ÉCOSCIENCE
18 (4): 329-340 (2011)

Forest succession rate and pathways on different surface deposit types in the boreal forest of northwestern Quebec[1]

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Abstract: Forest stands within the Quebec–Ontario paludification-prone Clay Belt are expected to converge to open unproductive black spruce (*Picea mariana*) stands regardless of initial tree composition with the prolonged absence of fire. We hypothesized that different surface deposits would display different stand transition characteristics, as recent research on the deglaciation history of the regions suggests that certain site conditions could exhibit different susceptibility to paludification. We quantified the rate and age of transitions of different succession stages for various surface deposits using a large spatio-temporal forest database. Our results suggest that a complete convergence to open and less productive black spruce stands can occur, but it may take a long time (*i.e.*, more than 500 y), especially on surface deposits less prone to paludification, such as coarse-textured soils. We also observed that if succession pathways start with open and less productive black spruce stands, their capacity to change to more productive stands is conditioned by the surface deposit. Consequently, based on preferential age of transition, transition rates, and succession pathways, we suggest an increased susceptibility to paludification as one goes from coarse-textured deposits to fine-textured deposits and finally to restructured clay deposits, which are regionally designated as Cochrane Till. In terms of forest management, surface deposit susceptibility to paludification should be taken into account in order to minimize soil organic accumulation and the loss of tree productivity.
Keywords: black spruce, boreal forest, Clay Belt, forest succession, paludification, semi-Markov chain.

Résumé : La ceinture d'argile québéco-ontarienne est susceptible à l'entourbement. Dans cette région, on s'attend à ce que les peuplements convergent vers des peuplements d'épinettes noires (*Picea mariana*) ouverts et peu productifs peu importe leur composition initiale. Cependant, des études sur l'Holocène et l'historique de la déglaciation suggèrent que la susceptibilité à l'entourbement pourrait varier en fonction du dépôt de surface et qu'ainsi les peuplements pourraient présenter des caractéristiques de succession différentes selon le dépôt. À l'aide d'une base de données forestières spatio-temporelles, nous avons quantifié le taux et l'âge de transition des peuplements entre différents stades de succession pour différents dépôts de surface de la ceinture d'argile. Nos résultats suggèrent qu'une convergence totale vers des peuplements d'épinettes noires ouverts et moins productifs peut se produire, mais qu'elle peut s'étaler sur une très longue période (plus de 500 ans), surtout dans le cas des dépôts peu susceptibles à l'entourbement comme les dépôts grossiers. De plus, nos résultats suggèrent que dans le cas des successions qui débutent avec des peuplements d'épinettes noires ouverts et moins productifs, leur capacité à atteindre un état plus productif est aussi liée au type de dépôt de surface. Sur la base des âges préférentiels de transition, des taux de transition et des types de peuplements impliqués dans la succession, nous suggérons un gradient croissant de susceptibilité à l'entourbement allant des dépôts grossiers aux dépôts fins argileux, et enfin, aux dépôts fins ayant subi une réavancée des glaces lors de la dernière grande déglaciation. Dans un contexte d'aménagement forestier, une bonne gestion de la couche organique du sol en fonction de la susceptibilité du dépôt à l'entourbement pourrait assurer le retour de peuplements productifs.
Mots-clés : ceinture d'argile, chaînes semi-markoviennes, entourbement, épinette noire, forêt boréale, succession forestière.

Nomenclature: Marie-Victorin, F.É.C., 1995.

[1]Rec. 2010-07-14; acc. 2010-08-01.
Associate Editor: Barry G. Warner.
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DOI 10.2980/18-4-3393

Introduction

Throughout much of the North American boreal forest, crown fires have long been considered to be the primary disturbance type (Heinselman, 1981; Bergeron, 1991; Johnson, 1992; Payette, 1992). Where the fire cycle is short, the high recurrence of fires may preclude succession with species replacement in the canopy (Dix & Swan, 1971; Black & Bliss, 1978; Johnson, 1992). On the other hand, in regions where the fire cycle is longer, there is enough time between successive fires for the establishment of a second cohort of trees, resulting in species replacement into the canopy (Foster & King, 1986; Bergeron & Dubuc, 1989; Gauthier, De Grandpré & Bergeron, 2000). In fact, where crown-fire cycles are long, patch or gap disturbances drive forest dynamics (Kneeshaw & Bergeron, 1998). Under these conditions, succession follows a pattern that begins with even-aged stands composed of intolerant species, initiated by stand-replacing disturbances, to uneven-aged stands mainly composed of shade-tolerant species (Carleton & Maycock, 1978; Cogbill, 1985; Bergeron & Dubuc, 1989; Bergeron, 2000; Gauthier, De Grandpré & Bergeron, 2000; Lecomte & Bergeron, 2005). Adaptations of some species, such as serotinous cones, can allow a shade-tolerant species like black spruce to regenerate after fire and form monospecific, even-aged stands that, while maintaining themselves for long periods of time after fire, undergo structural changes rather than compositional changes (Gauthier, De Grandpré & Bergeron, 2000; Harper *et al.*, 2002; Lecomte & Bergeron, 2005). In addition to time since the last stand-replacing disturbance, species longevity and shade tolerance, as well as site conditions, are the main factors explaining forest succession in the Canadian eastern boreal forest (Robichaud & Methven, 1993; Gauthier, De Grandpré & Bergeron, 2000; Harper *et al.*, 2002; Lecomte & Bergeron, 2005; Taylor & Chen, 2011).

Black spruce stands within the Quebec–Ontario Clay Belt are known to be prone to paludification and hence to develop a thick forest floor organic layer in the absence of fire (Taylor, Carleton & Adams, 1987; Fenton *et al.*, 2005). Paludification is caused by several factors and over time can lead to a decrease in stand productivity. One mechanism for this decrease is a rise in the water table that makes soils become colder and more anaerobic, and consequently decreases microorganism activity and nutrient availability (Van Cleve & Viereck, 1981; Taylor, Carleton & Adams, 1987). Time since fire and fire severity (amount of the organic layer left unburned after fire) have been found to be the major factors determining the thickness of the organic layer in black spruce stands of the Clay Belt area (Fenton *et al.*, 2005; 2006). Chronosequence studies have shown that as stands become paludified, forest stand composition converges to black spruce and to a very open, irregular, and unproductive stand structure (Harper *et al.*, 2002; 2005; Lecomte & Bergeron, 2005; Lecomte *et al.*, 2005; Fenton & Bergeron, 2006; Lecomte, Simard & Bergeron, 2006; St-Denis, Kneeshaw & Bergeron, 2010). Based on these observations, Lecomte, Simard, and Bergeron (2006) and Simard *et al.* (2008) have proposed a succession model for the northern Clay Belt, with stands being dominated after fire by jack pine (*Pinus banksiana*), trembling aspen (*Populus tremuloides*), or black spruce (Figure 1). This model is a function of 2 variables: fire severity (thickness of the organic layer left unburned after fire) and time since fire. As fire severity increases, regenerated stands are less dominated by black spruce and are more productive, while the opposite trends are observed with time since fire. In the southern Clay Belt, where broadleaf trees are more abundant, stand convergence to fir and white cedar is commonly observed (Cogbill, 1985; Bergeron & Dubuc, 1989; Gauthier, De Grandpré & Bergeron, 2000). However, Gauthier, De Grandpré, and Bergeron (2000) suggest that large wildfires in the boreal forest will limit these succession pathways, as well as the accumulation of a thick layer of organic matter, because paludification favours black spruce layering instead of fir regeneration. Girardin, Tardif, and Bergeron (2001) also point out the low capacity of white birch to establish itself when the forest floor organic layer is thick.

The succession model developed by Simard *et al.* (2008) was based primarily on succession in lowland sites. However, we know that succession trajectories and paludification may vary according to different surface deposits (Gauthier, De Grandpré & Bergeron, 2000; Lecomte & Bergeron, 2005). Moreover, field studies of Holocene ice-flow chronologies and their impact on surface deposits suggest that the northern part of the surface glaciolacustrine fine clay deposits in the study region were largely restructured by a southern late glacial surge and by iceberg furrows during the last deglaciation (Boissonneau, 1966; Veillette & Paradis, 1996; Veillette, 2007; Veillette & Thibaudeau, 2007). The restructured surface deposit area is characterized by an immature drainage network, which has contributed to the development of large peatlands (Veillette & Paradis, 1996; Veillette, 2007), suggesting that it is highly susceptible to paludification.

Considering a potential paludification susceptibility gradient for the different surface deposits in our study area, we expect succession dynamics to be influenced by site conditions, requiring a modification of the succession model proposed by Lecomte, Simard, and Bergeron (2006) and Simard *et al.* (2008). We used SIFORT (Système d'information forestière par tesselle), a large spatio-temporal forest database, to validate the results of the abovementioned chronosequence studies and investigate how stand composition and structure changed over a 23-y period for a large number of stands (Pelletier *et al.*, 1996). Using semi-Markov chains and transition matrices, we quantified transition rates between the different successional stages proposed by Lecomte, Simard, and Bergeron (2006) and Simard *et al.* (2008). Based on transition parameters and the rapidity at which forest stands converged to black spruce open stands, we also estimated the paludification susceptibility of different surface deposits, as in the study area paludification is the most important process driving structural changes in black spruce stands (Lecomte, Simard & Bergeron, 2006). Based on the observations of Harper *et al.* (2002), Lecomte and Bergeron (2005), and Lecomte, Simard, and Bergeron (2006), we hypothesized that regardless of initial stand composition and surface deposit type,

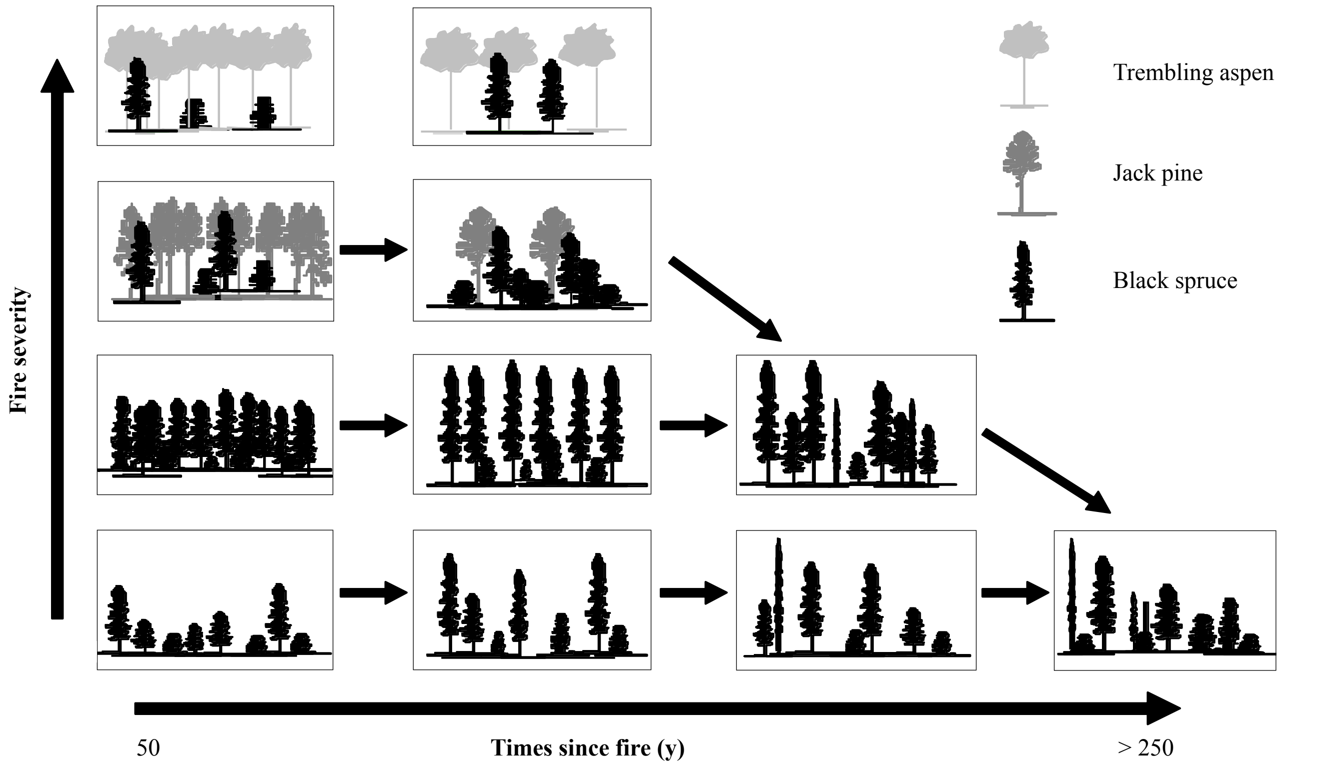

FIGURE 1. Succession model proposed by Lecomte, Simard, and Bergeron (2006) and by Simard *et al.* (2008).

all succession pathways (in the absence of fire) converge to black spruce–dominated stands. Considering mineral soil texture and deglaciation history of the surface deposits (restructuring and compaction of certain deposits), we also hypothesized, as suggested by Lecomte & Bergeron 2005 as well as Taylor & Chen 2011, that convergence rates to open black spruce stands would be higher on the restructured glaciolacustrine fine clay deposits than the other surface deposit types.

Methods

STUDY AREA

The study area is located in the Clay Belt physiographical unit of northwestern Quebec and of northeastern Ontario. The region is mainly covered by fine-textured clay deposits left by proglacial lake Ojibway (Vincent & Hardy, 1977). The area is over 10 000 km^2 and is located between 49° 00' and 51° 30' N and 78° 30' and 79° 31' W. The northern part of the study area was affected during the last glaciation by late southern glacial surges that restructured the glaciolacustrine fine clay deposits known as the Cochrane Till (Boissonneau, 1966). The topography is flat with a mean elevation of 250 m. The region has a mean annual temperature of –0.7 °C and a mean annual precipitation of 905.5 mm as recorded at the nearest weather station (Matagami, 49° 43' N, 77° 37' W) (Environment Canada, 2004). The forest stands are typical of the black spruce–feather moss ecological region and are dominated by monospecific black spruce stands. The black spruce stands display a diversity of stand structures (Harper *et al.*, 2002). Scattered hardwood and pine stands are also present. Apart from logging, the study area is mainly disturbed by fires. The fire cycle is estimated to have been 101 y before 1850, 135 y between 1850 and 1920, and around 398 y since the 1920s. The current mean stand age is estimated to be 148 y (Bergeron *et al.*, 2004). Industrial forest activities started in the area between 1940 and 1960.

DATABASE AND STAND SELECTION

The SIFORT database is a grid composed of rectangular cells measuring an average of 14 ha each (0.15" of latitude and 0.15" of longitude). Forest information is associated with each cell by overlaying the grid onto eco-forestry maps. The stand information for the stand located at the centre of the cell is then associated with the entire cell. The eco-forestry maps are a result of 3 aerial photographic campaigns and field surveys (1965–1974, 1983–1990, and 1992–1996). As the third survey was far more detailed than the first (the first, second, and third surveys used 12, 57, and 45 composition types, respectively), we regrouped the stand types and species' composition of the third survey so that it could be compared to the first survey. Similarly, we used the second and third surveys to deduce the presence of mixed black spruce and jack pine stands that were not identified in the first survey. Finally, to follow the structural changes that occur during black spruce stand development, black spruce stands were classified into 3 structural types based on cover density/stand height associations (Table I).

The different surface deposits in the database were grouped into similar deposit types based on texture and on deglaciation history. Three surface deposit types were determined: 1) Cochrane Till, which is made up of restructured

TABLE I. Forest cover and structural types retained[1] using the SIFORT database.

Forest cover type	Structural stage or species composition[1]	Abbreviation	Description	n	Relative abundance by surface deposit type (%) Cochrane Till	Clay	Coarse	Mean stand age in 1965 (y)[2]	Age interval used
Hardwoods	Trembling aspen	TA	> 75% of the forest cover is composed of aspen	260	0.2	2.6	2.7	68	72–169
Mixed stands	Aspen/ conifer	TAC	25% of the forest cover is composed of aspen and 50–75% of a mix of conifers or by black spruce	560	1.5	3.4	8.2	92	72–286
	Hardwood/ jack pine	HJP	25–50% of the forest cover is composed of a mix of hardwoods and 50–75% of jack pine	690	0.5	6.2	10.0	68	72–168
	Pine/conifer	JPC	25% of the forest cover is composed of jack pine and 50–75% of a mix of conifers or black spruce	939	1.3	7.9	12.1	79	74–218
Conifers	Jack pine	JP	> 75% of the forest cover is composed of jack pine	1935	1.6	13.1	41.1	65	72–168
	Balsam fir	BF	> 75% of the forest cover is composed of balsam fir	263	1.3	1.4	1.4	168	92–268
	Black spruce	BS	> 75% of the forest cover is composed of black spruce						
	Close and productive	CP	The dominant trees create a cover density greater than 60%	2056	8.3	15.8	4.4	103	75–168
	Partially open	PO	The dominant trees are ≥ 12 m and create a cover density between 25 and 60%	8033	54.1	30.8	10.8	159	72–283
	Open and unproductive	OUP	The dominant trees are < 12 m and create a cover density less than 60% (forested bogs are included here)	4752	31.1	18.8	9.2	138	72–267
Total				19 488	54.0	35.3	10.7	129	

[1] Larch, white birch, or mixed white birch and conifer forest cover types were not retained as they were present on less than 5% of the landscape.

[2] Mean stand ages have been calculated using the time since fire date, which was estimated by subtracting the date of the aerial photograph from the fire date recorded on the fire history maps (Bergeron *et al.*, 2004).

fine-textured glaciolacustrine clay deposits that contain a small proportion of coarse grains; this surface deposit covers the northern part of the study area; 2) fine-textured glaciolacustrine clay deposits that primarily cover the southern part of the study area; and finally 3) coarse-textured deposits composed of sand, coarse till, rock, and thin deposits. The coarse deposits are dispersed over the entire study area (Saucier *et al.*, 1994). Deposits that were classified as organic in the third survey were assigned to the clay or Cochrane Till deposit types depending on their geographical location (south or north), as forest stands observed on organic soils result in paludification and hence are not a permanent geomorphological feature. In this case, and at the scale of the photo interpretation of the stands, organic soils are less likely to develop on coarse-textured deposits considering their very weak susceptibility to paludification, except in particular topographic features. Finally, to determine the time since fire (stand age) for each cell, the SIFORT database was overlaid onto the fire history map of the study area (Bergeron *et al.*, 2004). Fires that occurred prior to 1880 were dated using the age of the trees established after the last fire or by dating fire scars on surviving trees. Historical records and aerial photographs were used for fires that occurred after 1880.

The cells that were non-forested (*i.e.*, lake, flooded area, sand pit, urban or agricultural area, transmission lines), had been disturbed by human activity (clear or partial cut, plantation, old fields), or had been severely disturbed by fires, insect outbreaks, or windthrow since 1965 according to disturbance indications in the SIFORT database were removed. Furthermore, cells classified as peatland in the 3 surveys were considered to be permanent peatlands related to the topography of the site and were likewise removed. Overall, it was possible to determine a time-since-fire age, an initial forest type (type at the first survey), and a succession type (type at the third survey) for 31 103 cells. To ensure that the initial forest types retained were representative of forest stand succession at the landscape scale, we analyzed only the forest types that occupied more than 5% of the landscape. Similarly, we retained by initial forest types only the succession types that represented more than 10% of the transitions observed. Finally, to satisfy statistical requirements of a goodness-of-fit test (Hosmer & Lemeshow, 2000), we truncated and log transformed the chronosequence. Retained stand age intervals by initial forest cover type are presented in Table I. In the end, 19 488 cells were used to establish the succession models and to estimate transition rates.

STATISTICAL ANALYSES, SEMI-MARKOV CHAINS, AND STAND PERSISTENCE

Taking into account the uncertainty associated with the aerial photo interpretation of forest cover types, the changes in classification attributes between the 2 surveys, and the uncertainty associated with historical fire maps, we limited our study to semi-Markov chains built around a model proposed in the literature and the moment of observed maximum change. Markov chains are stochastic processes through which a future state is predicted from the current state while ignoring previous states (Karlin, 1968; Kemeny & Snell, 1976). They are commonly used to model forest succession (Yemshanov & Perera, 2002; Taylor, Chen & Vandamme, 2009) as they accommodate most modelling requirements and may be built from low acquisition cost data, including forest aerial surveys. Simple Markov chains may not reflect the reality of forest succession, because tree longevity and growth favours the maintenance of forest stands in the same state for a certain amount of time. A more realistic approach is to use latent phases in succession and to consider semi-Markov chains that are in part related to the time elapsed in a state (Howard, 1971; Acevedo, Urban & Alban, 1995; Acevedo, Urban & Shugart, 1996). We tested model selection using Likelihood Ratio and change in Akaike's Information Criterion (AIC) in order to ensure that stand age and surface deposits were considered as critical variables for the establishment of the transition phase and the rate of transition (Hobbs & Hilborn, 2006). The AIC approach provides information regarding the effect of adding or using certain independent variables or effects (simple *versus* interaction or cumulative effects) in the model *versus* increasing capacity to approximate the dependant variable. This is done by calculating Akaike weights (w_r) amongst several models evaluated independently of their statistical level of significance. The Akaike weights take values from 0 to 1 and order the models from the poorest to the best on their ability to approximate the dependant variable. Models with a w_r higher than 0.9 were considered to be the best. We compared models that included the individual main effects of surface deposits and stand age, as well as their interaction, for each initial forest cover type. The Likelihood Ratio and AIC were calculated by performing logistic regressions using the LOGISTIC procedure in the SAS statistical package (software 9.1.3, SAS Institute Inc. 2002–2003, Cary, North Carolina, USA).

Based on the variables included in the best model selected, we determined the moment of maximum transition and the age at which the latent phase ended for each initial forest cover type that possessed a noticeable age effect using a simplification of Pearson's Chi square approach (Legendre & Legendre, 1998). We calculated a deviance between the age distribution of the overall stands observed during the first survey for each forest type and surface deposit combination (if the surface deposits noticeably influenced the transition events) and the age distribution of the stands that experienced state changes between the first and the third surveys. For each forest type–surface deposit combination, we searched for the age or age interval that showed a significantly higher proportion of stands in transition. These age intervals were considered to be indicative of the break age window. The onset of the break age window was considered to be the end of the latent phase. Note that the breaking age was set as the third survey stand age because we could not determine exactly when a change had occurred between the surveys but we did know that the third survey age was the maximum age at which this transition could have occurred. Similarly, the transition rate during the transition phase was calculated as the ratio of the number of stands that changed state between the first and third surveys and the total number of stands. The probability of transiting to different states when a transition did occur was established based on the proportion of all the succession types that could be reached in the third survey. Finally, to predict how quickly certain forest types will disappear on the landscape or reach a quasi steady state in the absence of fire, we examined the transition characteristics of each forest type over time by using matrix calculations for each surface deposit type with a time interval of 23 y. We considered the quasi steady state as being the state that will remain on the landscape for a very long time (> 500 y) in the absence of stand-replacing disturbance.

Results

Age and influence of surface deposits

Runs for each initial forest type (Table I), the model selection analyses presented in Table II, indicate that the model including the interaction between surface deposits and stand age was the best model for almost all of the 9 initial types. The interaction model possessed an Akaike weight (w_r) higher than 0.9 for 6 of the 9 initial forest cover types. The trembling aspen stands (TA) also seem to be largely influenced by surface deposit and stand age, with an interaction model scoring the transition event at 0.89. In contrast, the mixed conifer/jack pine and conifer/trembling aspen types showed the highest score for the surface deposit main effect model. However, the w_r for these last 3 initial forest cover types was still less than 0.9, indicating that a clear model selection was not achieved. Thus, the possibility that other models might better approximate these transition events should not be ignored.

Succession pathways

Our analysis of the 19 488 SIFORT cells found that, in the absence of fire, shade-intolerant pioneer species (jack pine or trembling aspen) succeeded in a unidirectional fashion into a mixed state composed of more-shade-tolerant species (mixed conifer/jack pine or conifer/trembling aspen), with these mixed stands then succeeding into diverse (closed or partially open) black spruce stand structures. The partially open black spruce stand structure was a key transition state that was part of most mixed stand pathways. The mixed stands either succeeded directly into partially open black spruce stands or succeeded first into closed black spruce stands and eventually into partially open black spruce stands. Pathways starting with black spruce displayed 2 different trajectories: a productive one, beginning with young productive closed stands that changed to open and less productive stands, and a second, less productive trajectory that started with young open stands that in general remained structurally unchanged, or exceptionally changed to a more productive state before ultimately breaking down and returning to an open stand structure (Figure 2).

There was a higher abundance of pioneer species such as jack pine and trembling aspen, and conversely a decreasing abundance of open unproductive black spruce stands,

TABLE II. AIC model selection parameters. See Table I for definition of the initial forest cover type abbreviation

Initial forest cover type	Models compared	Log likelihood	Degrees of freedom (DF)	AIC	W_r
TA	Surface deposit (SurfDep)	–160.8573	3	327.7146	0.11
	Log (Stand age)	–169.0658	2	342.1316	0.00
	SurfDep·Log (Stand age)	–155.7194	6	323.4388	0.89
TAC	Surface deposit (SurfDep)	–371.2189	3	748.4378	0.88
	Log (Stand age)	–375.6050	2	755.2100	0.03
	SurfDep·Log (Stand age)	–370.4898	6	752.9796	0.09
HJP	Surface deposit (SurfDep)	–452.9134	3	911.8268	0.00
	Log (Stand age)	–459.2255	2	922.4510	0.00
	SurfDep·Log (Stand age)	–435.3076	6	882.6152	1.00
JPC	Surface deposit (SurfDep)	–647.8922	3	1301.7844	0.74
	Log (Stand age)	–649.5900	3	1305.1800	0.14
	SurfDep·Log (Stand age)	–643.6803	9	1305.3606	0.12
JP	Surface deposit (SurfDep)	–1203.4981	3	2412.9962	0.00
	Log (Stand age)	–1304.8977	2	2613.7954	0.00
	SurfDep·Log (Stand age)	–1176.9629	6	2365.9258	1.00
BF	Surface deposit (SurfDep)	–107.396	3	220.7920	0.04
	Log (Stand age)	–112.6626	2	229.3252	0.00
	SurfDep·Log (Stand age)	–101.2278	6	214.4556	0.96
BS_CP	Surface deposit (SurfDep)	–1199.7748	3	2405.5496	0.00
	Log (Stand age)	–1083.0197	3	2172.0394	0.03
	SurfDep·Log (Stand age)	–1073.4783	9	2164.9566	0.97
BS_PO	Surface deposit (SurfDep)	–5390.2399	3	10786.4798	0.00
	Log (Stand age)	–5461.6214	3	10929.2428	0.00
	SurfDep·Log (Stand age)	–5378.4286	9	10774.8572	1.00
BS_OUP	Surface deposit (SurfDep)	–2807.9060	3	5621.8120	0.00
	Log (Stand age)	–2859.6796	3	5725.3592	0.00
	SurfDep·Log (Stand age)	–2785.0838	9	5588.1676	1.00

along a gradient from Cochrane Till to coarse deposits (Figure 2). Along the same gradient, we also observed a simplification of the main successional pathways, as illustrated by the fewer transitions (arrows) that occurred at higher rates (*i.e.*, > 0.2). However, on clay there were many secondary succession paths characterized by a transition rate between 0.2 and 0.1. Finally, we also observed a transfer of the steady state from the very open, unproductive black spruce stands to the partially open, more productive black spruce stands until equilibrium between these 2 states occurred on the coarse deposits. Overall, succession pathways occur on all surface deposits, but with different frequencies. In general, the rate of convergence to open black spruce states was fastest on the Cochrane Till, slowest on the coarse deposits, and of intermediate speed on the fine-textured deposits.

TRANSITION PARAMETERS

Stand age at the beginning of the transition phase was highly variable (Table III). The stands composed of pioneer species such as jack pine and trembling aspen and their associated mixed stands (*e.g.*, black spruce and pioneer species) generally started to change before they were 100 y old. However, mixed stands tended to change at a slightly older age than pure pioneer species stands. The closed and partially open black spruce stands that currently dominate the landscape generally changed at an age older than 100 y. Occasionally, young open unproductive black spruce stands succeeded into closed stands at ages between 60 and 200 y old. The length of this phase is strongly dependant on the type of surface deposit and on the initial openness of the stand. In the case of the clay and coarse deposits, equilibrium between the partially open and the very open black spruce stands occurred at an age of 120 y (Figure 3). Our chronosequence for this analysis did not allow us to determine if this equilibrium would be maintained if stands reached an age older than 290 y.

The transition rates were generally higher than 0.4, except for the unproductive black spruce convergent states, which displayed rates as low as 0.264 and 0. More specifically, the majority of the stands developing on the Cochrane Till showed higher transition rates than the ones on the other surface deposit types. One exception to this was the open unproductive black spruce state, which showed a higher rate of transition to a denser state on clay sites than on the Cochrane Till.

The persistence of stand states for each succession pathway and each surface deposit type are illustrated in Figure 3. In general, we observed that the convergence of the stands to a partially open or to an open state took less than 300 y. The rapidity with which the convergent open state was reached appeared to be related to the surface deposits, with the fastest rates on the Cochrane Till and the slowest on the coarse deposits. On coarse deposits, open

TABLE III. Transition parameters estimated from the first and third forest surveys for each forest cover and surface deposit type (n = 19488; base time interval = 23 y). Forest cover types as in Table II.

Forest cover type	Surface deposit type	Transition age (y)	Transition rate	Probability of a different forest cover type when transition occurs				
				JPC	TAC	BS		
						CP	PO	OUP
TA	Cochrane Till	72	0.712	0	1	0	0	0
	Clay	74	0.371	0	1	0	0	0
	Coarse	72	0.569	0	1	0	0	0
TAC	Cochrane Till	74	0.597	0	0	0.365	0.378	0.257
	Clay	76	0.592	0	0	0.444	0.223	0.333
	Coarse	81	0.442	0	0	0.261	0.739	0
HJP	Cochrane Till	72	0.417	1	0	0	0	0
	Clay	77	0.382	1	0	0	0	0
	Coarse	72	0.676	0.812	0	0	0.188	0
JPC	Cochrane Till	122	0.529	0	0	0	0.696	0.304
	Clay	87	0.586	0	0	0.354	0.477	0.169
	Coarse	90	0.514	0	0	0	0.750	0.250
JP	Cochrane Till	90	0.606	1	0	0	0	0
	Clay	78	0.577	1	0	0	0	0
	Coarse	90	0.497	1	0	0	0	0
BF	Cochrane Till	92	1	0	0	0.144	0.698	0.158
	Clay	92	1	0	0	0.138	0.632	0.230
BS_CP	Cochrane Till	146	0.863	0	0	0	0.620	0.380
	Clay	117	0.852	0	0	0	0.870	0.130
	Coarse	92	0.791	0	0	0	1	0
BS_PO	Cochrane Till	196	0.629	0	0	0	0	1
	Clay	167	0.508	0	0	0	0	1
	Coarse	196	0.422	0	0	0	0	1
Young	Cochrane Till	92	0.264	0	0	0	1	0
BS_OUP[1]	Clay	62	0.486	0	0	0.438	0.564	0
	Coarse	78	0.750	0	0	0.619	0.381	0
Old	Cochrane Till	283	0	0	0	0	0	1
BS_OUP	Clay	118	0.352	0	0	0	1	0
	Coarse	122	0.581	0	0	0	1	0

[1] These stands may have established after low-severity fires; they follow succession paths similar to pioneer species and may experience canopy closure in young stages before becoming taller and open again.

unproductive stands never occupied more than 50% of the landscape. In particular, Figure 3 illustrates that residence times of jack pine stands were longest on coarse deposits, intermediary on Cochrane tills, and shortest on clays. The time of residence for the trembling aspen stands was more variable between the different surface deposit types. Specifically, the trembling aspen stands and the mixed aspen stands showed longer residence times on the clay deposits than on the coarse deposits. Finally, considering that black spruce stands show 2 significantly different initial states in terms of canopy openness of the young stands, we estimated 2 possibilities of persistence. In the case of the trajectory starting with closed young black spruce stands, we observed an increasing time of residence from coarse deposits to Cochrane tills, while the opposite trend was observed for the trajectory starting with open young black spruce stands. In this last case, we observed an increasing canopy closing gradient with the possibility for complete stand closure on clay and coarse deposit sites but not on Cochrane Till.

Discussion

COMPOSITION AND STRUCTURAL CHANGES

Similar to previous chronosequence studies (Gauthier, De Grandpré & Bergeron, 2000; Harper *et al.*, 2002; 2003; 2005; Lecomte & Bergeron, 2005; Lecomte, Simard & Bergeron, 2006; Simard *et al.*, 2008), our succession models are in accordance with a convergence of species composition to black spruce–dominated stands regardless of the initial species composition (Figure 2). Since the rate of convergence decreased along a gradient of surface deposits that goes from the Cochrane Till to coarse deposit types, and because stands on the different surface deposit types showed a preference to either converge to open or closed black spruce stands, our results support the idea that paludification is the process that drives the succession pathways (Harper *et al.*, 2002; Fenton *et al.*, 2005; Lecomte & Bergeron, 2005; Fenton *et al.*, 2006), but that it may act differently according to different surface deposit types. For jack pine stands, as suggested by Donnegan and Rebertus (1999), the xeric nature of the deposit can explain in part the lower rate of convergence. Individual growth rates are slower on xeric surface deposits than on richer, mesic deposits, such as clays. This slower growth rate results in longer life spans for individuals on xeric than on mesic surface deposits. The difference in life spans for the different types of deposits explains both our findings and those of Cogbill (1985) and Harper *et al.* (2002), who also found a faster convergence of jack pine to black spruce on clay than on coarse deposits. In contrast to jack pine, the succession pathways for trembling aspen indicate that some of these stands will succeed to closed black spruce stands on the Cochrane Till (Figure 3). This suggests, as observed by Légaré, Paré & Bergeron (2005), that the presence of aspen can counteract the process of paludification, enabling aspen stands to change into productive closed black spruce stands before ultimately changing into open or partially open black spruce stands regardless of the surface deposit's susceptibility to paludification.

Depending on the stand composition type and surface deposit, our results concerning the onset of the transition phase (Table III) are similar to the ones proposed for the northern boreal mixedwood forest by Yemshanov and Perera (2002). Excluding fir and black spruce stands that are considered in the literature to be climax species, it appears that cover change will begin early in stand development. We note in the literature that cover changes usually begin between 50 and 150 y after the last stand-replacing disturbance, and that the persistence time period of the species on the landscape is highly variable, between 100 and 200 y depending on the succession stage studied (Carleton & Maycock, 1978; Cogbill, 1985; Gauthier, De Grandpré & Bergeron, 2000; Harper *et al.*, 2002; Yemshanov & Perera, 2002; Harper *et al.*, 2003; Pothier, Raulier & Riopel, 2004; Lecomte & Bergeron, 2005). Harper *et al.* (2002) found that trembling aspen could persist more than 200 y on coarse, thin deposits. Our results show that stands composed of pioneer species such as jack pine and trembling aspen start to change at around 70 to 120 y old. However, the time of residence we evaluated was consistently longer than the ones in the scientific literature, which are between 145 and 352 y. We recognize that the use of a constant transition rate for a given age may favour an over-evaluation of the time of residence in the landscape. Our method appears to be more applicable to short-lived species with fast transition rates (higher than 0.5). These species usually rapidly disappear to the benefit of more shade-tolerant species. The narrow analysis window (23 y) provided by the SIFORT database may also have limited our capacity to detect high transition rates occurring in a narrow break age window. The majority of the stands of certain cover types, such as trembling aspen, in our study area established themselves after fires during the 1910s and 1920s and were consequently younger (less than 75 y old) than the active transition phase during the 23 y of our database (approximately 1970–1993). Furthermore, in regard to the trembling aspen stands, Bergeron (2000) and a study currently in progress (S. Gautier-Éthier, pers. comm.) suggest a high recurrence of self-replacing forest dynamics in the Quebec boreal mixedwood forest. This could also partly explain the very long persistence observed for this type of stand (more than 200 y). Finally, considering that the mean stand age is lower on clay and coarse deposits compared to the Cochrane Till, the absence of complete landscape convergence to open black spruce stands on these surface deposit types could be attributed to a potentially shorter fire cycle (Bergeron *et al.*, 2004). As the organic layer growth rate is low on coarse deposits, the majority of stands on this surface deposit type never reached the unproductive open stand state in the period analyzed. On coarse deposits, stands mostly converged to partially open black spruce stands that could be attributed to the dryness of the site rather than to the process of paludification. In the study area, paludification on coarse deposits is rare and tends to be locally limited to particular topographic features such as rock crevices or depressions on hilltops.

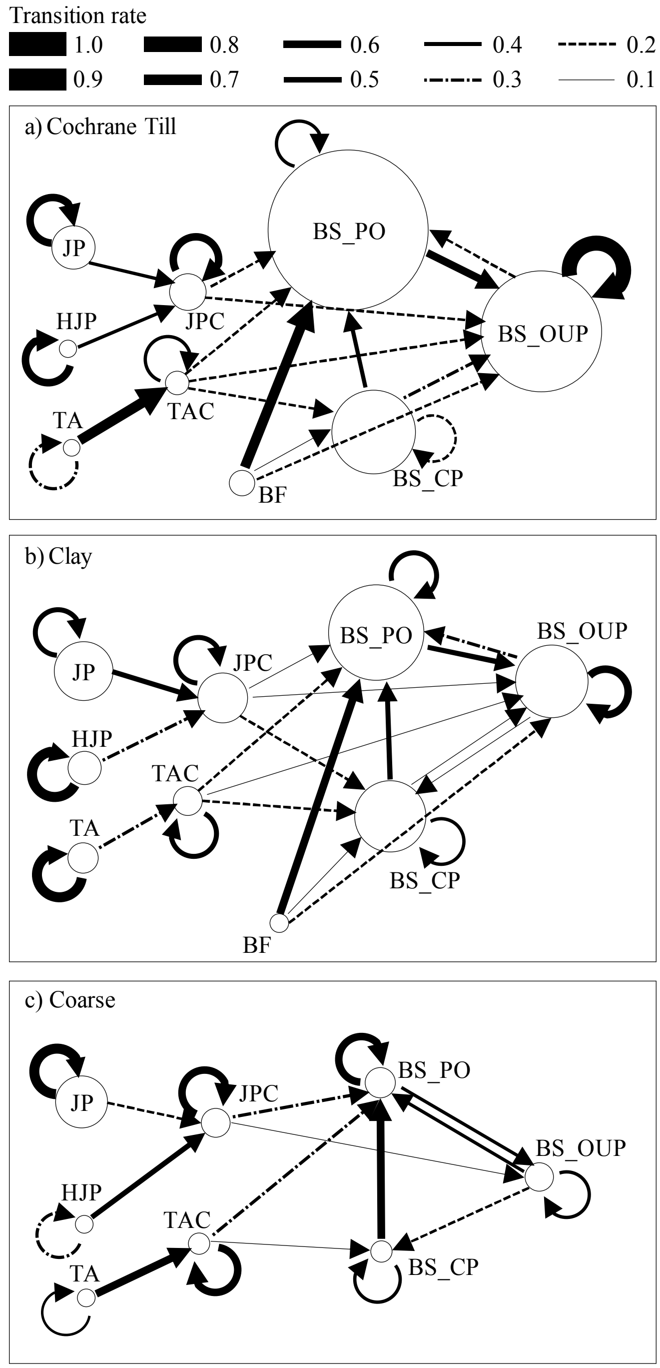

FIGURE 2. General transition pathways considering surface deposit type: a Lecomte and Bergeron (2005) and Simard *et al.* (2008) succession model validation. Arrow thickness is proportional to the transition rate between forest cover types. Circle size is proportional to the abundance of the forest cover type in 1965. Stand cover type abbreviations are balsam fir (BF), close productive black spruce (BS_CP), partially open black spruce (BS_PO), open unproductive black spruce (BS_OUP), jack pine (JP), mixed jack pine and conifer (JPC), mixed hardwood and jack pine (HJP), trembling aspen (TA), and mixed aspen and conifer (TAC).

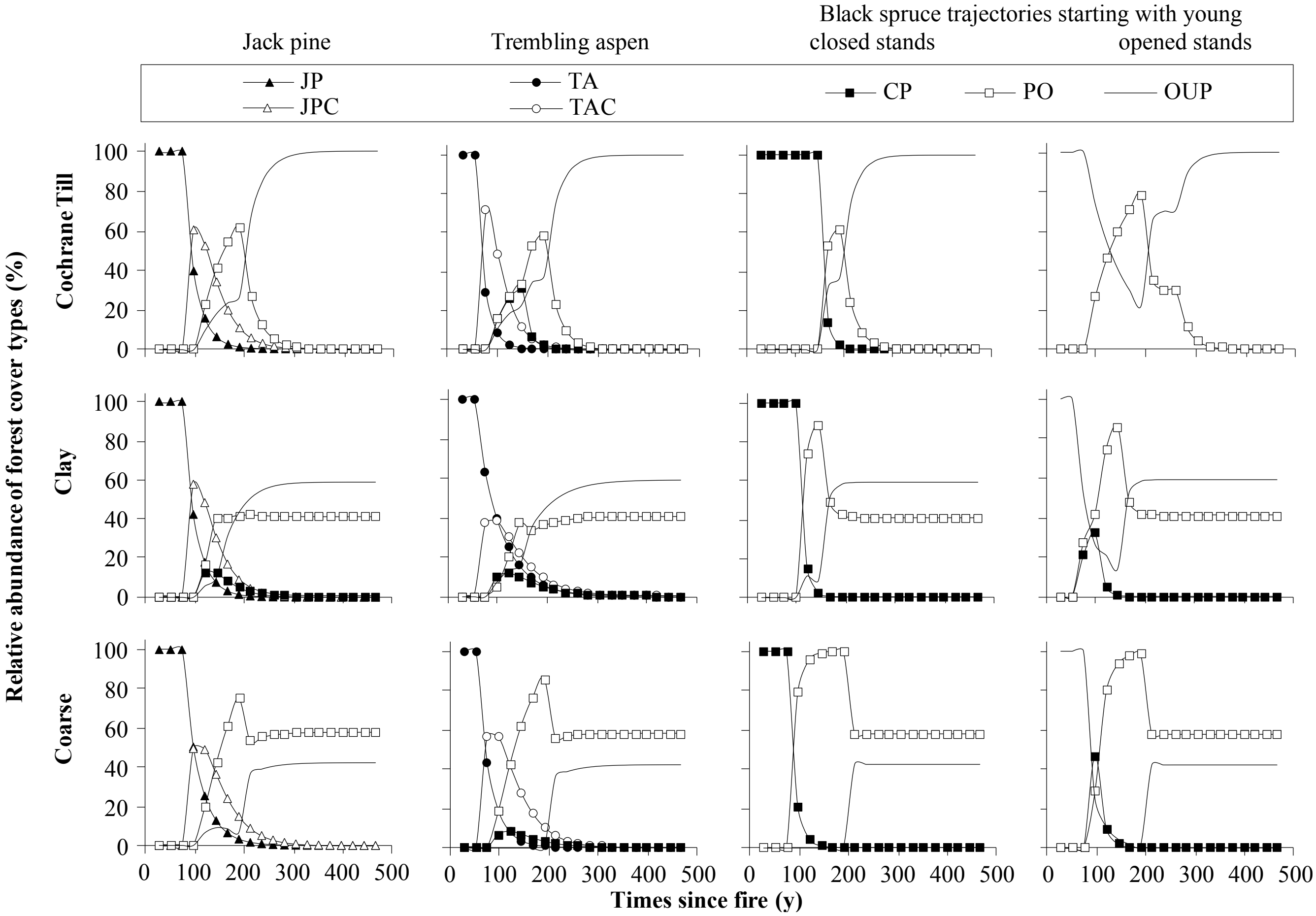

FIGURE 3. Landscape scale persistence (y) of the major forest cover types by surface deposit. For each surface deposit, graphs show complete succession paths from the pioneer species to the expected climax composition. Jack pine–dominated stands are indicated by black triangles and jack pine/conifer mixed stands by white triangles; trembling aspen–dominated stands are indicated by black circles and aspen/conifer mixed stands white circles; closed productive black spruce stands are indicated by black squares and partially open stands by white squares. Finally, the open and unproductive stands are illustrated by a continuous line without symbols.

The succession pathways established by our study also enabled us to investigate the major structural changes that happen in black spruce stands during their development. In our study area, these changes have mainly been studied by Harper *et al.* (2002; 2003; 2005), Lecomte and Bergeron (2005), Simard *et al.* (2008), and by St-Denis, Kneeshaw, and Bergeron (2010). These studies have shown that, in the absence of fire, changes in stand height and total basal area of dead and live trees are more important than changes in composition. These studies proposed a first opening phase between 75 to 175 y old followed by a second opening phase at 200 y old; these phases caused a decrease in tree height. There is no consensus on the different phases for stands established after low-severity fires, where the organic layer is thick from the onset of succession. It appears that a certain proportion of stands may be able, when they are relatively young (*i.e.*, less than 100 y old), to succeed to closed stands before eventually developing into open black spruce stands. The manner in which we have grouped the different black spruce into stand structural types appears to accurately reflect these structural changes through time. We observed, as did Lecomte, Simard, and Bergeron (2006) and Simard *et al.* (2008), 2 succession pathways, with one being closed in structure and the other open. We suspect, in light of Lecomte, Simard, and Bergeron (2006), that the closed pathway is initiated by severe fire, following which stands go from a closed stage to a partially open one before they eventually succeed to a very open and short canopy stage. The second open pathway is likely the result of low-severity fires where a certain amount of the forest floor organic layer is left unburnt. Stands in the open pathway start with an open canopy stage that is maintained through time, although some of these stands may succeed briefly to a partially open stand. For this last succession pathway, our evaluation suggests that the closing phase starts between 60 and 120 y and ends between 150 and 250 y after the last fire (Table III). However, since aerial photograph interpretation of the stand structure (tree density and height) is less accurate than direct field basal area measurements, it is hard to compare our results to those obtained by Harper *et al.* (2005) and Lecomte and Bergeron (2005). Another limitation is the use of fire history maps to evaluate the real age of black spruce stands that have escaped fire for a long time, as this approach may underestimate the age at which stands start to change and their persistence time on the landscape. Cyr *et al.* (2005) used ^{14}C dates to demonstrate that some forest stands assigned to a relatively recent fire episode (between 200 and 300 y ago) had in reality not burned for as long as 1000 y. Nevertheless, the 2 succession pathways of the black spruce stands appear to be dependent on the surface deposit type, the stand age (Fenton *et al.*, 2005; 2006), and the residual thickness of the organic layer left after the passage of a fire (Lecomte, Simard & Bergeron, 2006; Simard *et al.*, 2008).

PALUDIFICATION SUSCEPTIBILITY

In regard to the succession patterns and paludification mechanisms proposed by chronosequence studies undertaken in our study area (Gauthier, De Grandpré & Bergeron, 2000; Harper *et al.*, 2002; 2003; 2005; Fenton *et al.* 2005; 2006; Lecomte & Bergeron, 2005; Lecomte, Simard & Bergeron, 2006; Simard *et al.*, 2008), the rapidity of convergence to black spruce stands and the breaking age at which the active transition phase starts in our results suggest that different surface deposits show different susceptibilities to paludification. This susceptibility gradient is also suggested by the total convergence of the stands to an open unproductive black spruce stage, with time, on the Cochrane Till, as opposed to the equilibrium between open and partially open black spruce stands that was observed on non-reworked clays of the south and coarse textured deposits (Figure 3). The abundance of the black spruce stands on the Cochrane Till and the total absence of complete closure of the young open stands also suggest that the Cochrane Till sites are more sensitive to paludification than the other surface deposits. Several factors may explain the paludification of sites on the Clay Belt. The high paludification susceptibility observed on the Cochrane Till may be related to the region's deglaciation history, which created a poor drainage network and a high occurrence of iceberg furrows that already show a high degree of paludification (Boissonneau, 1966; Veillette, 1993; Veillette & Thibaudeau, 1995).

FOREST MANAGEMENT CONCERNS

Our study confirmed that productive closed stands composed of either black spruce, jack pine, or trembling aspen may succeed to more open unproductive black spruce stands with time. Considering that stands undergoing the paludification process develop a thick organic layer over time and become less productive (Simard *et al.*, 2007), forest managers should be concerned about the productivity of stands growing on surface deposits susceptible to paludification. Young, unproductive, open black spruce stands, associated to low severity fires by Lecomte, Simard and Bergeron (2006), also have a low capacity to succeed toward more productive stand types in the absence of severe disturbance of the soil organic layer. Quebec's current harvesting approach aims to protect soil integrity and to maintain natural regeneration in order to favour rapid canopy closure after harvesting. However, by protecting the organic layer established above the surface deposits, and hence mimicking the effects of low-severity fires, this approach may in fact be inhibiting canopy closure and inducing a loss in site productivity (Lafleur *et al.*, 2010). Our results suggest that the organic layer on surface deposits that are susceptible to paludification (*e.g.*, the Cochrane Till) should be heavily disturbed during or after harvesting in order to favour the establishment of productive stands (Lecomte, Simard & Bergeron, 2006; Lafleur *et al.*, 2010). Protection of the organic layer may be appropriate on surface deposits that are not as susceptible to paludification (*e.g.*, coarse-textured deposits).

Acknowledgements

We thank Quebec's Ministry of Natural Resources for allowing us to use the SIFORT database. We would also like to thank Tembec Inc. and Quebec's Funds in nature and technology research (FQRNT) for the funding they provided. Finally, we are also grateful to the Chaire industrielle CRSNG-UQAT-UQAM en aménagement forestier durable (CAFD), which provided financial and technical support.

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