Regional patterns of postfire canopy recovery in the northern boreal forest of Quebec: interactions between surficial deposit, climate, and fire cycle[1]

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Abstract: In many northern forest ecosystems, the postfire transition from a closed-crown forest to open woodland is often observed but poorly understood. This paper looks at the effect of interactions between surficial deposit, climate, and fire cycle on postfire forest recovery within a large territory (190 000 km^2) of the boreal forest of eastern Canada. Postfire recovery was estimated using the time elapsed to move from the burnt stage to the regenerated stage and the young forest stage. The main objective was to determine if forests situated in dry regions (characterized by a high proportion of dry coarse surficial deposits, low precipitation, and short fire cycle) tend to reestablish more slowly after fire, obtaining a more open stand compared with wetter regions characterized by a longer fire cycle. To identify the best explanatory model for postfire recovery, multinomial logistic regressions with the Akaike information criterion were conducted using a combination of physico-climatic factors. Our best model suggests that the most significant predictors of postfire recovery are time since fire (χ^2 = 1370.06), surficial deposit type (χ^2 = 651.95), the Canadian Drought Code (χ^2 = 247.75), and the growing season precipitation (χ^2 = 102.80). Fast recovery and dense forest regeneration are associated with subhydric till deposits only in the regions characterized by a long fire cycle (>500 years). Conversely, slow regeneration conducive to a sparse young forest was usually associated with regions characterized by a short fire cycle (<200 years) underlain by dry coarse deposits such as juxtaglacial but also mesic deposits in some cases. Our results also show that slow recovery and reduced forest regeneration are most likely to occur following fires that occurred in dry years, regardless of the deposit type and region.

Résumé : La transition, d'une forêt à couvert fermé vers un boisé ouvert, qui suit un feu dans plusieurs écosystèmes forestiers nordiques est souvent observée mais peu comprise. Cet article porte sur l'effet des interactions entre le dépôt de surface, le climat et le cycle de feu sur le rétablissement de la forêt après feu dans une vaste zone (190 000 km^2) de forêt boréale de l'est du Canada. Le rétablissement après feu a été estimé en utilisant le temps écoulé pour passer du stade de brûlis au stade de régénération et au stade de jeune forêt. Le principal objectif consistait à déterminer si les forêts situées dans les régions sèches (caractérisées par une proportion élevée de dépôts de surface grossiers et secs, une faible précipitation et un cycle de feu court) ont tendance à se rétablir plus lentement après feu, produisant ainsi un peuplement plus ouvert comparativement aux régions plus humides caractérisées par un cycle de feu plus long. Pour identifier le meilleur modèle explicatif du rétablissement après feu, des régressions logistiques multinomiales avec le critère d'information d'Akaike ont été effectuées en utilisant une combinaison de facteurs physico-climatiques. Notre meilleur modèle indique que les prédicteurs les plus significatifs du rétablissement après feu sont le temps écoulé depuis le feu (χ^2 = 1370,06), le type de dépôt de surface (χ^2 = 651,95), l'indice de sécheresse canadien (χ^2 = 247,75) et la précipitation durant la saison de croissance (χ^2 = 102,80). Un rétablissement rapide et une végétation forestière dense sont associés à des dépôts de till subhydrique seulement dans les régions caractérisées par un cycle de feu long (>500 ans). À l'inverse, une régénération lente propice à une jeune forêt clairsemée était habituellement associée aux régions caractérisées par un cycle de feu court (<200 ans) et la présence de dépôts grossiers secs, tels que le dépôt juxtaglaciaire, mais aussi de dépôts mésiques dans certains cas. Nos résultats indiquent aussi qu'un rétablissement lent et une faible régénération forestière vont très probablement suivre les feux qui se produisent lors d'années sèches, peu importe le type de dépôt et la région.

[Traduit par la Rédaction]

Received 31 January 2012. Accepted 14 June 2012. Published at www.nrcresearchpress.com/cjfr on 17 July 2012.

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[1]This article is one of a selection of papers from the 7th International Conference on Disturbance Dynamics in Boreal Forests.

Introduction

Since the beginning of the Holocene, the floristic composition and vegetation structure of the boreal forest have been driven by periodic naturally occurring large fires ignited by lightning (Rowe and Scotter 1973). In turn, the fire regime, which is variable in time and space, is itself influenced by the regional climate, the landforms, and also the susceptibility of fuels to drought (Johnson 1992; Payette 1992). To sustain forest services and predict ecosystem responses to global changes, the understanding of the mechanisms and pathways of disturbance effects on ecosystem recovery is essential in devising effective strategies for ecosystem management (Hamrick 2004). In addition to the fire regime, the regeneration of the boreal forest is strongly influenced by ecophysiological and physicoclimatic factors (Payette et al. 2008). As a top-down factor, climate has a major influence on rates of photosynthesis, growth potential and establishment of trees, and other forest processes, acting through temperature, radiation, and moisture regimes over medium and long time periods (Thompson et al. 2009). Topography and soil conditions also directly influence postfire recovery through the water flow regime in the soil (drainage) or through microclimates that in turn determine seedbed quality as well as fire cycle (Greene et al. 1999; Cyr et al. 2007).

Black spruce (*Picea mariana* (Mill.) B.S.P.) and jack pine (*Pinus banksiana* Lamb.) are characteristic of the black spruce – feathermoss domain in eastern Canada. They are fire-adapted species, usually able to reestablish themselves quickly and abundantly after fire due to their semi- or serotinous cones (Greene et al. 2004). Punctuated by the fire cycle, defined as the time necessary to burn an area equivalent to the study area (Johnson and Gutsell 1994), this loop is generally well observed within the closed-crown spruce forest zone, creating uniform and dense landscapes dominated by black spruce. Moreover, reduced postdisturbance regeneration has been widely reported within the closed-crown forest leading to an open lichen–woodland characterized by a low-density (<25% cover) stand interspersed with lichens (mainly *Cladonia* spp.; Girard et al. 2008, 2009). In some cases, development of the low-density stand could be the result of natural and anthropogenic disturbances (Payette et al. 2000; Jasinski and Payette 2005). Successive disturbances, such as logging followed by fire or spruce budworm outbreaks followed by fire (or in the reverse order), which occur before trees reach sexual maturity or before the seedbank is replenished, may strongly reduce tree density and cause regression of the closed-crown forest (Girard et al. 2008, 2009).

On the other hand, the soil moisture regime is equally important to the germination and survival of black spruce due to its high vulnerability to water stress (Black and Bliss 1980; Moss and Hermanutz 2009). Therefore, the open-type stand can also originate from edaphic constraints related to the thinness, excessive stoniness, and xeric drainage of the surficial deposits (hereafter SDD or deposit refers to surficial deposits and their drainage; Table 1), which would restrict both establishment and growth of trees. However, sites with strong edaphic constraints are not all occupied by open lichen–spruce woodland (Asselin et al. 2006). SDD are defined as sediments or materials that accumulated or were deposited after component particles were transported by ice, water, wind, or gravity (Fullerton et al. 2003). SDD play a key role in the distribution and development of vegetation in the boreal forest (Robitaille and Allard 2007) as well as in the spatial variation of the fire cycle (Mansuy et al. 2010). Considering the strong effect of the SDD on spatial variations in the fire cycle, we expect that different SDD types will show differences in development and density patterns in their postfire recovery. Altogether, these assumptions suggest that dry regions, due to drought as well as shorter fire cycles, may be more prone to reduced establishment and poor regeneration.

Consequently, the main objective of our study is to evaluate the influence of environmental factors driving the regional drying potential (physicoclimatic factors such as SDD, slope, altitude, temperature, precipitation, the number of degree-days, and the Canadian Drought Code) and the regional fire risk on postfire recovery in the boreal forest. Our first hypothesis predicts that forest development following fire is reduced within dry regions (i.e., high proportion of dry SDD, low precipitation, and short fire cycle) compared with a more humid region with a longer fire cycle. The second hypothesis predicts that postfire forest cover within dry regions is likely to exhibit a low-density cover (open) compared with a more humid region. To test these hypotheses, we will (1) determine which combination of physicoclimatic factors best explains postfire recovery using a comparison of multinomial logistic model regressions, (2) use the best model to predict the rate and age of transitions of different succession stages as an indicator of forest development, and (3) then compare the proportion of the open versus closed forest 45 years after fire (the older stage available with our data) as an indicator of forest density. Covering 190 000 km^2, the scope of this study has potential implications for devising strategies for ecosystem management in the northern boreal forest regarding forest vegetation succession and the landscape characteristics linked to the fire cycle.

Materials and methods

Study area

The study area, located in the Canadian Shield (Precambrian rock formation), encompasses a vast territory of roughly 190 000 km^2 between 70°W and 76°W and 49°N and 53°N (Fig. 1). The black spruce – feathermoss bioclimatic domain dominated by black spruce and jack pine largely covers the study area, while north of 52°N, the vegetation belongs to the black spruce – lichen domain (Fig. 1). The entire study area is relatively inaccessible and little affected by human activities. The largest city in the area is Chibougamau with 30 000 inhabitants. South of 51°N, the forest is under management licences and intensive fire protection by the SOPFEU (Société de Protection des forêts contre le Feu; intensive implies that all fires are fought). The dynamics of the vegetation and spatial variations of the fire cycle observed throughout the study area mostly repond to climatic and biophysical factors (Mansuy et al. 2010). This paper focuses on the three regions illustrated in Fig. 1 compiled from a classification of the landscape units based on the mean fire cycle in Mansuy et al. (2010). The landscape units are one of the elements in the hierarchical ecological classification system developed by the Ministère des Ressources naturelles et de la Faune du Québec (Robitaille and Saucier 1996). The

Table 1. Classification of the surficial deposit–drainage (SDD) combinations based on their mean fire cycle and their texture, stoniness, thickness, morphology, drainage, and associated soil drying potential (modified from Mansuy et al. 2010).

Dominant deposits	Fire cycle (years (95% CI))[a]	Texture[b]	Stoniness[c]	Thickness (m)[d]	Morphology[e]	Drainage[f]	Drying potential[g]	Area (%)[h]	Code[i]
Juxtaglacial and disintegration moraine	144 (96–288)	Sa	GPB	≈1	Knob-and-kettle	M	+ + + +	3	DRY
Ablation till >1 m and rogen moraine	146 (100–273)	SaSi	GB	1–5	Hummocky	X	+ + +	7.1	DRY
Juxtaglacial and disintegration moraine	157 (190–282)	Sa	GPB	≈1	Knob-and-kettle	X	+ + + + +	11.3	DRY
Outwash	173 (118–327)	SaSi	G	≈1	Relatively flat	X	+	2.7	DRY
Bedrock <25 cm	171 (116–323)	Null/SaSiC	Rock	0.25	Steep-sided/concave	X	+ + or –	3.2	ROC
Undifferentiated till >1 m	178 (123–322)	SaSiC	SPGB	5–1	Wavy	M	– –	45.7	MES
Undifferentiated till between 25 cm and 1 m	213 (150–368)	SaSiC	SPG	0.25–1	Wavy	M	–	11.3	SUB
Undifferentiated till >1 m	246 (168–460)	SaSiC	SPGB	5–1	Wavy	L	– – –	1.1	SUB
Undifferentiated till >1 m	290 (230–510)	SaSiC	SPGB	5–1	Wavy	H	– – – –	3.9	SUB
Undifferentiated till between 25 cm and 1 m	425 (269–1017)	SaSiC	SPG	0.25–1	Wavy	X	–	2.4	SUB
Organic >40 cm	279 (184–568)	Organic	Null	1–2	Wavy	H	– – – – –	8.3	ORG

[a]Fire cycle given with 95% confidence intervals (CI) for the period 1940–2006 from Mansuy et al. (2010).

[b]Texture is defined in terms of the size distribution of primary particles <2 mm. From the smallest to the largest particles: C, clay (0.25–40 µm); Si, silt (40–63 µm); Sa, sand (63–2000 µm). The sequence of letters in the column indicates the importance of each element in the combination.

[c]Stoniness is defined in terms of the size of the particles >2 mm. From the smallest to the largest particles: G, gravel (2–5 mm); P, pebble (75–250 mm); S, stone (25–600 mm); B, boulder (>600 mm)

[d]The average thickness of the deposit from the bedrock.

[e]The morphology is the general shape of the deposit observed in the field.

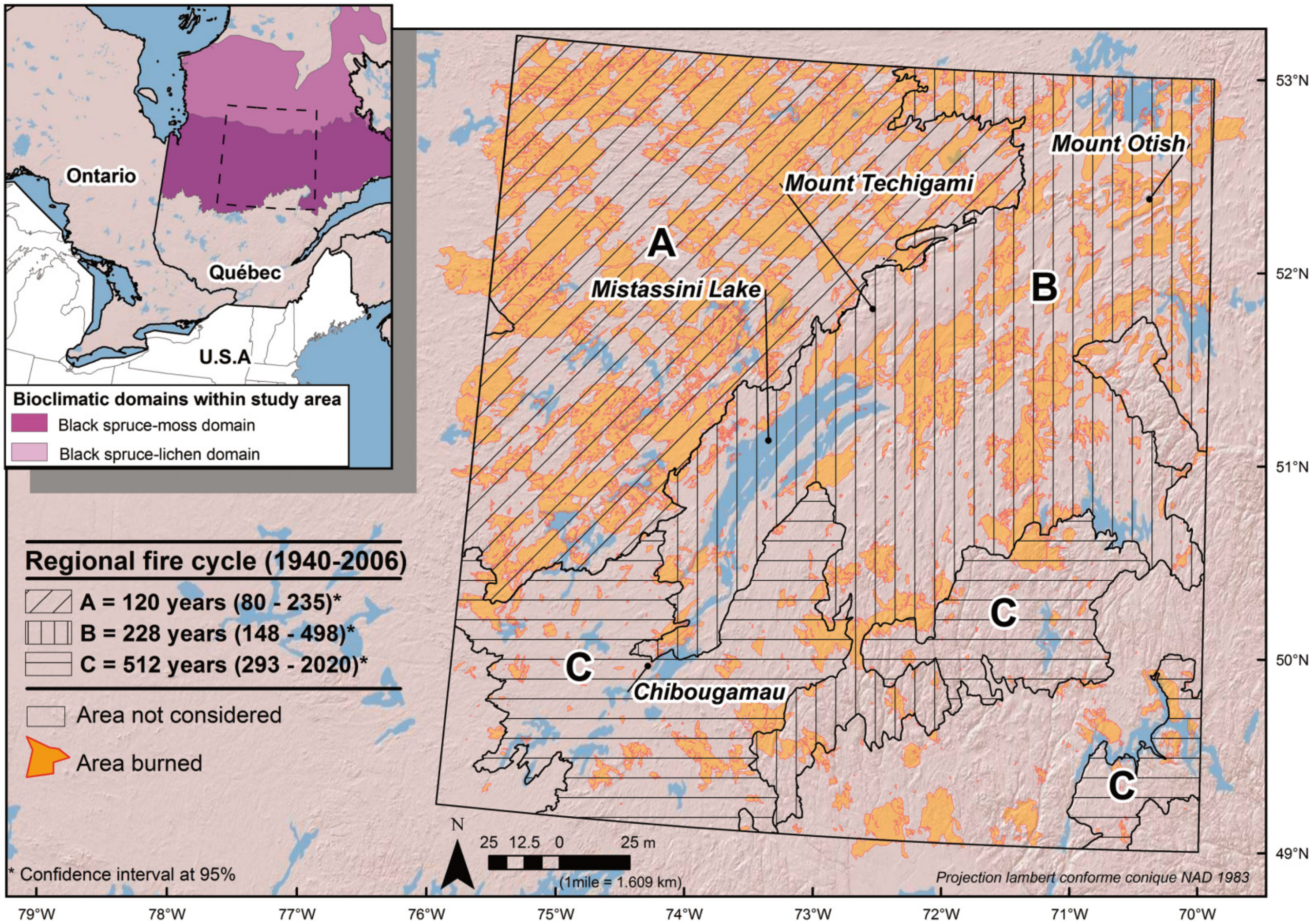
[f]Drainage classes: X, xeric; M, mesic; H, hydric; L, lateral.

[g]Drying potential refers to the speed at which water drains from the soil and the potential availability of surface water for fuel types. A high drying potential is indicated by "+" and a low drying potential is represented by "–".

[h]Percent area estimated with the 6133 sampled points.

[i]Code summarizes the quality of the stoniness and the texture: DRY, dry because very sandy and very coarse; ROC, rock; MES, mesic; SUB, subhydric; ORG, organic.

Fig. 1. Location of the study area with the main bioclimatic domain in the Province of Quebec. The enlarged square refers to the study area subdivided into three regions, A, B, and C, based on the mean fire cycle (from the burn rate estimated between 1940 and 2006 in Mansuy et al. 2010). The shaded polygons (yellow in the online version) represent the area burned between 1940 and 2006.



physicoclimatic description of the three regions that follows is predominantly adapted from the final report on the northern limit for timber allocation (Ministère des Ressources naturelles et de la Faune 2000) and from Robitaille and Saucier (1998) and Mansuy et al. (2010).

Region A spreads out westward and northwest of Lake Mistassini (Fig. 1) and consists of undulating hillocks with an average altitude of 350 m. The SDD are mainly composed of stony and sandy textured glacial deposits, which explains the abundance of xeric areas, particularly north of 52°N. The mean annual temperature ranges from –1.5 to –1.8 °C and the mean annual precipitation varies between 680 and 800 mm. The fire cycle is considered short with a mean value of 120 years between 1940 and 2006.

Region B is located northeast and east of Lake Mistassini and consists of high hilly territory (Mounts Techigami and Otish). The mean altitude ranges roughly between 700 and 750 m with some peaks higher than 1000 m. The SDD are mainly composed of glacial till and various moraines with rocky outcrops that occupy approximately 30% of the zone. The mean annual temperature varies from –6.0 to –1.5 °C and the mean annual precipitation is between 800 and 950 mm. South of Mount Otish, the land becomes slighty hilly with a mean altitude of roughly 250 m characterized by hillocks and a few hills covered by thick undifferentiated till. The mean annual temperature is about –1.5 °C and the mean annual precipitation is roughly 900–1000 mm. The fire cycle is considered medium-long with a mean value of 228 years between 1940 and 2006.

Region C covers three zones, all south of 51°N. The most western zone consists of slightly undulating plains with a mean altitude of 350 m. Located between the Geer moraines and drumlins are depressions generally occupied by peat bogs that occupy 20% of the surface area (20% of ORG in Region C; Table 2). The two most eastern zones consist of hilly terrain with a mean altitude of 600 m. The narrow and deep valleys (400 m deep), oriented north–south, cut across the plateau and are characterized by rocky escarpments. Thick undifferentiated till characterizes flat surfaces and valley bottoms, whereas thin till covers the steep slopes and the rocky outcrops on the summits. For the three zones, the mean annual temperature ranges from –2.5 to 0 °C and the mean annual precipitation varies between 800 and 1000 mm. The fire cycle is considered long with a mean value of 512 years between 1940 and 2006.

Forest recovery data

The data are compiled from mapping the Ecoforestier inventory program (Létourneau et al. 2008). Data are polygons of 8 ha minimum treated with ArcGIS 9.3 (ESRI Inc., Red-

Table 2. Types and descriptions of the explanatory variables used in the analyses.

Variable (abbreviation)	Type	Description	Scale	Source
Physical				
Surficial deposit–drainage (SDD)	Class	Five surficial deposit–drainage combinations	See Table 2	Mansuy et al. 2010
Slope (SLOPE)	Continuous	Mean slope (%) at the landscape unit scale	2% to 15%	Robitaille and Saucier 1998
Altitude (ALT)	Continuous	Mean altitude (m) at the landscape unit scale	353 to 800 m	Robitaille and Saucier 1998
Geographic				
Region (REG)	Class	Three regions based on mean fire cycle	A, B, C (Fig. 1)	Mansuy et al. 2010
Climatic				
Degree-days (DD)	Continuous	Annual growing degree-day summation over 5 °C	894 to 1342 °C	BioSIM 10
Growing season precipitation (GSP)[a]	Continuous	Total precipitation (mm) during growing season	352 to 497 mm	BioSIM 10
Growing season temperature (GST)	Continuous	Mean temperature (°C) during growing season	13.4 to 15.8 °C	BioSIM 10
Temperature mean (TM)	Continuous	Annual mean temperature (°C)	−3.7 to 0.8 °C	BioSIM 10
Canadian Drought Code (DC)[b]	Class	The years with drought code >240 (mean + SD) were considered particularly dry	Dry or normal years (Fig. 4)	BioSIM 10
Temporal				
Time since fire (TSF)	Continuous	Time since last fire	1 to 67 years	Mansuy et al. 2010

[a]Growing season is defined as the period between 3 consecutive days without frost ($T_{min} > 0$ °C) and 3 consecutive days with frost ($T_{min} < 0$ °C).
[b]The driest years recorded with BioSIM 10 (Régnière and St-Amant 2007) are 1945, 1952, 1953, 1957, 1961, 1962, 1963, 1967, 1981, 1982, 1987, 1988, 1989, 1995, 2002, 2005, and 2006 (Fig. 4).

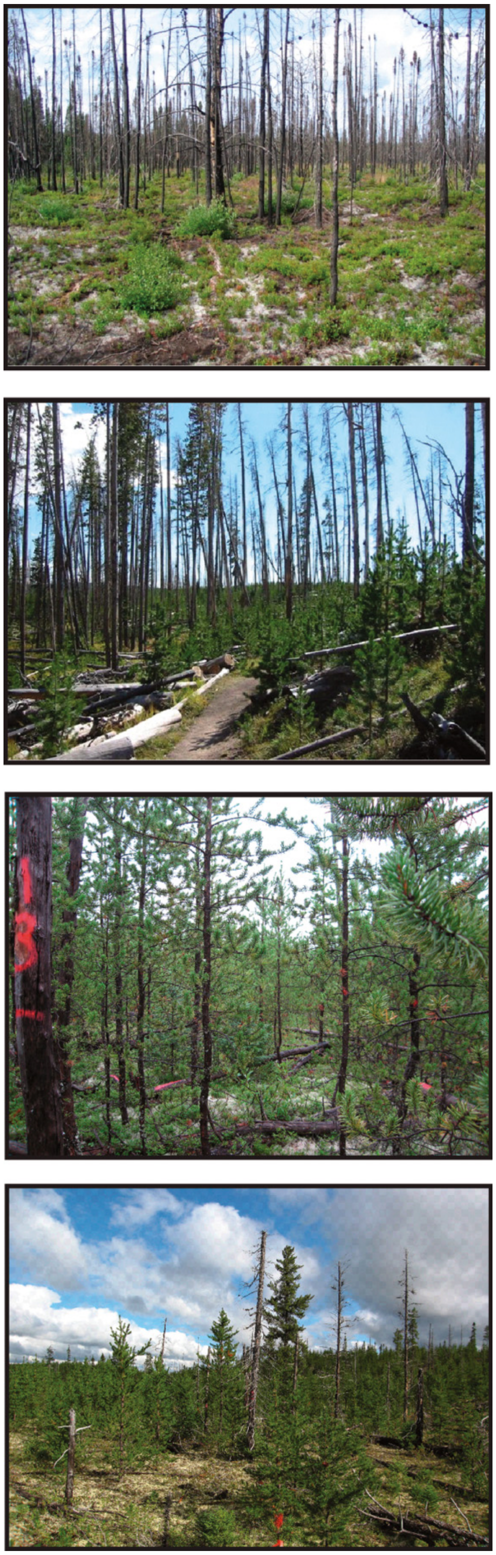
lands, California). This inventory aims to extensively describe the vegetation and physical characteristics of the northern boreal forests of Quebec. North of 51°N, information on vegetation is gathered from satellite images, while in the south, it is derived from photo-interpretation. In the south, photo-interpretations are validated routinely by ground-truthing. To assess the quality of northern data, 1000 stands were selected randomly and described using the same photo-interpretation rules as used in the south. There was a good agreement between the two mapping strategies, as revealed by a Kappa statistic (measure of interrater agreement) higher than 60%, for any of the variables used in this study (maturity stage, disturbance type, and surficial deposit; see below). As our data do not distinguish between species, the analysis will be done on the vegetation as a whole, which is comprised of approximately 90% coniferous species such as black spruce and jack pine. To obtain a measure of postfire recovery, we considered four successional stages in accordance with the mapping standards used in Quebec (Létourneau et al. 2008, 2009) and with the first three decadal forest inventories. The successional stages correspond to different tree heights and canopy densities (Fig. 2) as follows. (1) Burnt (BURNT): stand affected by a recent fire with no trace of regeneration more than 2 m in height. (2) Regenerated (REG): initial regeneration stage with seedlings and saplings growing in diameter with a height between 2 and 7 m. The stand has no or very few stems with a diameter of 9 cm and greater. (3) Young (DENSE): stand measures 7 m and greater and the majority of the stems have a diameter greater than 9 cm. It has a density (as estimated by ground cover estimation from photo-interpretation) higher than 25%. (4) Young sparse (SPARSE): stand measures 7 m and greater and the majority of the stems have a diameter greater than 9 cm. However, it has a density (as estimated by ground cover estimation from photo-interpretation) less than 25%. As our data span only 67 years after fire, we did not consider the mature stage of development in the analysis.

Explanatory variables

To model postfire recovery and predict the probability of each successional stage over time, we tested several types of variables including SDD, slope, altitude, degree-days, temperature, precipitation, the Canadian Drought Code, the three regions described above (expressing three levels of fire risk), and time since fire. Sources and scales of the whole data set used in the analyses are described in Table 2 but some variables are also described here.

The Canadian Drought Code, a component of the Canadian Fire Weather Index system (DC) (Van Wagner 1987) is a useful indicator of the seasonal drought effects on forest fuels and the amount of smouldering in deep duff layers and large logs. To assess whether particularly dry years can affect the postfire recovery compared with so-called normal years, the 67 years of data have first been categorized into two classes, normal or dry based on the DC. The average DC has been computed with BioSIM (Régnière and St-Amant 2007) for each year based on the monthly mean of May, June, July, and August and for each region (with the random points inside each region). The years above the threshold of 240 (240 = average DC + standard deviation) are considered

Fig. 2. Examples of the four successional stages used as an indicator of forest recovery. From top to bottom: burnt, regenerated, young dense, and young sparse. This paper aims to estimate the time required to shift from one state to another and the role of the surficial deposits in this succession (photograph credits: top two panels, François Girard; bottom two panels, MRNFQ).



as “dry”. Years below the threshold of 240 are considered as “normal”.

To have sufficient well-represented classes to estimate forest recovery for each type of SDD, we grouped together the combinations of SDD by similar fire cycles from tables 1 and 2 in Mansuy et al. (2010) (Table 1). The SDD were grouped to illustrate the soil drying potential based on their texture, stoniness, drainage, and morphology. For this paper, among the SDD with a short fire cycle (<200 years), we distinguished the coarse-sand deposits (DRY) from the rock outcrops (ROC) and the mesic thick tills (MES) given the possibility that they may have a different effect on postfire forest recovery despite a similar fire cycle (Table 1). Among the SDD with a long fire cycle (>200 years), we distinguished the subhydric thin tills (SUB) from the pure organic deposits (ORG) for the same reasons.

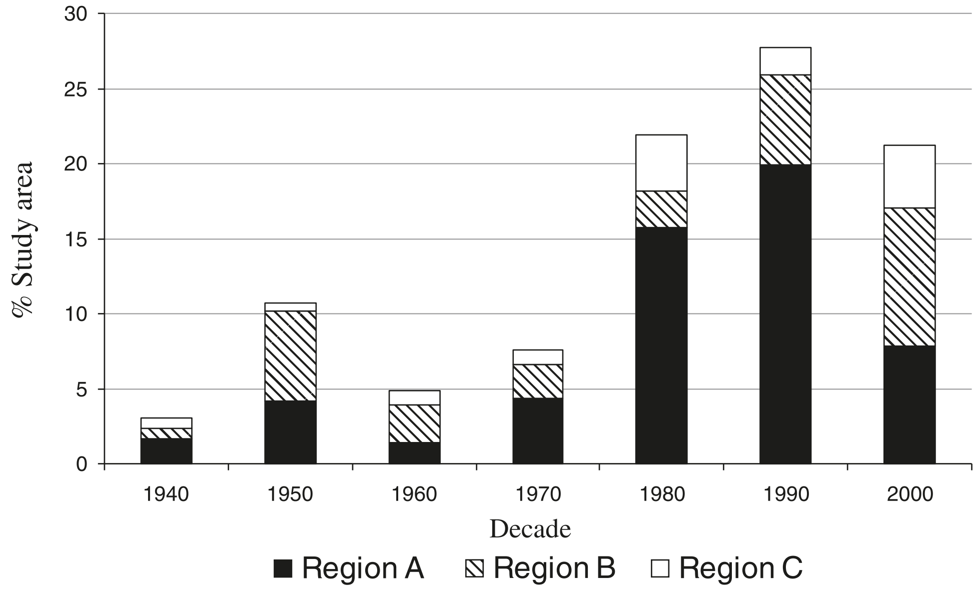
To estimate the time since last fire (TSF) for the period between 1940 and 2006, we used the provincial fire spatial database provided by the Ministère des Ressources naturelles et de la Faune du Québec. Most of these fires were classified with an exact ignition date by the SOPFEU. For remotely located fires, for which the perimeter was obtained using remote sensing (accounting for 30% of the fires), the fire dates are approximations subsequently integrated into classes of 5 years. For these fires, the middle value of each class was considered as their fire date. The fire perimeter was also validated with ground-truthing data using the Kappa statistic with more than 90% success. The fire polygon database was included in ArcGIS 9.3 with the following attributes: location, size, and date. Then, we attributed to each random point a TSF from 1 to 67 years. In the study area, 1094 fires occurred between 1940 and 2006, with fire sizes ranging from 5 to 225 918 ha (mean size = 5442 ± 15 101 ha). Despite the large fires (>50 000 ha), less than 13% of the total number of fires are responsible for burning over 65% of the study area between 1940 and 2006 (Fig. 1). In addition, 61% of the total area burned occurred in region A, 23% in region B, and 16% in region C. Seventy-four percent of the total area burned occurred since 1980 of which 45% occurred in region A (Fig. 3).

Model selection and logistic regression

We randomly sampled the study area with 30 000 points with ArcGIS 9.3 in manner similar to the methodology used in Mansuy et al. (2010). We considered the stands that originated from fire only between 1940 and 2006, and among them, the points representing nonforest land (water, island, wetland, barrenland, dam, road, etc.) were not included in the analyses. Finally, our data set consists of 6133 points for which we assigned the four successional stages and all of the explanatory variables cited in Table 3. Our statistical method can be organized into three steps.

First, to test if the variables, combined or not, can explain the postfire recovery, we built 11 a priori multinomial logistic models with the explanatory variables and then we compared the models with the Akaike information criterion (AICc) with R (R Development Core Team 2007). Differences in AICc values, delta AIC (Δ_i), and Akaike weights (W_i) among models were used to identify the model that was best supported by our data. Models with large Δ_i values are less plausible given the data, and W_i provides an additional meas-

Fig. 3. Percentage of the study area burned by decade from each region. One decade represents 10 years of collected data (1940–1949, etc.) except for 2000, which represents only 7 years (2000–2006). Seventy-four percent of the total area burned occurred since 1980 when 45% occurred in region A.



ure of strength of evidence for a model (Burnham and Anderson 2002; Mazerolle 2006). Then, we ran the multinomial logistic regression to find the most significant variables among the best selected model. Logistic regression emerged as a valuable statistical tool for analyzing spatial and temporal patterns of vegetation cover change (Taylor and Chen 2011). It tests the global null hypothesis that none of the independent variables in the model are related to changes in probability of event occurrence and fit a logistic regression model by using the maximum likelihood estimation method (Agresti 2002). If X_i are explanatory variables and p is the response probability to be modeled, the logistic model has the form

$$\log p/(1-p) = B_0 + B_1X_1 + B_2X_2 + B_3X_3 + \ldots + B_mX_m$$

where B_i is the regression coefficient. For a response with k levels (four in our case: BURNT, REG, DENSE, and SPARSE), a logistic regression is used to describe k – 1 pairs with three levels relative to a reference level. We selected the SPARSE level as a reference level. All variables presented in Table 3 were tested as explanatory variables.

Second, we used the probabilities generated by the output of the best model to predict the rate and age of transitions to different succession stages as an indicator of forest development over TSF for each type of SDD and each region. To show the probability of reaching the 7 m and more stage, regardless of the cover density, we summed the probabilities of reaching the sparse and dense stages. Using the year dryness classification (dry or normal from Fig. 4), we also included a comparison between the driest years and all years together.

Third, as an indicator of forest density, we compared the predicted proportion of dense versus sparse forests at 45 years after fire (the oldest stage available with our data) to see if this ratio had changed compared with the old landscape (burned before 1940). Finally, we also compared the chances of being in a dense or sparse stage, focusing on the odds ratios $\Psi = \exp(\beta)$, where βs are the estimated coefficients for the significant independent variables in the logistic regression model. The odds ratio is a more intuitive and easily understood way to capture the relationship between the continuous variables (Hosmer and Lemeshow 1989; Jalkanen and Mattila 2000).

Results

Model selection and individual effect of variables

Among the 11 a priori models tested (Table 3), Mod11, which combines all of the geographical, temporal, physical, and climate variables, is the most significant for describing postfire recovery. Notice that Δ_i tends to decrease drastically (meaning a better model) as soon as the climatic, physical, and temporal variables are combined with a $\Delta_i < 272.09$ for Mod11, Mod10, and Mod9 compared with other models with $\Delta_i > 2864.73$ (Table 3). However, comparing Δ_iMod9 = 272.09 with Δ_iMod10 = 12.17, we see that DC significantly improves the model. Models with a single variable are not significant. Nevertheless, Mod2, which alone contains the TSF variable, appears as the third strongest model (Δ_iMod2 = 2864.73).

In addition, the logistic procedure displays a table that shows the effect for each variable included in the best model (Table 4). The χ^2 test statistics and associated p values indicate that each of the 10 variables significantly improves the model (all $p < 0.05$). TSF, as expected ($\chi^2 = 1375.79$), and SDD ($\chi^2 = 651.57$) are clearly the most significant variables followed by DC ($\chi^2 = 248.34$) and the growing season precipitation (GSP) ($\chi^2 = 102.33$). The remaining variables are less significant with $\chi^2 < 100$ in the following order: the altitude (ALT), the interaction of the region and the deposits (REG × SDD), the annual mean temperature (TM), the degree-days (DD), the growing season temperature (GST), and the slope (SLOPE). REG alone is not significant but is kept in the model. Our best model fits particularly well with our

Table 3. Description and model selection based on Akaike's information criterion (AIC).

Candidate model	Name	Parameters[a]	AICc	Δ_i[b]	W_i
REPONSE ~ REG × SDD + TDF + DD + GSP + TM + GST + SLOPE + ALT + DC	Mod11	72	8836.84	0	1
REPONSE ~ REG + SDD + TDF + DD + GSP + TM + GST + SLOPE + ALT + DC	Mod10	48	8849.02	12.17	0
REPONSE ~ REG + SDD + TDF + DD + GSP + TM + GST + SLOPE + ALT	Mod9	45	9109.74	272.90	0
REPONSE ~ DD + GSP + TM + GST + DC	Mod8	21	12725.61	3888.77	0
REPONSE ~ DC	Mod7	6	13268.74	4431.90	0
REPONSE ~ REG × SDD	Mod6	45	12195.00	3358.16	0
REPONSE ~ SDD	Mod5	15	12307.82	3470.97	0
REPONSE ~ SDD + SLOPE + ALT	Mod4	21	12209.53	3372.68	0
REPONSE ~ REG	Mod3	9	13493.62	4656.78	0
REPONSE ~ TDF	Mod2	6	11701.57	2864.73	0
REPONSE ~ 1	Mod1	3	13571.45	4734.60	0

Note: Models are ranked based on their AICc scores where the smallest AICc represents the best model. RESPONSE refers to the four successional stages as explained in the text. Abbreviations are explained in Table 2. "×" indicates an interaction between the variables REG and SDD.

[a]Parameters refers to the number of estimated parameters for a given model.

[b]Delta AICc (Δ_i) is the difference in AICc scores between the best model and another competing model from the same set of candidate models. $\Delta_i \leq 2$ as substantial evidence in support of a model. Δ_iMod11 = 0 and Akaike weight $W_i = 1$ is interpreted as meaning that model Mod11 has a 100% probability of being the best model among the set of candidate models, given the data (Burnham and Anderson 2002).

data, since 85.5% of predicted values are consistent with the observed values (Appendix A, Fig. A1).

Rate and age succession over time

As an indicator of postfire forest development, the predicted transition probability values for the four successional stages were estimated over TSF for each type of SDD within each region (Appendix A, Table A1). However, to simplify the text for the reader, we chose to present only the greatest extremes in terms of forest recovery to highlight the effects of SDD and REG (Fig. 5). To show the probability of reaching the 7 m and more stage, we summed the SPARSE and the DENSE stages. When the data allow for it, we also included a comparison between the driest years and all of the years together. The effect of dry years was included in analyses only if there were enough dry years in the region. This was not the case in region C, which burns less than regions A and B (Fig. 1). Region B, which is not discussed in this section, shows intermediate results between regions A and C (Appendix A, Table A1).

Looking at the whole study area, the regenerated stage surpasses the burnt stage from 25 years after fire (Fig. 5*a*). Then, the regenerated state dominates the chronosequence up until 42 years after fire. At 45 years after fire, the 7 m and more stage is above all other stages (0.52). In region A, the pattern of the recovery is similar regardless of the deposit (Figs. 5*b* and 5*c*). The regenerated stage surpasses the burnt stage from 28 years after fire on the DRY deposit and 23 years on the SUB deposit. The transition from the regenerated stage to the 7 m and more stage is carried out at the same time for both deposits (40 years for DRY and 42 years for SUB). Meanwhile, 45 years after fire, the probability of attaining the 7 m and more stage tends to be much higher for the DRY (0.61) than for the SUB deposit (0.41). In region C, the pattern of forest recovery is different from that in region A, but it is also influenced by the deposits (Figs. 5*d* and 5*e*). For the SUB deposit in region C, the probability of attaining the 7 m and more stage tends to be much higher and faster than the for the DRY deposits in region C and any other case (Appendix A, Table A1). The curve shows a net increase from 15 years after fire, passing the regenerated state at 37 years after fire, and reaching 0.68 of probabilities above all other stages at 45 years after fire (Fig. 5*e*).

Generally, the effects of the driest years for the DRY and SUB deposits within region A are similar to those observed throughout the whole study area. The driest years slow the transition (up to 10 more years to switch from the burnt state to the regenerated one compared with all of the years together), meaning a higher probability of staying longer in the burnt stage and a lower probability of reaching the regenerated stage.

Open versus closed forest 45 years after fire

Figure 6*a* shows that the predicted proportion of dense forest, 45 years after fire, increases (28%, 31%, and 60% for regions A, B, and C, respectively) with a decreasing risk of fire. The driest years reduce the proportion of dense forest for the three regions (25%, 28%, and 52% for regions A, B, and C, respectively). Within regions, the proportion of dense forest increases when the drying potential of the deposit decreases, except with the ORG deposit, which always shows a

Fig. 4. Annual Canadian Drought Code (monthly maximum of the year) computed with BioSIM 10 (Régnière and St-Amant 2007). The years 1945, 1952, 1953, 1957, 1961, 1962, 1963, 1967, 1981, 1982, 1987, 1988, 1989, 1995, 2002, 2005, and 2006 above the the threshold of 240 (mean + SD) were considered particularly dry (see details in the text).

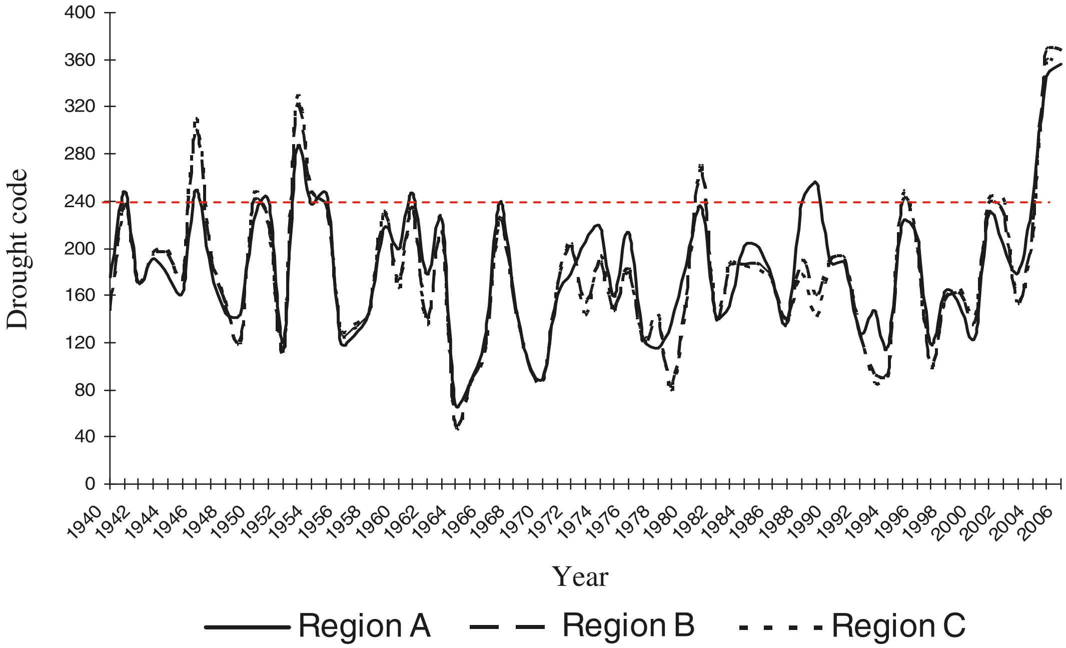


Table 4. Summary of the logistic regression (variables significant at $p < 0.05$).

Variables	df	Wald χ^2	Pr > χ^2
TSF	3	1370.06	<0.0001
SDD	12	651.95	<0.0001
DC	3	247.75	<0.0001
GSP	3	102.80	<0.0001
ALT	3	79.96	<0.0001
REG × SDD	24	53.13	0.0006
TM	3	43.18	<0.0001
DD	3	34.61	<0.0001
GST	3	27.10	<0.0001
SLOPE	3	23.20	<0.0001
REG	6	12.78	0.0465

Note: Abbreviations are explained in Table 2. Based on the Wald test, the table shows the significance for each variable included in the best model (Mod11) individually (Table 3). "×" indicates an interaction between the variables REG and SDD.

proportion of dense forest close to zero. The SUB deposit shows the highest proportion of dense forest (41%, 45%, and 62% in regions A, B, and C, respectively). Conversely, the DRY deposit presents the lowest proportion of dense forest (22%, 25%, and 40% in regions A, B, and C, respectively). Other deposits are intermediate between these two extremes. We notice that the predicted regional pattern is similar to the proportions observed in the old landscape (burnt before 1940; Fig. 6*b*) in relative terms. The rank of each region on the canopy density (the mean proportion of dense forest) is clearly preserved (57%, 72%, and 88% for regions A, B, and C, respectively). The predicted proportions of dense forest are obviously lower than those observed in the old landscape because the forest is older in the latter case. Similarly to the predicted proportions, the SUB deposit shows the highest proportion of dense forest in the three regions (94% in region C). However, unlike the predicted proportions, the DRY deposit shows a higher proportion of dense forest than the ROC deposit.

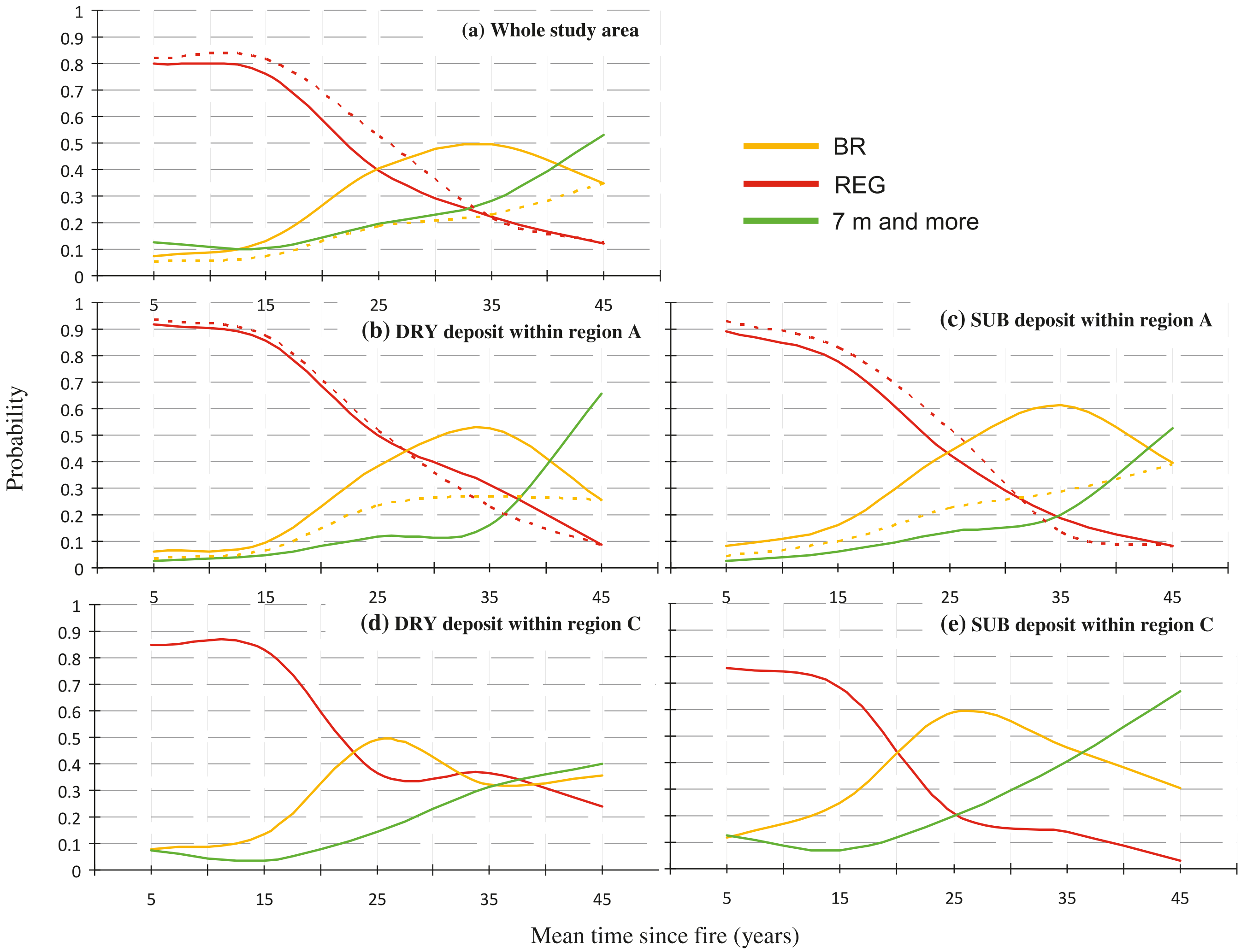
In addition to the region and the deposit, other variables influence whether a forest will be in the dense or sparse stage (Table 5). All of the continuous variables are statistically significant at $p < 0.05$. As suggested in Table 4, GSP is highly significant with an odds ratio of 29.3. Concretely, one unit increase in GSP increases the probability of being a young dense forest over that of being a young sparse one by 29.3%. Similarly, one unit increase in TM increases the chance of being a young dense one compared with young sparse one by 4.2%. On the other hand, ALT, DD, and GST with an odds ratio between 0.97 and 0.99 have a very slight risk of decreasing the chance of being in a young dense state compared with a young sparse state.

Discussion

Interaction of processes at the regional scale

Our results suggest that the regional pattern of postfire vegetation recovery is controlled by a complex combination of physical and climatic factors. Therefore, postfire recovery appears highly variable in space and time but also in density across the entire study area. Among the variables tested in this paper, time since fire, deposit, the Canadian Drought Code, growing season precipitation, and the annual mean temperatures are the most significant predictors of postfire successional stages. The time since fire is a "no surprise" significant factor because fire is well known to be the main natural disturbance driving ecological succession in the boreal forest (Heinselman 1981; Johnson 1992). A longer fire interval will actually allow tree reestablishment, while a short in-

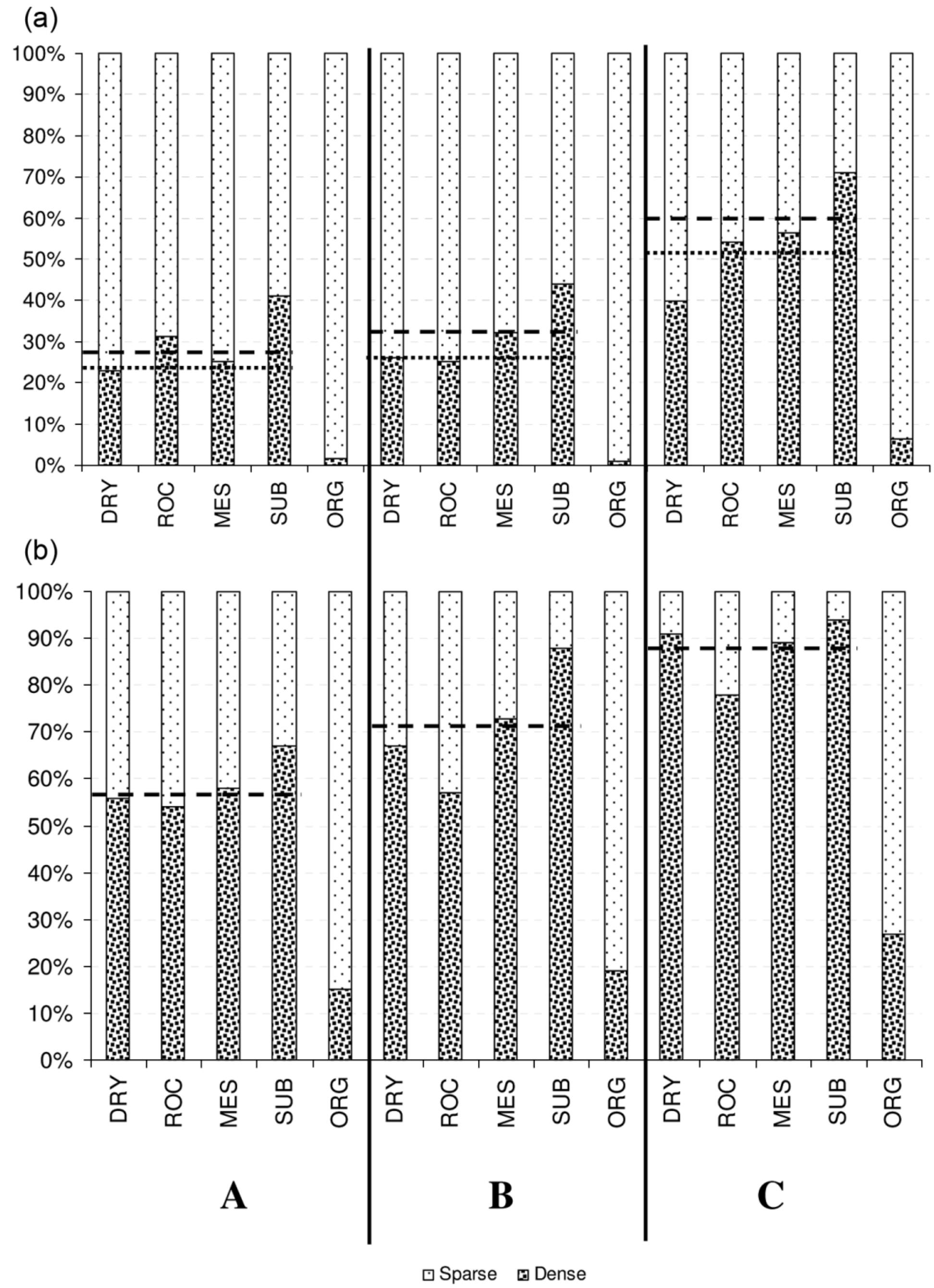
Fig. 5. Predicted transition probability values for the three successional stages (we summed the SPARSE and the DENSE stages) over mean time since fire for (*a*) the whole study area, (*b*) the driest (DRY) deposits in region A, (*c*) the subhydric (SUB) deposits in region A, (*d*) the driest deposits in region C, and (*e*) on the subhydric deposits in region C. Solid lines describe all of the years and dotted lines describe only the "dry" years (annual DC >240) when the data permit (Fig. 4).



terval could lead to an opening of the forest leading to open woodland in the burned areas (Payette 1992; Girard et al. 2008). In the context of short fire intervals, as one can assume for region A with a 121-year fire cycle, the black spruce stems may not have sufficient time to reach sexual maturity and produce sufficient seeds following the occurrence of the next fire (Girard et al. 2009).

This paper confirms the key role of deposits as bottom-up factors controlling forest succession (Lecomte and Bergeron 2005; Kang et al. 2006). The deposits affect both the speed and the density of tree establishment after fire through differential creation of microsite conditions influencing the soil moisture regime (Taylor and Chen 2011). Dry deposits within dry regions appear to be the worst site type for forest recovery in our study area. The driest ones, composed of sandy-gravel deposits such as juxtaglacial deposits, eskers, or decrepitude moraines, are most likely to limit seedling establishment and subsequent forest development, thus generating an open forest. Indeed, fast drainage accentuated by a slope or coarse material could make the mineral soil particularly exposed after fire, causing high seedling mortality at the start of the regeneration period (Greene et al. 2004). Interactions of a high proportion of dry deposits within a dry region (such as region A, which combines a high proportion of DRY deposits, mean annual precipitation <800 mm, with a short fire cycle) could create extreme fire-weather conditions for fuels to dry and increase their flammability regardless of the type of deposit (Mansuy et al. 2010). In this situation, even sites with better drainage conditions (mesic or subhydric) may have a forest recovery pattern similar to the driest deposits leading to a high probability of maintaining or creating open-forest conditions over time (Fig. 6; Appendix A, Table A1). However, even in region C (which is more humid and has a very long fire cycle), control of forest recovery by the inherent characteristics of the driest deposits rather than regional top-down processes is still detectable. Conversely, fast and dense forest regeneration is observed on SUB deposits only in region C, which is characterized by a long fire cycle (>500 years), making region C the best situation for closed-crown forest recovery in our study area. Consistent

Fig. 6. (*a*) Predicted proportion of dense versus sparse forest 45 years after fire for each deposit by region. (*b*) Observed proportion of dense forest versus sparse forest 45 years after fire for each deposit by region in the landscape burned before 1940. The dotted line shows the mean proportion of dense forest for each region (ORG deposit not included). The dashed line shows the mean proportion of dense forest for each region during the driest years (ORG deposit not included; available only in Fig. 6*a*).



with other studies, organic deposits in our study area led in most cases to unproductive low wetland environments (peatlands) that remain stable over time (Appendix A, Table A1).

Regional climate conditions also influence the speed of forest recovery as well as cover density. Our analyses clearly show that the transition period from the burnt stage to the regenerated one is slowed during the driest years compared with the "normal" years, whatever the deposit or the region considered. This suggests that the rate of forest development is influenced by climatic and soil moisture conditions during this initial stage after fire. A drought involving low water retention in the deep compact organic layers the first 3–5 years after fire could be critical for black spruce survival (Moss and Hermanutz 2009; Johnstone et al. 2010). In addition, if the spruce fail to reestablish during this time span after fire, lichen expansion is likely to reduce spruce extension and growth (Sirois and Payette 1989; Hébert et al. 2006). Therefore, the Canadian Drought Code seems to be a good indicator of potential forest recovery, since it allows us to describe the critical parameters for the survival of spruce after fire such as the moisture of deep organic layers and the hydric stress depth (Turner 1972; Girardin et al. 2004). In addition,

Table 5. Odds ratio of the continuous variables for the young dense state compared with the young sparse one (variables significant at $p < 0.05$).

Variable	Response	df	Estimate	SE	Wald χ^2	Pr > χ^2	Odds ratio exp(estimate)[a]
ALT	DENSE/SPARSE	1	–0.008	0.002	16.361	<.0001	0.992
SLOPE	DENSE/SPARSE	1	0.126	0.046	7.407	0.007	1.134
TM	DENSE/SPARSE	1	1.449	0.566	6.550	0.011	4.258
GST	DENSE/SPARSE	1	–0.017	0.007	5.524	0.019	0.983
GSP	DENSE/SPARSE	1	3.378	1.075	9.877	0.002	29.303
DD	DENSE/SPARSE	1	–0.025	0.010	6.015	0.014	0.975

Note: Abbreviations are explained in Table 2.

[a]The exp(estimate) value corresponds to the odds ratio for a unit increase of the corresponding variable (the odds ratio is equal to the odds raised to the power of the increment of interest). Odds ratios greater than 1 mean that the event is more relatively likely to occur than not for one group as opposed to another.

cover density seems particularly responsive to the regional variation in precipitation and temperature, as is usually the case in the boreal forest (Greene et al. 1999; Girard et al. 2011). As shown in Table 5, an increase in the growing season precipitation and temperature is likely to regenerate a dense stand rather than a sparse one. That is why we observe better regeneration in region C compared with region A, which are climatically distinct. The potential for regeneration after fire is of course also under the control of intrinsic characteristics of the vegetation before fire, such as the density and age of trees as well as the seedbank (Greene et al. 1999). However, due to a lack of information on the predisturbance stand conditions, the influence of these factors has not been tested here. In this regard, a comparison of our results with a study conducted at the stand level in the same area suggests similar effects of SDD and climate on tree recruitment 10–30 years after fire (R. Van Bogaert et al., in preparation). Similarly, we did not include past fire severity in the analysis because we did not have this information.

Current regional postfire recovery

Although species such as jack pine and black spruce are well adapted to fire, the absence or decrease in postfire regeneration in the boreal forests of Quebec has been observed with the extension of the open spruce–lichen woodlands toward the south over the last 50 years (Payette et al. 2008; Girard et al. 2009). Our data do not allow us to draw conclusions about the transition from a closed forest to an open forest cover (or the decrease in the density of trees compared with the prefire stands). Indeed, it is difficult to compare a 67-year-old recent portion of the landscape where most of the fires occurred over the last 20 years with an old forested portion of the landscape where the date of the last fire remains unknown. Meanwhile, we first notice that the regional pattern predicted using the best model is somewhat similar to that of the old landscape (Fig. 6) Thus, the high probability of having sparse forest in region A as well as the overall canopy recovery could therefore be linked at least partly to the prefire stand composition associated with regional physicoclimatic processes rather than drastic recent changes in the successional pathways. It is also possible that this phenomenon is increasing (i.e., transition from a closed crown forest to an open forest), as there is a higher proportion of open forest in the recent landscape than in the old one. To support this idea, several studies have already demonstrated the recent impacts of climate change on boreal forests (Thompson et al. 2009; Bergeron et al. 2010; Johnstone et al. 2010). Recent studies suggest that seedlings will be more susceptible to episodic soil drying and less competitive for belowground resources in future climates in the boreal region (Angert et al. 2005; Way and Sage 2008; Moss and Hermanutz 2009). This may be particularly true for black spruce, which is more vulnerable to prolonged and repeated drought than jack pine (Sirois 1993). Therefore, the opening of the landscape on the driest sites may be accompanied by a replacement of black spruce by jack pine (Le Goff and Sirois 2004). On the other hand, global changes will not only influence the fire regime by "fire-weather" but also influence soil drainage, thereby affecting long-term water tables (Yi et al. 2009). Whereas some characteristics of deposits, such as composition and elevation, are stable over time, other attributes, such as drainage and water table, are responsive to climate change and will certainly influence future forest establishment.

Another major natural disturbance not addressed in this paper may interfere with the succession processes and possibly compromise the reestablishment of the closed-crown forest within our study area. A recent spruce budworm outbreak has been detected along a corridor (70°W–72°W and 49°N–52°N; Girard et al. 2011). Although the preferred host of the spruce budworm is balsam fir (*Abies balsamea* (L.) Mill.), recent studies have shown a large decrease in growth and survival following defoliation of black spruce in the boreal forest of eastern Canada (Simard and Payette 2005). Hennigar and MacLean (2010) have shown that recent warming episodes might accelerate the seasonal development of outbreaks and might also cause catastrophic loss in growth.

Conclusion

The dynamics of change in the boreal forest vary tremendously in time and space, which makes generalizations or predictions difficult to make (Chapin et al. 2010). Nevertheless, this study helps us to better understand the complex interactions between surficial deposits and forest mosaics. The combined effects of deposits, climate, and regional fire cycle appear to effectively control the rate of succession as well as forest density. Similarly to Mansuy et al. (2010), we have shown that their joint effects can somehow be synergistic when a high proportion of dry-coarse deposits accentuates the ambient drought within a region characterized by a short fire frequency. In this case, forest recovery is likely to be slow and maintain an open cover over time. Conversely, fast and dense forest recovery is most likely on subhydric deposits within the southern region characterized by a long fire cycle (>500 years). The scope of this study (190 000 km^2) provides substantial knowledge for forecasting future vegetation mosaic on a regional scale in the boreal forest. In addition, because fire-prone regions in which the drying factors are already additive are more susceptible to undergoing higher fire activities in the future (Wotton et al. 2010), policy-makers should anticipate forest recovery in response to fire regime changes. With the expected global changes, new perspectives are needed to explore the interactions between fire-weather patterns, soil moisture regimes, and vegetation recovery dynamics.

Acknowledgements

This research was made possible thanks to the financial and in-kind support provided by the Ministère des Ressources naturelles et de la Faune du Québec (MRNFQ). We acknowledge the important contribution of the MRNFQ, from whom most of the data were obtained; without their contribution, this study would not have been conducted. We thank Julie Fortin (Direction de l'environnement et de la protection des forêts) for providing the provincial fire data and Antoine Leboeuf (Service de l'acquisition de l'information forestière) for providing the surficial deposit data. We also thank Pamela Cheers for editing the manuscript and Alix Rive and François Girard for their useful comments. We are most grateful to the Université du Québec à Montréal and the Canadian Forest Service for their logistical support. We also thank NSERC Strategic Grants, FQRNT Fonds Forestier, and UQAM (Bourse d'excellence) for their financial support.

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Appendix A

Figure A1 and Table A1 appear on the following pages.

Reference

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Fig. A1. Proportion of the four successional stages observed throughout the study area (dashed line) versus the 95% confidence interval of the predicted probability (solid line) computed with the best logistic model (Mod11). The association of predicted probabilities and observed responses table contains four measurements for assessing the predictive ability of our model. With 85.5% concordant and Somers' D = 0.714, our model is highly predictive. Somers' D index is used to determine the strength and direction of relationships between pairs of observed and predicted variables. Its values range from –1.0 (all pairs disagree) to 1.0 (all pairs agree). The Gamma and Tau-a tests are a variant of Somers' D index (Agresti 2002).

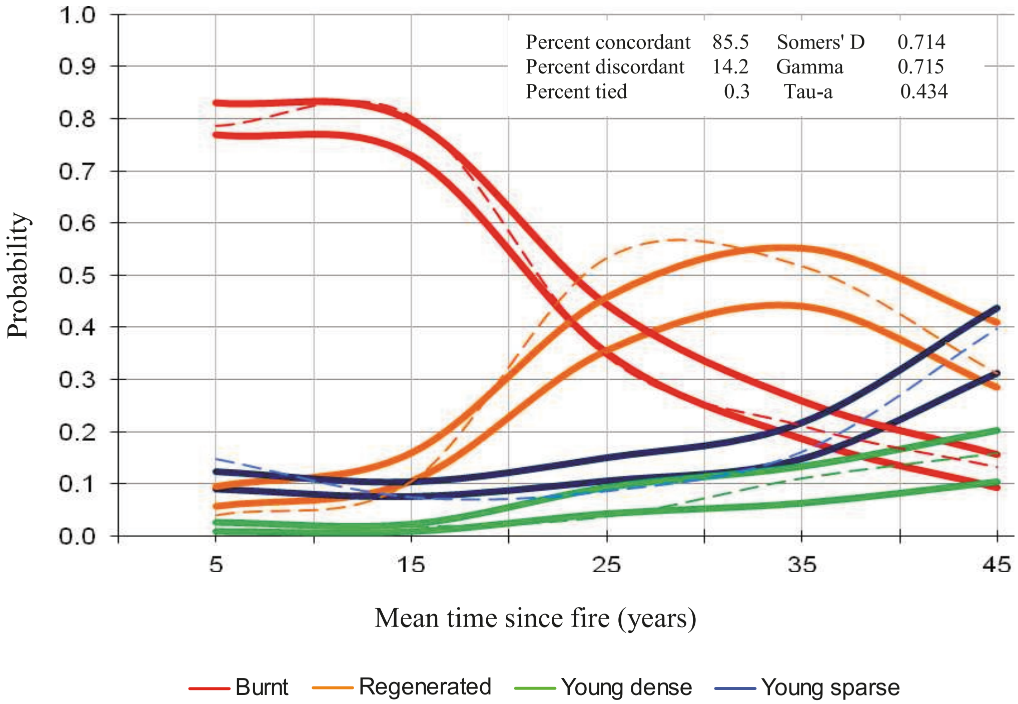

Table A1. Predicted transition probability values for the four successional stages over mean time since fire for each type of deposit (SDD) within the three regions for all years.

		Region A				Region B				Region C			
SDD	Time since fire (years)	BR	RE	YD	YS	BR	RE	YD	YS	BR	RE	YD	YS
DRY	5	0.94[a]	0.04	0.00	0.02	0.85[a]	0.11	0.01	0.04	0.82[a]	0.09	0.03	0.05
	15	0.89[a]	0.07	0.01	0.03	0.78[a]	0.19	0.01	0.02	0.81[a]	0.16	0.02	0.02
	25	0.57[a]	0.32	0.06	0.05	0.40	0.47[b]	0.03	0.10	0.33	0.44[b]	0.09	0.14
	35	0.37	0.48[b]	0.07	0.08	0.12	0.75[b]	0.05	0.08	0.35	0.34[b]	0.12	0.20
	45	0.12	0.28	0.15	0.45[d]	0.18	0.43[b]	0.09	0.30[d]	0.22	0.32[b]	0.17	0.28
ROC	5	0.83[a]	0.11	0.01	0.04	0.88[a]	0.04	0.04	0.04	0.63[a]	0.12	0.07	0.18
	15	0.64[a]	0.19	0.04	0.13	0.64[a]	0.27	0.07	0.02	0.79[a]	0.13	0.04	0.04
	25	0.34	0.43[b]	0.11	0.12	n.d	n.d	n.d	n.d	0.17	0.35[b]	0.20	0.29
	35	0.16	0.56[b]	0.14	0.15	0.09	0.46[b]	0.36	0.09	0.02	0.42[b]	0.21	0.35
	45	0.04	0.25	0.19	0.52[d]	0.10	0.16	0.36	0.38[d]	0.00	0.13	0.41	0.45[d]
MES	5	0.91[a]	0.06	0.01	0.02	0.87[a]	0.09	0.01	0.03	0.83[a]	0.09	0.03	0.06
	15	0.84[a]	0.11	0.02	0.03	0.75[a]	0.22	0.01	0.02	0.80[a]	0.17	0.01	0.02
	25	0.52[a]	0.36	0.07	0.05	0.24	0.60[b]	0.04	0.11	0.26	0.55[b]	0.06	0.13
	35	0.29	0.52[b]	0.11	0.08	0.14	0.72[b]	0.05	0.09	0.31	0.47[b]	0.07	0.15
	45	0.08	0.30	0.18	0.44[d]	0.15	0.43[b]	0.12	0.30	0.19	0.38[b]	0.20	0.23
SUB	5	0.88[a]	0.09	0.01	0.02	0.83[a]	0.08	0.05	0.04	0.78[a]	0.12	0.08	0.02
	15	0.76[a]	0.17	0.02	0.05	0.61[a]	0.30	0.07	0.02	0.69[a]	0.26	0.04	0.01
	25	0.41	0.46[b]	0.07	0.06	0.20	0.54[b]	0.16	0.09	0.23	0.57[b]	0.14	0.05
	35	0.18	0.64[b]	0.11	0.07	0.13	0.59[b]	0.22	0.06	0.16	0.50[b]	0.26	0.08
	45	0.07	0.39[b]	0.16	0.38[d]	0.15	0.23	0.37[c]	0.25	0.04	0.33	0.52[c]	0.11
ORG	5	0.29	0.04	0.01	0.66[d]	0.07	0.01	0.00	0.92[d]	0.16	0.02	0.01	0.81[d]
	15	0.17	0.10	0.02	0.71[d]	0.09	0.02	0.00	0.88[d]	0.20	0.05	0.01	0.74[d]
	25	0.07	0.11	0.03	0.79[d]	0.00	0.01	0.00	0.99[d]	0.02	0.04	0.01	0.93[d]
	35	0.02	0.14	0.05	0.79[d]	0.01	0.02	0.00	0.98[d]	0.05	0.03	0.01	0.91[d]
	45	0.00	0.02	0.03	0.95[d]	0.00	0.00	0.00	0.99[d]	0.00	0.01	0.02	0.96[d]

Note: The driest deposits characterized by a short fire cycle DRY (dry because very sandy and very coarse), ROC (rock), and MES (mesic) have a tendency to slow down the succession (longer time to move from one stage to another) and are more likely to reach the sparse young state. The SUB (subhydric) deposits stand out clearly from the latter, since it is the only deposit to offer young dense forest 45 years after fire but only in regions B and C. As suggested in Fig. 6, the ORG (organic) deposits lead to a sparse forest in all cases.

[a]Likely to be in the burnt (BR) state than all other states for each time step.

[b]Likely to be in the regenerated (RE) state than all other states for each time step.

[c]Likely to be in the young dense (YD) state than all other states for each time step.

[d]Likely to be in the young sparse (YS) state than all other states for each time step.