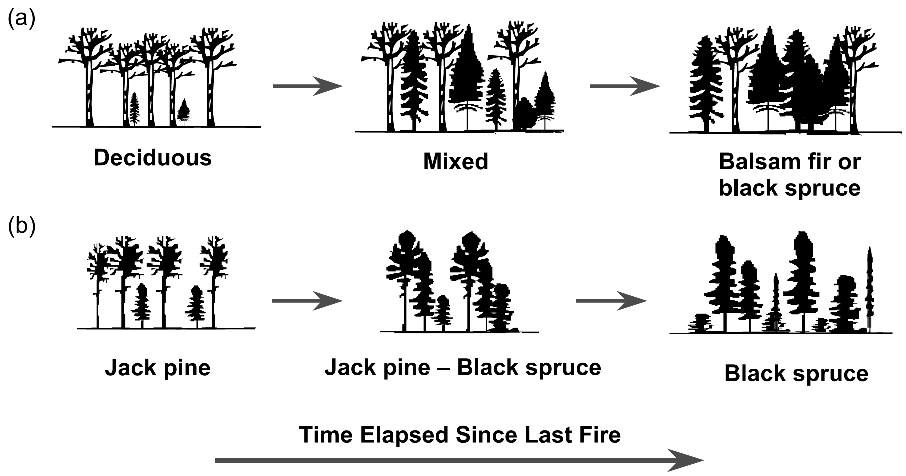
Discussion

Factors governing fire frequency

Although the climate change that has occurred since the end of the Little Ice Age is known to have had a major impact on fire-cycle length in the boreal forest (Engelmark et al. 1994; Larsen 1997; Weir et al. 1999; Bergeron et al. 2001), other historical and spatial factors can contributed to the heterogeneity of the fire regime. Studies have shown that regional development and logging operations (Lefort et al. 2002; Weir and Johnson 1998) could cause changes in the fire regime as do vegetation composition (Hély et al. 2000, 2001) and hydrology (Larsen 1997). Surprisingly, there was no evidence that there were distinct fire cycles for these spatial factors (bioclimatic subdomain, land uses, surficial deposit, and mean water break), and therefore, they did not explain the mixed distribution observed at the outset. These elements, therefore, did not appear to have served as major barriers to the spread of fires as has been reported in other studies (Wein and Moore 1979; Agee et al. 1990; Larsen 1997; Hély et al. 2001). Given that the major fires seem to have occurred in years characterized by extreme conditions (Lefort 1998; Lesieur 2000), only unfavourable climatic conditions, such as heavy rainfall, appear to have the capacity to put out fires, particularly crown fires. Although fire intensity may be lower in mixed and deciduous stands, fires do not appear to be less frequent in those stands (see mean age of stands in Tables 5 and 6). As with forest stands, some surficial deposits, such as glaciofluvial, may induce changes of intensity, but they are not widespread enough in the region to engender a significant difference in the duration of the fire cycle.

With regard to anthropogenic factors, human impacts began a few decades earlier in the southern part of the territory, but this factor had an influence only for a very short time period (~1940 to the present). This appears to explain the absence of a significant difference in fire-cycle length between the two regions. The same is likely true for the road

Fig. 4. Main patterns of species replacement for Smurfit-Stone private land when the time between two disturbances is sufficiently long: (*a*) deciduous stands replaced by balsam fir and to a lesser extent by black spruce; (*b*) jack pine replaced by black spruce.



system, which is more developed in the southern area; a more extensive road system would have permitted more effective detection and faster access for firefighting purposes. It appears that the different timing of the start of forestry operations in the two regions was not determinant for the fire cycle during the study period; alternatively, there could have been an effect that was too weak to be detected.

Since spatial factors do not explain the variation in the fire cycle, climate change patterns appear to be the key element contributing to the decrease in fire frequency (Bergeron and Archambault 1993; Bergeron et al. 2001). Climatic conditions seem to be less conducive to forest fires in this region than in the past (Lesieur 2000). This interpretation corroborates predictions made for this region of a decline in fire frequency in the future (Bergeron 1998; Flannigan et al. 1998; Lefort et al. 2002).

Vegetation dynamics

Our results support the hypothesis that species replacement occurs when the fire-return interval is sufficiently long, i.e., when the interval between fires exceeds the mean tree longevity for the post-fire cohort. As in other boreal forest regions (Day 1972; Heinselman 1981; Cogbill 1985; Bergeron and Dubuc 1989; Bergeron 2000; Gauthier et al. 2000), patterns of replacement found in the Smurfit-Stone territory are fairly simple.

Transition matrices revealed two main distinct patterns of replacement on the two main surficial deposit types, although they are not found in the same proportion on both soil types. With the first pattern (Fig. 4*a*), deciduous and mixed stands were replaced in many cases by balsam fir and, to a lesser extent, by black spruce. The low capacity of shade-intolerant deciduous trees to recruit in the understory of closed-canopy stands (Dix and Swan 1971; Bergeron and Charron 1994) aptly explains this change in dominance toward more shade-tolerant species (Kimmins 1987). Using a 230-year chronosequence, Bergeron (2000), Gauthier et al. (2000), and Bergeron and Dansereau (1993) suggested that deciduous stands are gradually replaced by conifer-dominated stands 100 years after the last fire. However, on account of its longevity, white birch is able to maintain itself, though more sporadically, in stands more than 100 years old (Bergeron and Dubuc 1989; Bergeron 2000; Gauthier et al. 2000). In spite of this, if there is no fire disturbance over a long period, most of the deciduous and mixed stands will be replaced by balsam fir dominated stands and, to a lesser extent, by black spruce dominated ones (Bergeron and Dansereau 1993; Gauthier et al. 1996; Bergeron 2000). Historical and abiotic factors undoubtedly play a role in relation to the presence of one or the other of these species. The replacement patterns are therefore not unique (Taylor et al. 1987; Bergeron and Dubuc 1989; Bergeron 2000).

A greater transition rate towards balsam fir dominated stands can be explained partly by lower fire intensity in deciduous and mixed stands. A greater number of balsam fir would survive the disturbance, allowing this species to reinvade quickly. Afterwards, balsam fir would be at an advantage because of its greater capacity to become established on leaf litter as compared with white spruce (Simard et al. 1998) and black spruce; although we know of no research on direct comparisons with black spruce. A number of studies (Knapp and Smith 1982; Klein et al. 1991) suggest that the root system is more extensive for *Abies* than for *Picea*. This would enable balsam fir seedlings to penetrate the thick leaf litter more readily and become established more successfully than black spruce. Over a longer period (simulated transition of 30 years), the higher transition rate, particularly towards balsam fir, confirms the limited capacity of white birch and trembling aspen to regenerate in the understory and the ability of balsam fir to become established and develop in the understory until a gap is created (Kneeshaw and Bergeron 1998; Kneeshaw et al. 1998). Moreover, the observed and predicted decrease in fire frequency for the region (this paper; see also Bergeron et al. 2001; Flannigan et al. 1998) will undoubtedly accentuated this phenomenon as balsam fir is favoured, at the landscape level, by long fire intervals (Bergeron and Leduc 1998; Gauthier et al. 2000).

However, as the fire cycle is lengthening and the spruce–fir proportion in the landscape is increasing, the landscape is becoming more favourable to secondary perturbations like spruce budworm outbreaks (Blais 1983; Bergeron and Leduc 1998). Gap created by severe budworm defoliation can initiate secondary succession composed of shade-intolerant deciduous species (Kneeshaw and Bergeron 1999) as seen in our transition matrices. In other cases, the opening of the canopy can release suppressed balsam fir and black spruce from the understory (Baskerville 1975; Morin 1994; Kneeshaw and Bergeron 1999) and favoured the return of shade-tolerant species.

With the second pattern of species replacement in the canopy (Fig. 4*b*), jack pine is replaced by black spruce. The observed patterns of replacement are consistent with the chronosequence studies (Cogbill 1985; Bergeron and Dubuc 1989; Gauthier et al. 1996; Bergeron 2000; Gauthier et al. 2000; Harper et al. 2002). Day (1972) described an analogous replacement pattern for lodgepole pine and Engelmann spruce. Although the replacement of jack pine by black spruce seems to indicate delayed recruitment of black spruce, the change in dominance is more likely attributable to differential growth rates (Van Cleve and Viereck 1981). It should be noted that the widespread absence of balsam fir in jack pine stands is probably due to the absence of individuals that survived the fire. In the long term, the accumulation of acidifying litter from jack pine appears to cause an impoverishment of the soil, favouring the establishment of species that are less demanding in terms of nutrients, such as black spruce. Hence, owing to the inability of jack pine to recruit in the understory (Eyre 1938), jack pine stands are gradually replaced by stands with a greater proportion of black spruce and are eventually dominated by black spruce. Our results suggest, however, that it takes at least 50 years before black spruce dominate or codominate jack pine stands (see also Harper et al. 2002).

Over the long term, reduced fire frequency in this area of the boreal forest (Bergeron et al. 2001) could cause a decrease in the extent to which this successional pattern occurs. Since jack pine appears to be limited to areas where the species was present prior to the most recent disturbance (Bergeron 1991), a substantial decrease in the area burned will likely lead to a decline in the zones occupied by jack pine. Since jack pine stands are already poorly represented in the landscape except on glaciofluvial deposits, a decrease in this replacement pattern would have a considerable impact. However, in the event that jack pines disappear from certain sites, the high mortality rate of balsam fir following high-intensity fires will keep this species from following this pattern. In such a case, black spruce would become the main replacement species.

As expected, very few changes occurred in stands dominated by balsam fir and black spruce, which suggests that these stands are in a state of equilibrium. This is primarily due to their great shade tolerance and their capacity to regenerate continuously under their own canopy (Dix and Swan 1971; Galipeau et al. 1997). Black spruce and balsam fir can also regenerate through layering, allowing them to maintain themselves under their own canopy for a long time after the last disturbance. Thus, even if few stands have changed stand type, this does not mean that these stands are not changing. Changes are occurring in term of structure rather than composition (Harper et al. 2002). The results of the modelled transitions show that over a longer period, balsam fir may replace black spruce in some cases. However, the presence of highly acidifying ericaceous and *Sphagnum* species that are often associated with black spruce may inhibit germination of balsam fir in these environments. The absence of seed trees may likewise limit the presence of balsam fir, given the poor seed dispersal capacity of this species (Frank 1990).

A few balsam fir and black spruce dominated plots nonetheless underwent a transition towards stands with a greater proportion of deciduous trees (deciduous and mixed). These transitions were likely caused by insect outbreaks (DeGrandpré et al. 1993; Kneeshaw and Bergeron 1999) as indicated by the high mortality of host species (unpublished data). The Smurfit-Stone archives enabled us to confirm a posteriori that spruce budworm (C*horistoneura fumiferana* (Clem.)) outbreaks occurred in the territory in past years. Thus, although fire is the main disturbance in the boreal forest (Johnson 1992), insect outbreaks likewise play an important role in allowing secondary succession to happen (Morin et al. 1993; Bergeron and Leduc 1998; Kneeshaw and Bergeron 1998). Since the last inventory period was done during or shortly after an outbreak period, this means that the only living trees used in the classification of forest stands were nonhost species, specifically white birch and to a lesser extent trembling aspen. Hence, this increase in the deciduous component of plots was due to the high mortality of host species (balsam fir and (or) spruce) rather than a recruitment of deciduous trees. A similar situation occurred with plots that lost their forest designation and, therefore, were classified as nonforested. In this case, the mortality rate was high for the associated species as well, and the basal area in the first inventory was near the lower limit (5 m^2/ha) required to receive the designation of "forest land". However, despite the fact that stands can be affected significantly by spruce budworm defoliation (Kneeshaw and Bergeron 1999), the relatively high fire frequency in this region of the boreal forest has historically limited the magnitude of insect outbreaks (Bergeron and Leduc 1998).

Although a number of studies provide some evidence that species replacement occurs in the boreal forest canopy (Heinselman 1981; Cogbill 1985; Bergeron and Dubuc 1989; DeGrandpré et al. 1993; Leduc et al. 1995; Gauthier et al. 1996, 2000; Bergeron 2000), these studies were based on a chronosequence approach. The present study is the first to provide direct evidence of species replacement with sufficient time following fire from repeated inventory type data on a large scale. On glaciofluvial deposits, the plots that underwent a transition had a significantly greater time since last fire, which suggests that they were closer to the stand breakup age in the first inventory. With regard to glacial deposits, the significantly longer study period for plots that underwent a transition enabled them to reach the stand breakup age.

However, the time since last fire does not appear to be the only factor that explains the probability of a transition for a given stand. Since there is considerable variability in species replacement and since each community changes independently, species replacement is not linked to the time since last fire through a linear relationship (Harper et al. 2002). Hence, simply knowing the time since last fire does not permit predictions about whether or not a transition will occur in a given plot. Other variables, such as fire intensity, knowledge of the pre-disturbance species, the initial composition, the presence and density of advance regeneration, a drainage index and a finer scale description of the surficial deposits, might have made it possible to better explain the transitions. The collection of some of these data is now part of the Smurfit-Stone inventory program. Monitoring of permanent plots should also make it possible to better target the transition period for several stand types.

In the modelled transitions, the integration of a differential mortality factor would probably have enabled better prediction of the decline in existing species. Similarly, the addition of nonmerchantable stems (<9 cm DBH) in the ACB computation would have made it possible to integrate and to determine the regeneration potential of the species that will form the future stand. These two variables should help to illustrate, in a nonlinear fashion, the replacement of species in the canopy and to possibly increase the stand transition rate.

Conclusions and management implications

The boreal forest has long been perceived as an ecosystem that is periodically disturbed by fires (~100 years) with cyclic regeneration. These characteristics have been used for a long time as justification for carrying out clear-cutting on short rotations. Our results indicate that species replacement in the canopy occurs in the eastern boreal forest of Canada when the time between disturbances is sufficiently long. In the studied period, 25% of the plots underwent a transition. Most of the replacement involved an increase in coniferous trees, mainly balsam fir. However, in jack pine stands, the replacement pattern was solely through black spruce. The proportion of stand undergoing transition is in part a function of the time since last fire. Under a relatively long fire cycle, smaller disturbances also have an impact on those transitions. For instance, in our case insect outbreak has allowed shade-intolerant deciduous trees to reinvade gaps created by budworm defoliation in some cases.

Our results have also suggested that there are few barriers (mean water break, vegetation, surficial deposits) that act to limit the spread of fires in the studied region. Thus, fires tend to cover large areas. However, studies have also shown that within a single fire, there is a large variation in terms of fire intensity (Kafka et al. 2001; Bergeron et al. 2002). For instance, as much as 50% of large fires have suffered from intermittent crown fires, which leave many living trees. In terms of management, it implies that large regenerating areas would be interspersed by zones of green tree retention.

Our results also indicate that the fire cycle is lengthening since the end of the Little Ice Age. As a result, the proportion of stands that exceed the age of senescence of pioneer species (~100 years) should also increase. Already, 45% of the forests should be over 100 years old and 20% over 200 years old if there were no harvesting in the study area. More stands are, therefore, likely to undergo species replacement. As the fire cycle is lengthening, the transition rate is likely to increase. Therefore, the proportion of overmature and old-growth stands in the landscape should be an important part of the landscape. It might also cause the system dynamics to shift from one mainly controlled by large-scale disturbances to one including also an important component of fine-scale disturbances. This perspective calls into question the widespread practice of clear-cutting over large areas in the boreal forest, as this approach emulates a short fire cycle. Moreover, this practice does not take into account the regional fire return interval or the presence of advanced regeneration in the understory. Even-aged management with short rotations remain a valid option for regions where the disturbance return interval limits species replacement, especially when there is insufficient advanced understory. However, for regions where the fire return interval is long enough and regeneration is present, partial cutting and selective cutting would be more appropriate approaches for conserving and deriving benefit from the understory. Therefore, planting could be minimized or even avoided in many situations. The decrease in the volume harvested would be offset by more frequent removals and a decrease in silvicultural work. The two pattern of replacement observed in this study, which have been determined for sites regenerated naturally, may also be used as a guideline for management strategies emulating natural disturbance (see Harvey et al. 2002). Thus, these approaches would allow the structure of overmature and old-growth forests, as well as forest under regeneration, to be recreated in the landscape. Forest management that emulates natural processes could thus be a cost-effective and ecologically sound solution for complying with environmental standards.

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