

Scale-dependent determinants of heterogeneity in fire frequency in a coniferous boreal forest of eastern Canada

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Abstract Despite the recognized importance of fire in North American boreal forests, the relative importance of stochastic and determinist portions of intra-regional spatial variability in fire frequency is still poorly understood. The first objective of this study is to identify sources of spatial variability in fire frequency in a landscape of eastern Quebec's coniferous boreal forest. Broad-scale environmental factors considered included latitude, longitude, human activities and belonging to a given bioclimatic domain, whereas fine-scale factors included slope, position on the slope,

aspect, elevation, surficial deposit and drainage. The average distance to waterbodies was also considered as a potential intermediate-scale source of variability in fire frequency. In order to assess these environmental factors' potential influence, they were incorporated into a proportional hazard model, a semi-parametric form of survival analysis. We also used a digital elevation model in order to evaluate the dominant aspect within neighborhoods of varying sizes and successively incorporated these covariates into the proportional hazard model. We found that longitude significantly affects fire frequency, suggesting a maritime influence on fire frequency in this coastal landscape. We also found that position on the slope was related to fire frequency since hilltops and upperslopes were subject to a lower fire frequency. Dominant aspect was also related to fire frequency, but only when characterized within a neighborhood delimited by 4,000 to 10,000-m radii (5,027–31,416 ha). A 2–6-fold variation in fire frequency can be induced by geographic and topographic contexts, suggesting a substantial intra-regional heterogeneity in disturbance regime with potential consequences on forest dynamics and biodiversity patterns. Implications for forest management are also briefly discussed.

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Introduction

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

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

The environmental factors controlling the spatial heterogeneity of fire regimes are numerous and vary from one ecosystem to another. They also depend on the spatial scales being considered. We will talk about top-down controls when the fire regime is mainly affected by environmental factors that might be described on broad spatial scales. Climate and belonging to major vegetation and physiographical formations would be included in the top-down controls associated with fire regimes commonly reported in the literature (Wein and MacLean.

1983; Johnson 1992; Payette 1992). Environmental factors described on a local scale, such as stand type or stand age, density of vegetation, surficial deposits, drainage, slope gradient and aspect, to give but a few examples, are bottom-up controls (Lertzman and Fall 1998; Heyerdahl et al. 2001). Bottom-up controls are frequently reported in Mediterranean-type ecosystems (Moritz et al. 2004; Mermoz et al. 2005; Broncano and Retana 2004), in temperate forests (Kushla and Ripple 1998) or in landscapes with very complex topography (Gavin et al. 2003; Dorner et al. 2002). Although some bottom-up controls are sometimes mentioned in the case of coniferous boreal forests (Kafka et al. 2001), it seems that boreal fire regimes are mostly subject to the influence of extended droughts that produce the conditions favourable to fire spread over vast areas (Bessie and Johnson 1995). Other environmental factors are more difficult to categorize within one of these two classes. Some studies indeed mention physiographical factors on intermediate spatial scales. They are usually environmental factors that influence the ignition or spread of fires within landscape units ranging in size from a few square kilometres to several hundred square kilometres; for example, proximity to surrounding firebreaks (Larsen 1997; Cyr et al. 2005), proportion of the area covered by wetlands or connectivity of forest blocks conducive to fire spread (Hellberg et al. 2004) or relative proportions of softwood and hardwood stands (Bergeron et al. 2004; Krawchuck et al. 2006).

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

The principal objective of this study is to highlight environmental factors responsible for the spatial variability of time elapsed since previous fires in a boreal forest landscape in eastern Canada. Our hypothesis is that the overall variability is partly determined by environmental factors inducing heterogeneity in fire frequency within the landscape concerned. We predict that fire frequency is mainly affected by a top-down control and that it is more the

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

Methods

Study area

The study area covers 15,961 km² of boreal forest in eastern Quebec, specifically in the North Shore region, between longitudes 67.00° W and 69.00° W and between latitudes 49.00° N and 50.25° N (Fig. 1). This region has a cold, maritime climate with an average annual temperature of 1.4°C and average precipitation of 1,018 mm, measured in Baie Comeau in the southwest corner of the study area. Precipitations are evenly distributed during the year, and are about 70% rain (Anonymous 1996). The topography is moderately uneven with high hills with rounded summits and many rocky escarpments. The highest hills, located in the northeastern part of the area, are just over 700-m high while other sparsely distributed hills reach above 500 m. The average elevation ranges within landscape subunits vary between 150 m and 200 m. Three of these landscape subunits, as described by Robitaille and Saucier (1998), make up for almost the totality of the whole study area. The average slope is 15%. The hydrography is complex

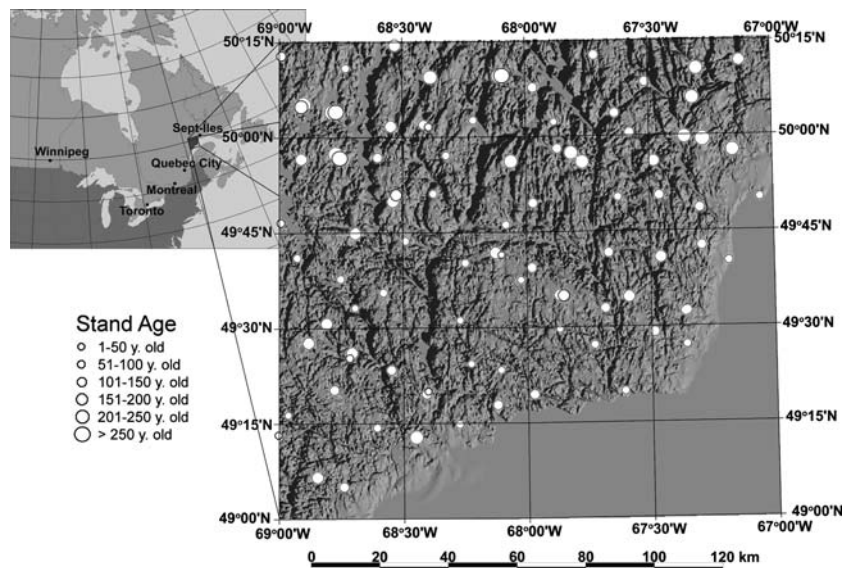
with numerous small lakes and rivers of varying sizes, some of them very large. The configuration of the topography produces a drainage system with a mainly north–south orientation (Robitaille and Saucier 1998). There are rocky outcrops on slightly more than a third of the total land area, while the rest of the land area consists mainly of thin tills on sloping areas and thick tills at the bottoms of slopes. To a lesser extent, there are glaciofluvial deposits on valley floors (Robitaille and Saucier 1998).

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

Fire history

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

Fig. 1 Study area – Topography and spatial distribution of sampled stands (elevation amplified 10 times)



dendroecological surveys carried out during MRNFQ forest inventory campaigns.

Samples were then taken in the study area according to a systematic random plan (Fig. 1). The entire study area was subdivided into 80 sectors measuring 15 km by 15 km, within which two accessible points (less than 1,000 m away from the roads) and covered with forest were randomly positioned and reached with the help of a GPS. One or two sites could be sampled, depending on time constraints during the field campaign, but were weighted accordingly to ensure that the sample was representative in the subsequent statistical analyses. A total of 94 points made up the final sample. The SOPFEU map archives were used to directly assign a fire date to some recent fires, i.e. 12.8% of cases. Dendroecological analyses were used to estimate the time interval elapsed since the most recent fires for the rest of the sample, based on data gathered in the MRNFP decadal inventories (37.2%) and during the sample-gathering campaign carried out for this study (50%). The time intervals since the most recent fires, estimated with the help of the dendroecological surveys were inferred based on the conventional methods of Arno and Sneek (1977). Between 10 and 15 dominant trees were cut at root collar and dated at each site. Fire dates were deemed sufficiently reliable if they concerned even-aged stands of a pioneer species commonly establishing itself after a fire. A minimum age (censored data) was assigned to

uneven-aged stands, i.e. where a 20-year interval included less than 60% of the sampled dominant trees. However, a visual examination of each stand's age structure suggested that this 20-year interval was too restrictive in the case of some of the older stands that seemed in fact even-aged, probably because of an increasing imprecision of dating with stand age, we thus chose to extend it to 30 years for stands older than 200 years. A minimum age was also assigned to stands consisting primarily of one species that usually does not establish itself after a fire such as balsam fir, independently of their age structure.

Survival analyses

Survival analyses are a statistical tool used to take censored data into consideration (Allison 1995). Such consideration is particularly important in a region such as the North Shore where, because of a relatively long fire cycle, there is a high percentage of old-growth and uneven-aged stands to which only a minimum age corresponding to the age of the oldest tree can be assigned. The influence of environmental variables on fire frequency was estimated using a proportional hazard model, more commonly known as the Cox regression model (Cox 1972). The Cox regression model belongs to a category of semi-parametric regressions, which gives it a high level of robustness given that the baseline hazard of burning function does not have to be specified beforehand, as

in the case of parametric regressions (Allison 1995), because it is derived from the empirical time-since-fire distribution obtained from dendroecological sampling and archival data (see Johnson and Gutsell 1994, for details related to the equivalence of these distributions). This allows for control of the temporal variability in fire frequency caused by climate change or human activities in the area and furthermore, allows to test for the influence of spatial variables that might cause departures from the baseline hazard of burning function. As stated by Johnson and Gutsell (1994), it should be noted that the term *hazard of burning* refers to the statistical notion of *hazard rate*, i.e. the instantaneous probability of fire, and must not be mistaken for *fire hazard* which, for the foresters, rather refers to the potential of fire based on fuel load, structure and phenology. Finally, any significant influence of an environmental factor revealed by the

Cox regression will be interpreted as one on *fire frequency*, which is an averaged quantification of hazard of burning over a given period of time (see also Reed et al. 1998). The term fire frequency, therefore, will exclusively be used in the rest of this paper for the sake of clarity.

The Cox regressions were made using the PHREG procedure of the SAS software (v9.1; SAS Institute Inc, 2003), which estimates the parameters of the model through partial likelihood. Independent variables integrated into the model were chosen by stepwise selection. Table 1 shows the environmental variables that were taken into consideration to develop the initial survival model. Even though it has been shown to be an important determinant of fire frequency in other regions (Larsen 1997; Kasischke et al. 2002), stand type was not considered in the survival model since aspen (*Populus tremuloides*) is

Table 1 Details of environmental variables considered in the initial survival model

Vegetation	Stand type ^a	Mixed	Local scale	Nominal
		Coniferous	Local scale	
	Bioclimatic domain ^b	Balsam fir – white birch	Broad scale	Nominal
		Black spruce – pleurozium	Broad scale	
Geography	Longitude		Broad scale	Continuous (decimal degrees)
	Latitude		Broad scale	Continuous (decimal degrees)
	Distance from Saint-Lawrence River		Broad scale	Continuous (meters)
Physiography and Topography	Surficial deposit ^c	Rocky outcrop	Local scale	Nominal
		Thin till	Local scale	
		Thick till	Local scale	
		Glaciofluvial	Local scale	
	Slope aspect ^c	West–east axis (x)	Local scale	Continuous (x,y)
		South–north axis (y)	Local scale	
	Position on the slope ^c	Hilltop/upperslope	Local scale	Nominal
		Midslope	Local scale	
		Depression/lowerslope	Local scale	
		Flat	Local scale	
Mean waterbreak distance ^d		Intermediate	Continuous (metres)	
Drainage ^c		Local scale	Ordinal; from 1 (excessive) to 6 (organic)	
Elevation		Local scale	Continuous (metres)	

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

^b From Robitaille and Saucier (1998)

^c Evaluated following the protocol used in Quebec's provincial forest inventories (Saucier 1994)

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

an early successional species (Lesieur et al. 2002), generally replaced during the fire-free intervals typical of this region. Its presence would thus probably be related to short fire-free intervals even though it is very unlikely to be a causal factor leading to short fire frequency because of its assumed lower flammability.

Nominal variables were coded as sets of dummy variables while aspect, which varies within a circular scale, had to be converted into a couple of coordinates (x , y) in order to be incorporated in the linear context of the Cox regression. Each aspect class (north, north-east, east, south-east, south, south-west, west and north-west) was thus positioned on a trigonometric circle of radius 1 centred at the origin where the angle corresponds to the azimuth of the dominant aspect of the surrounding slopes. The horizontal axis (x) therefore corresponds to the west–east axis, while the vertical axis (y) corresponds to south–north axis. Sites located within a topographical context where west, east, south and north slopes predominated were assigned the coordinates of $(-1,0)$, $(1,0)$, $(0,-1)$ and $(0,1)$, respectively, while sites located within a topographical context where south-west, north-west, south-east and north-east slopes predominated were assigned the coordinates $(-0.7071, -0.7071)$, $(-0.7071, 0.7071)$, $(0.7071, -0.7071)$ and $(0.7071, 0.7071)$, respectively ($\sin(45^\circ) = \cos(45^\circ) \approx 0.7071$). It should be noted that aspect is only characterized at the station level in this initial model. In order to assess the importance of collinearity among all the variables in the data set, we computed Spearman's nonparametric correlations. This allowed us to evaluate whether some of them should be discarded or interpreted more carefully should they reveal a significant effect on fire interval. Many variables that went into the stepwise selection are significantly correlated, although most of these correlations are not very strong (Spearman's ρ between 0.2 and 0.35), except for a few that are closely related by nature (Appendix 1). A particular attention has been paid to the stand type, which is in some systems a key determinant of fire frequency that was voluntarily discarded from this model for the reasons stated above. The mixed stands of this area, which represent less than 5% of our sample, seem to occur a little more frequently in the southern part, while resinous stands seem to be slightly excluded from locations close to waterbodies, although the

correlations are weak at 0.214, just above the 5% probability threshold. As most correlations are either weak, easily explainable or seemingly irrelevant with regards to fire behaviour, we decided to submit our original dataset to the stepwise selection procedure without any modifications.

The initial model was then improved through a multiscale examination of aspect as a potential source of spatial heterogeneity in fire frequency. A geographic information system (ArcView GIS 3.2a; ESRI Inc. 2000) was used to determine the dominant aspect around each pixel of the digital elevation model (93-m resolution). A series of contextual variables corresponding to the *dominant aspect* within a circular area with a radius varying between 93 m and 15,000 m (3.1 ha to 70,685.8 ha; Fig. 2) were successively incorporated into the regression model obtained after the stepwise selection described above. Each of these contextual variables was tested individually and a Bonferroni correction for 20 simultaneous tests was applied to the 5% significance threshold. Spearman's correlations among this second set of variables were also computed and suggested no confounding bias (Appendix 2). Of course, dominant aspects at varying spatial scales are correlated among them, but should not interfere with each other since they are incorporated individually into the second survival model.

Results

First survival model

In the first group of variables considered in the Cox regression model, only longitude and hilltop/upperhill were significantly related to fire frequency (Table 2). Longitude entered first into the regression model and maintained most of its contribution after the hilltop/upperhill category was incorporated during the second round of the stepwise selection. No other variables could be included into the model after these two rounds of stepwise selection.

The fire frequency ratios resulting from the Cox regressions (called *hazard ratios* or *risk ratios* in statistical literature) can be used to quantify the influence of each variable on fire frequency (Allison 1995). The fire frequency ratio associated with longitude (0.5200; Table 2) indicates a decreasing

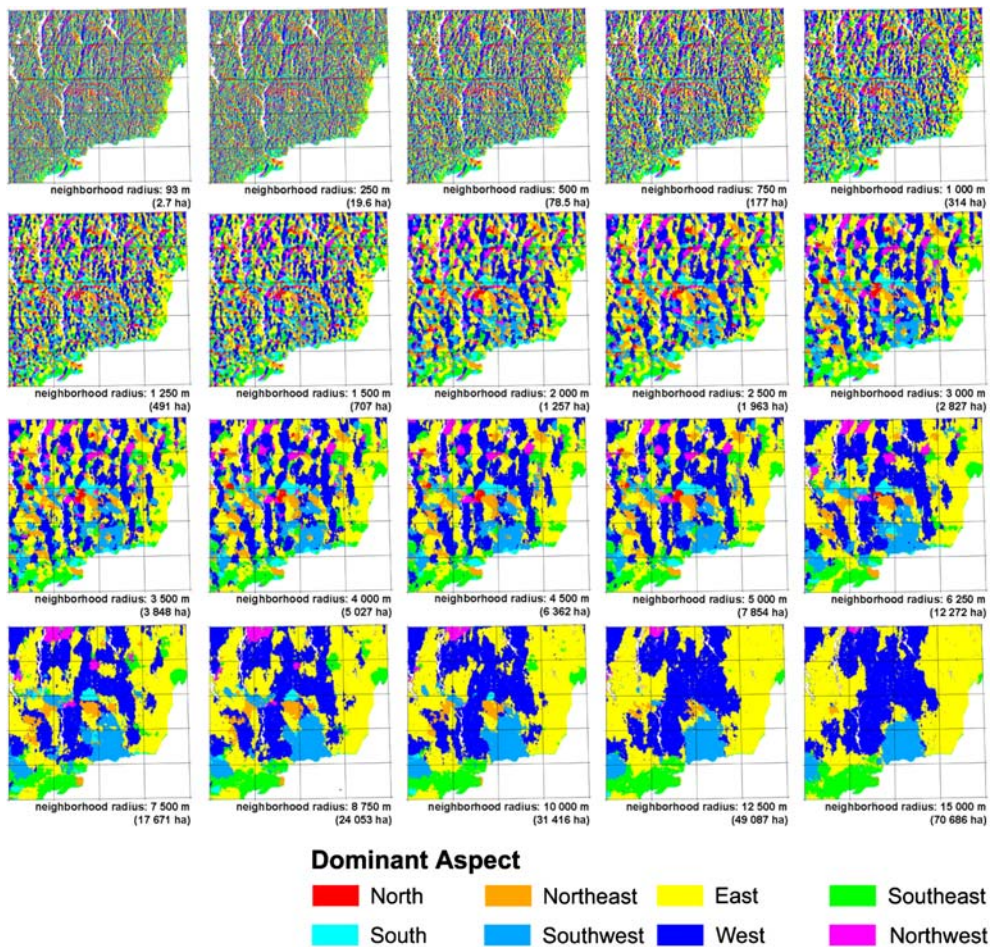


Fig. 2 Dominant aspect (for all elevations) considering various neighbourhood sizes

gradient in fire frequency from west to east, because a one-degree increase in longitude corresponds to a decrease in fire frequency of nearly half the original fire frequency. On the other hand, hilltops and upperhills, characterized by a fire frequency ratio of 0.4710, thus seem to burn roughly half as much as sites on other positions on the slope. Median fire-free intervals (Table 3) are indeed longer in the eastern portion (>191) of the study area than in the western part of it (179), although it is impossible to obtain a precise estimate in the western part because of the preponderance of stands for which only a minimum age is known. At a more local scale, sites on hilltops or upper slopes are characterized by a longer median fire-free interval (214) than sites on other positions on the slope (175).

Second survival model

After taking longitude and hilltop and uphill into consideration, it is possible to detect a statistically significant relationship between dominant aspect of surrounding slopes and fire frequency, but on certain spatial scales only (Fig. 3). The strength of statistical relationships between fire frequency and dominant aspect was indeed above the 5% threshold when determined within a radius of between 4,000 m and 10,000 m with a peak at 8,750 m, the only scale at which the relationship remains significant after a Bonferroni correction for 20 simultaneous tests.

The individual fire frequency ratios corresponding to each of the *x* and *y* coordinates (not shown), associated respectively with the east–west and

Table 2 Summary of stepwise selection of independent variables of the initial survival model

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

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

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

^c Covariate's contribution included in the model

Table 3 Median fire-free intervals as a function of geographic and physiographic context

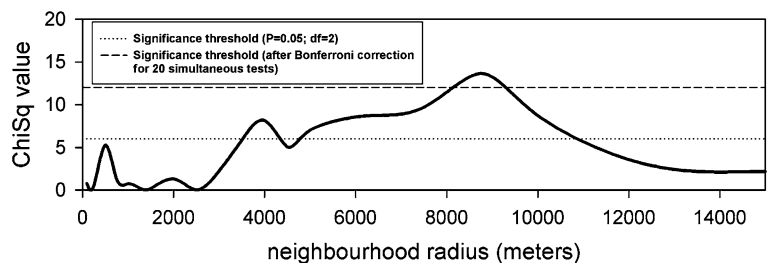
	Median fire-free interval (years)	<i>N</i>	% Censored ^a
East (longitude > -68°)	> 191 ^b (1 st quartile = 157)	40	69.2
West (longitude = -68°)	179 (1 st quartile = 90)	54	41.3
Hilltop/upperslope	214	32	62.5
Other (flat, depression/lowerslope, midslope)	175	62	46.9
Fire-prone topographic context ^c	108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

^a “% Censored” corresponds to the percentage of stands to which only a minimum age was attributed. These stands were either uneven-aged or consisting of a species that generally doesn’t establish after a fire (e.g. balsam fir)

^b Only an underestimation of the median fire-free interval is available since we only know the minimum age of the older stands (censored data). The first quartile has been added for comparison purposes

^c Topographic context characterized within a 8750-m radius. Fire-prone topographic contexts are dominated by south, south-west or west facing slopes. Intermediate topographic contexts are dominated by south-east or north-west facing slopes. Fire-resistant topographic contexts are dominated by north, north-east or east facing slopes

Fig. 3 Strength of statistical relationship between dominant aspect and fire frequency as a function of the neighbourhood radius considered



south–north axes, were combined to evaluate the direction and amplitude of the influence of dominant aspect. Each vector presented in Fig. 4 illustrates a fire frequency gradient related to dominant aspect at a single spatial scale, the fire frequency being at its maximum where slopes predominantly face the azimuth corresponding to the direction of the vector (thus, at its minimum in the opposite direction). Moreover, the length of each vector indicates the amplitude of this gradient in the form of a ratio. In more concrete terms, the vector associated with the 8750-m scale indicates that sites that are located in environments dominated by south-west facing slopes burn about 3 times more often than the average site, controlling

for other covariates (longitude and hilltop/upper-hill). Because a linear relationship between the independent variables and the criterion variable is assumed in the Cox regressions (Allison 1995), these results also indicate that the areas where north and north-east slopes predominate are about 3 times less likely to burn than the average site, with a linear gradient between these two extremes. These results are reflected in the median fire-free intervals (Table 3) of the various longitudinal and topographical contexts characterized at the 8,750-m scale (the spatial scale where the statistical relationship is maximized) and in the percentage of stands for which only a minimum age is known (% censored).

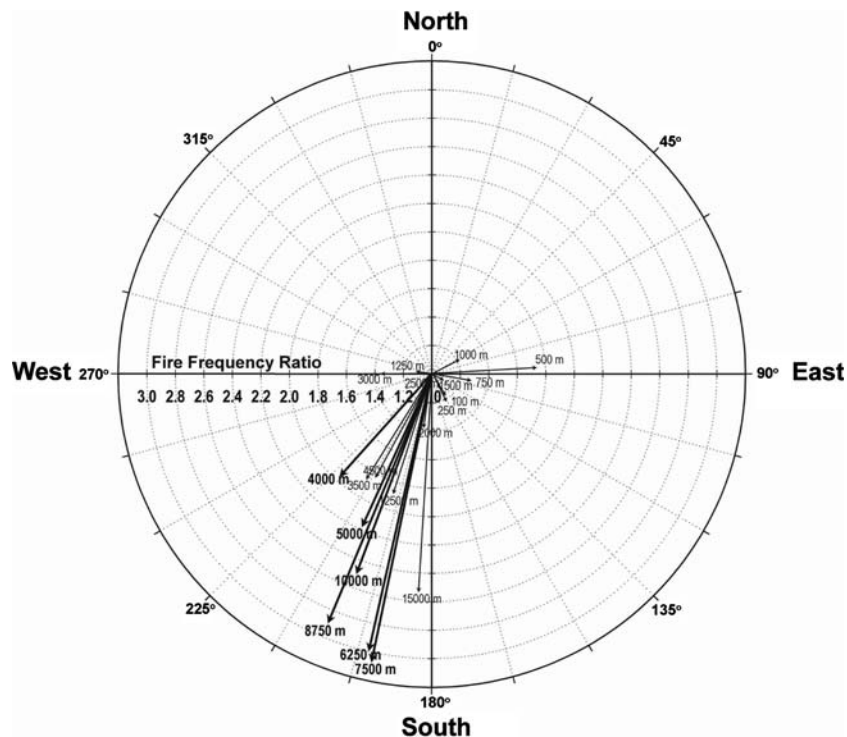


Fig. 4 Fire frequency gradients as a function of dominant aspect and neighbourhood radius considered. Radial axis indicates the amplitude of the gradient while the angular axis represents the direction in which the fire frequency is at its maximum, e.g., a vector of length 3 pointing in a south–south-west direction indicates that sites located in areas dominated by

slopes facing this azimuth burn three times as much as the average site and that sites located in areas dominated by slopes facing the opposite azimuth (north–north-east) burn three times less often than the average site, with a linear gradient between these extremes. Neighbourhood radii corresponding to significant spatial scales are in bold characters

Discussion

Intra-regional longitudinal gradient

The inter-regional variability of fire frequency in North American boreal forests is already well documented, particularly because of the growing number of regional long-term fire history reconstructions carried out in recent years (Heinselman 1973; Masters 1990; Johnson and Larsen 1991; Bergeron et al. 2001; 2004; 2006; Lesieur et al. 2002; Grenier et al. 2005). In the case of eastern Canada's boreal forests, a decreasing gradient in fire frequency from west to east has been observed (Gauthier et al. 2001), which is mostly related to a precipitation gradient caused by the gradual transition of a continental climate to a one under increasing maritime influence (Grondin 1996). The longitudinal gradient detected in our study suggests the same kind of phenomenon at a smaller

spatial scale. The explanation of this longitudinal gradient is indeed likely related to climate since longitude varies independently of other covariates (Appendix 1), except elevation, which does never come close to the significance threshold in the stepwise selection (Table 2), and distance from the shore, which is in this case a variable of very similar nature that would have led to the same kind of hypothesis. For these reasons, and even though we cannot completely discard the possibility of collinearity with another environmental factor that was not considered in this study, we think that the climate-related hypothesis remains the most plausible. As a matter of fact, similar fire frequency gradients correlated with longitude were observed in Alaska (Dissing and Verbyla 2003) and in the James Bay region of Quebec (Parisien and Sirois 2003) and were attributed to climate-related phenomena. This latter study, conducted in an area of similar size, attributes

this to the sea breeze effect, which consists of moist cold air blown inland. A notable difference between Parisien and Sirois' study and the present one is the direction of this possible sea breeze effect which would be, in this case, in the opposite direction of the prevailing winds during fire season. Dissing and Verbyla (2003) also suggest that the cool and more stable atmospheric conditions typical of maritime climates may suppress convective activity generated by heterogeneity in albedo of large landscape features, such as recently burned areas and large inland waterbodies within a matrix of coniferous forest, that is sometime sufficient to increase lightning strike activity (Knowles 1993). The survival model indicates that this possible maritime influence is substantial because, within this area, each degree of longitude from west to east would correspond to a decrease in fire frequency by a factor of almost 2.

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

Many studies have highlighted the impact of topography described on a local scale on fire frequency, particularly aspect (Clark 1990; Kushla and Ripple 1998; Beaty and Taylor 2001; Heyerdahl et al. 2001; Vazquez and Moreno 2001; Broncano and Retana 2004; Mermoz et al. 2005). Even though aspect sometimes exerts a strong control over the distribution of fuel types, e.g. when a significantly larger proportion of deciduous stands are found on southern slopes (Kasischke et al. 2002), slopes with more direct exposure to solar radiation and prevailing winds usually are more vulnerable to fire because of the generally favourable influence of these two factors on the quality of fuels. However, this influence of aspect on fire frequency usually seems much greater in systems subject to small but frequent fire events, such as Mediterranean-type ecosystems, or in mountainous systems. Although they exist, there are not many references to the influence of aspect on fire frequency in continental coniferous boreal forests despite the large number of available studies of fire regimes. In fact, topography is acknowledged to have a more important influence on fire severity than on fire frequency *per se* (Kushla and Ripple 1997). The continuity of quality fuels in coniferous boreal forests, which fosters the development of high-intensity crown fires, especially in prolonged drought

periods during which most major fire events occur, probably explains to a large degree the modest influence of topography on fire frequency when described on a local scale.

Nonetheless, based on the results of this study, it seems that topography can have a significant influence on fire frequency in this non-mountainous yet rather rough boreal landscape. However, it is necessary to describe the topography more contextually and to include a rather large area with a radius of between 4,000 m and 10,000 m. Because fire frequency responds to a gradient running from areas with predominant south-west aspects, where fire frequency is highest, to areas with predominant north-east aspects, where fire frequency is lowest, we assume that mechanisms underlying these results are indeed related to the quantity of solar radiation and possibly, to a lesser degree, to the direction of the prevailing winds. Collinearity with other significant covariates doesn't seem to be an issue (Appendix 2).

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

on fire frequency. Moreover, fire spread is probably facilitated earlier in the season in areas with predominantly southern exposure as snow melts earlier and faster on these slopes, creating heterogeneity in terms of the length of the fire season within the study area.

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

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

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

As a general rule, coniferous boreal forests are subject to large-area fire regimes. In the case of the

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

Conclusions

The amplitude of the intraregional heterogeneity in fire frequency highlighted in our results is considerable. It is also likely permanent, since it is related to the physical environment. This suggests many potential implications. Strictly from a management perspective, a better understanding of the intraregional heterogeneity of fire frequency and effective spatial scales can increase our capacity to predict future fire occurrences within managed landscapes. This knowledge could be used in the development of bio-economical risk analyses that may be useful for forest management planning in general and for fire management specifically (Hirsh et al. 2001; Brillinger et al. 2003; Bonazountas et al. 2005). On the other hand, the ecological implications of such a heterogeneity are also numerous. Such heterogeneity in fire frequency indeed affects time-since-fire distributions at the landscape level, stands' attributes and spatial distribution throughout the landscape, as

well as potentially promotes different successional pathways (Frelich and Reich 1995). This leads us to believe that areas which are relatively geographically close to one another may be home to distinct biological legacies left by distinct disturbance regimes.

Considerable attention has been given to the inter-regional variability of fire regimes in boreal forests in recent years (Bergeron et al. 2006; Lefort et al. 2004; Stocks et al. 2002; Flannigan et al. 1998) largely in reaction to the widespread application of consistent management practices over vast areas which results in a standardization of boreal forest that may have serious impacts on ecosystemic diversity. It has indeed been suggested that we should diversify our forest management practices based on the inter-regional variability of natural disturbance regimes in order to preserve this diversity (Attiwill 1994; Gauthier et al. 1996) and apply a coarse filter, or in other words, a pragmatic conservation biology-based approach that recognizes the impossibility of taking the specific needs of each species into account (Noss 1987, Hunter et al. 1988; Hunter 1990; Franklin 1993). We suggest that the intraregional heterogeneity of fire frequency may be an additional level of variability that could be considered through forest management based on the natural dynamics of boreal forest disturbances.

Moreover, forest zoning is often suggested in order to meet the multiples objectives inherent to sustainable development (Seymour and Hunter 1999; Andison 2003; D'eon et al. 2004). This involves spatialization of the various types of forest management where spatial patterns in large scale natural disturbance must be taken into consideration (Angelstam 1997; Baker 1992; Le Goff et al. 2005). In fact, heterogeneity in fire frequency could be considered beforehand in order to optimize such zoning according to the desired objectives.

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

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