Successional pathways on different surficial deposits in the coniferous boreal forest of the Quebec Clay Belt

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Abstract: To infer successional pathways on different surficial deposits in northwestern Quebec, we combined the chronosequence approach to the study of within-stand species' vertical distribution. The deposits sustained different frequencies of postfire stand composition types and successional trajectories. After fire, *Picea mariana* (Mill.) B.S.P. dominated all stands on organic deposits, while shade-intolerant species dominated the canopy in over 30% and 60% of stands, respectively, on fine- and coarse-textured deposits. In the absence of fire, *P. mariana* eventually dominates the canopy of all stands on every deposit. However, as the frequency of *Larix laricina* (DuRoi) K. Koch and *Abies balsamea* (L.) Mill. in old stands (>100 years) are, respectively, positively and negatively correlated with the deposits' paludification potential, changes in composition in this landscape appear to be driven by the species' tolerance to shade and paludification. Structural changes were characterized by the replacement of closed dense stands by open stands. The diversity of *P. mariana* stand structures within the youngest age-classes suggests that fire severity may also explain the diversity of stand structures within this landscape. As among-stand structural diversity decreases with increasing time elapsed since fire, converging structural development pathways may be occurring in this landscape.

Résumé : Pour inférer les trajectoires successionelles dans le nord-ouest du Québec, nous avons combiné l'approche dite de "chronoséquence" à l'étude de la distribution verticale, au sein des peuplements, des tiges et des espèces. Les dépôts de surface contrôlent des fréquences différentes de composition après feu et des trajectoires successionelles différentes. Après feu, *Picea mariana* (Mill.) B.S.P. domine tous les peuplements sur dépôts fins tandis que des espèces intolérantes à l'ombre dominent la canopée de 30 % et 60 % des peuplements sur respectivement les dépôts à texture fine et grossière. En absence du feu, *P. mariana* domine la canopée de tous les peuplements sur chaque dépôts de surface. Toutefois, puisque la fréquence de *Larix laricina* (DuRoi) K. Koch et *Abies balsamea* (L.) Mill sont respectivement positivement et négativement reliées avec le potentiel d'entourbement des dépôts de surface, les changements de composition au sein de ce paysage sont déterminés par la tolérance des espèces à l'ombre et l'entourbement. Les changements de structure des peuplements se caractérisent par un remplacement des peuplements denses et fermés par des peuplements ouverts. Au sein des jeunes classes d'âge, la variabilité de la structure des peuplements dominées par *P. mariana* suggèrent que la sévérité du feu pourrait être important pour expliquer la diversité de structure des peuplements au sein de ce paysage. Puisque la variabilité structurale entre les peuplements diminue avec une augmentation du temps depuis le dernier feu, des trajectoires structurales convergentes se manifestent peut-être au sein de ce paysage.

Introduction

The view of boreal forest dynamics has gradually shifted in recent decades. Many studies have suggested that the high fire frequency in the boreal forest, coupled with the high similarity between pre- and post-fire stand compositions, inhibited directional succession and that succession therefore tended to be cyclical (Dix and Swan 1971; Johnson 1992). However, in the past two decades, independent reports have indicated a high spatial and temporal variability in fire frequency within the Canadian boreal forest (Flannigan et al. 2001; Bergeron et al. 2004*a*).

In conjunction with fire reconstruction studies, chronosequence, permanent plot, and careful stand reconstruction studies have indicated that in the prolonged absence of fire, species replacement can occur, notably the replacement of *Pinus* species and deciduous species by shade-tolerant *Picea* and *Abies* species (Carleton and Maycock 1978; Frelich and Reich 1995; Lesieur et al. 2002). This pattern of succession has been postulated to be mainly driven by minor disturbances at the scale of single trees (insect and fungal attack, windthrow), which gradually chisel away at the even-structured closed stands that typically arise after large disturbances such as fire. These small-scale gap processes engender changes in

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stand composition by favouring shade-tolerant species, which are already established in the understory (Bergeron 2000).

As forest dynamics become progressively influenced by small-gap processes, stand structural development leads to the evolution of even-structured stands into uneven-structured stands (Kneeshaw and Burton 1997; Kneeshaw and Bergeron 1998; Bergeron 2000). Structural development is usually associated with the abovementioned changes in composition, which result in the taller early-successional species being replaced by the shorter shade-tolerant species. However, in the eastern Canadian boreal forest, *Picea mariana* (Mill.) B.S.P., a shade-tolerant species, can form monospecific postfire stands by producing serotinous cones (Harper et al. 2002; Dix and Swan 1971). Given that *P. mariana* can regenerate abundantly by seed and layering under a conspecific canopy, stand structural changes can occur without species replacement (Groot and Horton 1994; Harper et al. 2002).

In the northern part of the boreal forest, a process known as paludification, which involves a build-up of organic matter, may be important in explaining changes in stand composition and structure. The consequences of paludification include the creation of a water-saturated environment characterized by low temperature, decreased microbial activity, and decreased availability of important nutrients, notably nitrogen (N) and phosphorus (P) (Heinselman 1981; Van Cleve and Viereck 1981; Taylor et al. 1987). Since some species are able to persist under this unfavourable environmental regime, while many others exhibit decreased vigour and annual growth, the process of paludification may be important in determining stand successional direction. Furthermore, paludification may also affect the structural development of stands. In some boreal regions, local-scale gaps are hastily closed by the growth of shade-tolerant coniferous species from the understory into the canopy (Kneeshaw and Bergeron 1998; Bergeron 2000), which maintains relatively closed-canopy stands (Kneeshaw and Burton 1997). However, in regions where paludification is an important process, the degradation of site quality induced by paludification (Heinselman 1963; Glebov and Kurzukhin 1992) may hinder the capacity of tree saplings to grow and hence close the canopy. Since paludification is related to the water-holding capacity of the underlying surficial deposit (Prescott et al. 2000), the comparison of successional pathways among the main surficial deposits should yield some insight as to whether the process of paludification exhibits a bottom-up control of successional trajectories in this landscape.

Given the presumed interaction between surficial deposits and successional processes, improved knowledge of natural succession on the different surficial deposits should ameliorate the prediction of the composition and structure of forest stands that would characterize the natural landscape under different fire cycles. To improve our knowledge of succession for this part of the boreal biome, we combine the chronosequence approach to the study of within-stand diameter distribution to infer future developmental stages. Although both methods have been critiqued in the literature, we believe our approach of combining these techniques and using a large data set (over 750 stands) partially overcomes their respective shortcomings.

We hypothesized that in the absence of fire (1) species and individual replacement in the canopy can occur in this part of the boreal forest and is driven by the individual species' shade and paludification tolerance and (2) as a result of the combined effects of disturbances other than fire and paludification, even-structured closed stands that characterize young successional stages will, as succession proceeds, develop and maintain an open canopy and uneven-structured diameter distribution.

Materials and methods

Study area

The study area (49°N–51°20′N; 78°30′W–79°50′W) is located within the Clay Belt of northwestern Quebec, Canada, and is within the *P. mariana* – feathermoss bioclimatic domain (Robitaille and Saucier 1998). The Clay Belt is a physiographic unit composed mostly of clay deposits left by proglacial Lake Ojibway; organic soils and glaciofluvial deposits are also common. (Veillette 1994), Although a few rocky outcrops are scattered across the landscape, the topography is generally flat. Average annual temperatures (1971–2000) recorded at the closest weather station to the north (Matagami, 49°43′N, 77°37′W) and to the south (La Sarre, 48°46′N, 79°13′W) of the study area are, respectively, –0.6 and 0.8 °C with an average of 857 and 905 mm of precipitation annually (Environment Canada 2005). Most of the area is dominated by *P. mariana*, which forms monospecific, structurally diverse stands, whereas occasional deciduous- and pine-dominated stands are dispersed across the landscape (Harper et al. 2002). Fire cycle length has increased from 101 years before 1850 to 398 years since 1920; mean stand age is 148 years (Bergeron et al. 2004*b*).

Databases

The Quebec Ministry of Natural Resources (QMNR) gathered the data used to describe successional changes. Since the QMNR inventories the forest for forestry purposes, stands on slopes of more than 40% (rare in the study area) and with a canopy height less than 7 m were not sampled. In the study area, 953 circular plots of 400 m^2 were sampled in 1987, 1989, or 1996. The plots were sampled every 250 m along 1.5-km transects. In each 400-m^2 plot, every tree with a diameter >10 cm was identified to species and tabulated in diameter classes of 2 cm. In a concentric subplot of 40 m^2, trees with diameters <10 cm were measured in the same manner. Additionally, in each plot the age at breast height of three dominant trees was measured. With an eco-forestry database, we divided the stands into four surficial deposit types (thin, coarse, fine, and organic), four slope types (0%–3%, 4%–8%, 9%–15%, 16%–30%), and five canopy closure classes (0%–20%, 20%–40%, 40%–60%, 60%–80%, >80%) (similar to those being established by the Quebec provincial forest inventory program; Harper et al. 2002). We assigned a date since last fire to every forest stand by overlaying fire reconstruction maps (Bergeron et al. 2004*b*) onto the forest inventory and by validating the fire map date with the oldest age determined for the three dominant trees aged per stand. The fire reconstruction maps were developed by dating postfire tree cohorts for fires before 1880 and using archives and aerial photographs for fires after 1880 (Bergeron et al. 2004*b*).

Overall we were able to confidently attribute a surficial deposit type, a slope class, and a time since last fire (TSF) date to 797 stands (Appendix A). Because of an insufficient number of stands, we excluded young stands (<50 years, 4 stands) and stands on thin soils (12 stands). As compared to previous landscape-scale studies in this area (Harper et al. 2002; Bergeron et al. 2004*b*), the forestry inventory data set, with respect to surficial deposits and stand age, appears to be representative of the forested portion of the landscape under study (Appendix A).

Data analyses

Ordination

To obtain a two-dimensional integrated representation of stand tree composition and to directly relate stand composition to a set of environmental factors, a canonical correspondence analysis (CCA) (direct gradient analysis) was computed using the relative abundance of each species (percentage of total basal area) (CANOCO Version 4; ter Braak 1986; ter Braak and Šmilauer 1999). The environmental variables (TSF, surficial deposit, slope class) were loaded by forward selection. Significance of each variable was computed using a Monte Carlo test ($\alpha = 0.05$). The downloading option was used for rare species. Since the CCA with all the stands demonstrated that surficial deposit was an important factor in determining stand composition, separate CCAs were computed for each surficial deposits.

Age-class classification

To investigate changes in stand composition and structure in relation to TSF, we divided our stands into four age-classes (50–100, 100–150, 150–200, and 200+ years). To investigate seedling and sapling bank recruitment in the prolonged absence of fire, we calculated for each surficial deposit the proportion of stands older than 100 years where each species was present in the diameter classes <9 cm.

Within-stand canopy advanced regeneration trends

To assess canopy advanced regeneration (canopy-regen) relations within stands, we subdivided the trees in the stands into either canopy trees or advanced regeneration trees. As previous studies have demonstrated that canopy height decreases in the absence of fire (Harper et al. 2002), we chose an alternative method to the traditional static forestry definition of advanced regeneration (i.e., trees smaller than a certain diameter). To accomplish the canopy-regen division, we firstly subdivided the trees into six diameter classes (0–4.9, 5–8.9, 9–12.9, 13–16.9, 17–20.9, and >21 cm). Secondly, to determine where the canopy-regen boundary would be set between these diameter classes, we established that this boundary, starting with the largest diameter class and moving down, would be set when the cumulative surface area was at least 20% of the total stand basal area. The “20% boundary” was chosen as on average the largest diameter class (<21 cm), which represents 20% of the total stand basal area. Given our procedure and because of the variability in stand structure, we obtained five different canopy-regen types, which differ in the location of their respective canopy-regen delimitation. For the majority of stands (>98%), we excluded the smallest diameter class because of their associated high mortality rates. However, in a few very old (>200 years) or young stands (50–100 years), trees >10 cm did not make up 20% of the total stand basal area; for these stands the advanced regeneration is solely for trees with a diameter <5 cm. To assess canopy-regen relations within stands, for each surficial deposit and for each species dominating the canopy, we calculated the proportion of stands where each species was present or dominated the advanced regeneration.

Table 1. Summary statistics of the four canonical correspondence analyses (CCA) performed using a forward selection of environmental variables.

Surficial deposit	Total inertia of CCA	% variance explained by time since last fire	% variance explained by surficial deposit	% variance explained by slope
All	1.9	14	9	1
Coarse	2.1	11		0
Fine	1.65	12		5
Organic	0.2	0		0

Stand structural development

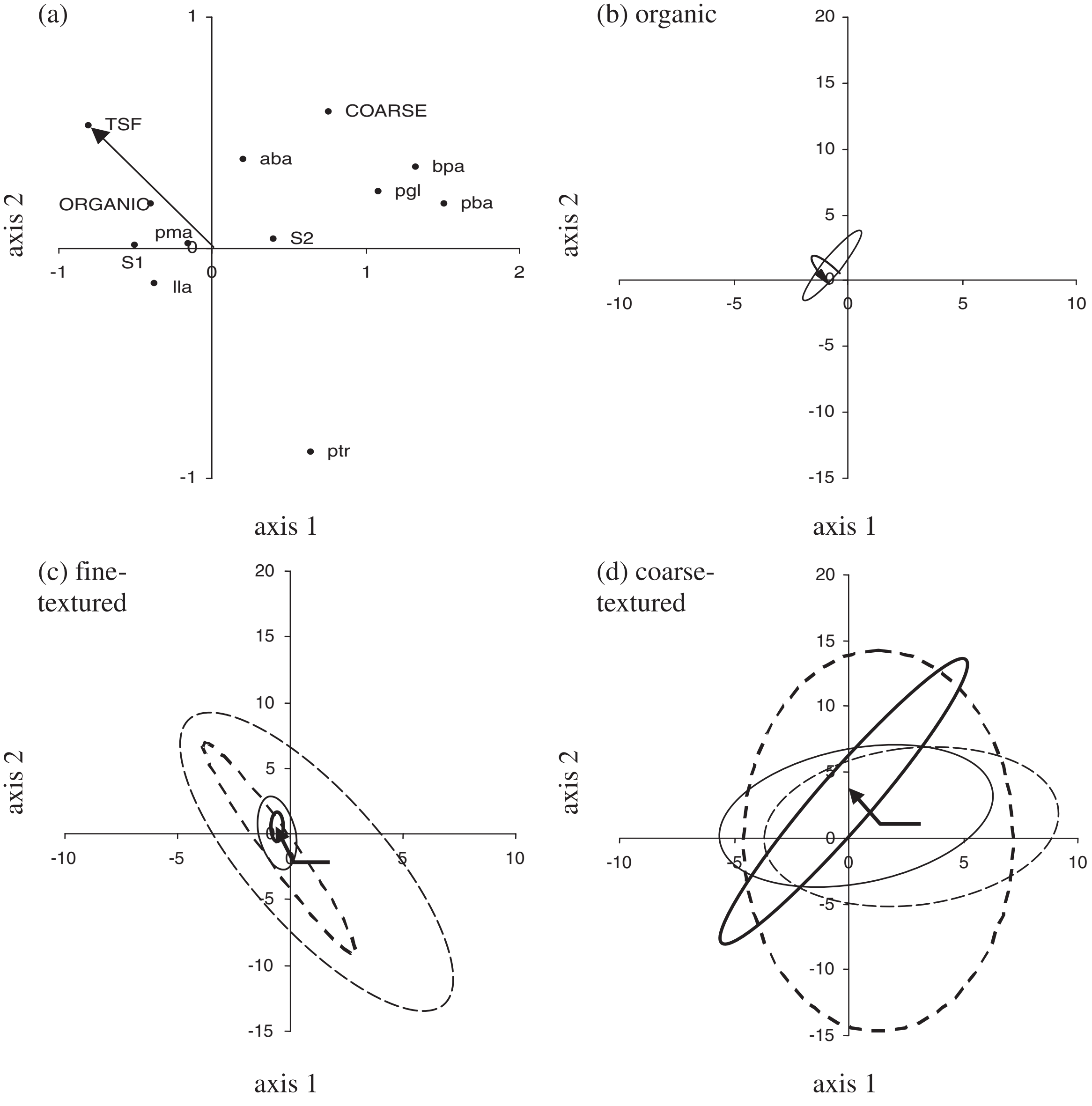
Stand structural development was assessed by calculating for each age-class the average and coefficient of variation of each of the following six variables: (1) diversity of diameter classes (Shannon’s index), (2) coefficient of skewness for diameter, (3) mean diameter (cm), (4) density (stems/ha), (5) surface area (m^2/ha), and (6) volume. To investigate whether structural changes or stand structural variability within age-class could be due to the variability in surficial deposit, stand composition, or slope, we isolated stands where *P. mariana* dominated the canopy and advanced regeneration. We then compared how the structural attributes varied between the surficial deposits and between the two main slope classes (0%–3% and 3%–8%) on fine-textured deposits.

Results

General ordination trends

Our CCA with all stands demonstrated that (1) the canonical axes 1 and 2 explained, respectively, 20% and 4% of the variance in species composition and (2) TSF explained 14% of the variation, surficial deposit 9%, and slope 1%. The total inertia of the individual CCAs for each surficial deposit indicate that stands on coarse-textured deposits display the highest variability in species composition and the ones on organic the least variability (Table 1). For all surficial deposits, time since fire (TSF) was again the most important explanatory variable. The ordination diagram with all the stands revealed that (1) TSF is negatively correlated with axis 1 and positively correlated with axis 2 and (2) the differentiation as to surficial deposit is a significant factor, with sites on coarse-textured deposits on the upper right side of the ordination diagram and sites on organic and fine-textured deposits negatively correlated with axis 1 (Fig. 1*a*). The position of *P. mariana* near the centre indicates that this species is present on all substrates regardless of the age of the stand. The position of *Pinus banksiana* Lamb., *Betula papyrifera* March., and *Picea glauca* (Moench) Voss. in the upper right of the ordination diagram indicates their early-successional status and (or) preference for coarse-textured deposits. The position of *Populus tremuloides* Michx. in the lower right of the ordination diagram demonstrates its early successional status and preference for fine-textured deposits. The intermediate positive position of *Abies balsamea* (L.) Mill. on

Fig. 1. Canonical correspondence analysis of the tree composition (relative abundance of basal area). (*a*) Tree species and explanatory variables. Stands are regrouped by (*b*) organic, (*c*) fine-textured, and (*d*) coarse-textured deposits and represented as age-class 80% confidence ellipses, light broken line (50–100 years), dark broken line (100–150 years), light line (150–200 years), and dark line (>200 years) (because of the similarity in the age-class ellipses, stands on organic soils are represented as one ellipse). Vectors represent a connection of the age-class ellipse centroids going from youngest to oldest. Species codes are as follows: aba, *Abies balsamea*; bpa, *Betula papyrifera*; lla, *Larix laricina*; pba, *Pinus banksiana*: pgl, *Picea glauca*; pma, *Picea mariana*; ptr, *Populus tremuloides*. Environmental variables are as follows: TSF, time since last fire; coarse, centroid of stands on coarse-textured deposits; organic, centroid of stands on organic deposits; S1, centroid of stands on slopes between 0% and 3%; S2, centroid of stands on slopes between 3% and 8%.



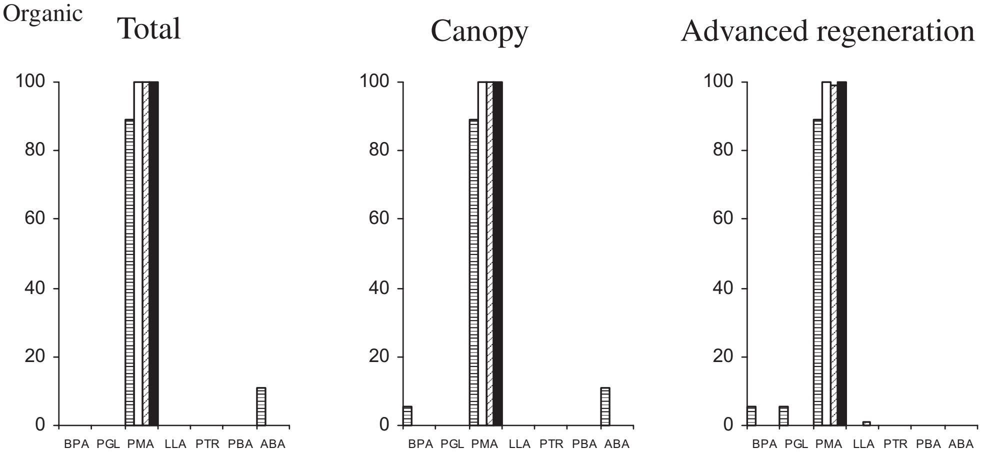
axis 1 and its positive position on axis 2 indicate that it is associated with long fire intervals on coarse-textured deposits. *Larix laricina* (DuRoi) K. Koch, being positioned in the lower left corner of the ordination diagram indicates its preference for fine-textured and organic deposits. The size and position of the age-class 80% confidence ellipses for each surficial deposit suggests that the absence of fire induces a converging decrease in stand composition diversity (Fig. 1*b*, 1*c*, 1*d*).

Age-class classification trends

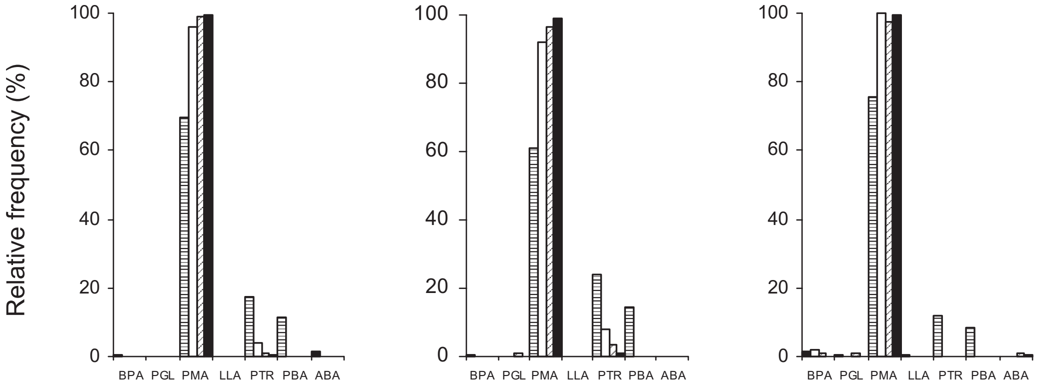
On organic deposits, apart from two young stands, *P. mariana* dominates the total and canopy stand basal area in all age-classes (Fig. 2). In the older stands, excluding *P. mariana*, only *L. laricina* occasionally dominates the advanced regeneration. On fine-textured deposits, *P. mariana* dominates the canopy, advanced regeneration, and overall basal area of nearly all the stands older than 100 years, while *Populus tremuloides* and *Pinus banksiana* dominate the canopy basal area of about 30% of the youngest stands. On coarse-textured deposits, shade-intolerant species dominate the canopy basal area of over half the stands within the youngest age-class. *Picea mariana* dominates the canopy of all the oldest stands, while *A. balsamea* dominates the total and advanced regeneration basal area of 25% of the stands older than 200 years.

Fig. 2. Proportion of stands where each species is dominating the total, canopy, and advanced regeneration basal area, per 50-year age-class, for (*a*) organic, (*b*) fine-textured, and (*c*) coarse-textured deposits (for species codes see Fig. 2). Barred bars represent stands aged between 50 and 100 years, open bars stands between 100–150 years, grey bars stands between 150 and 200 years, and black bars stands older than 200 years.

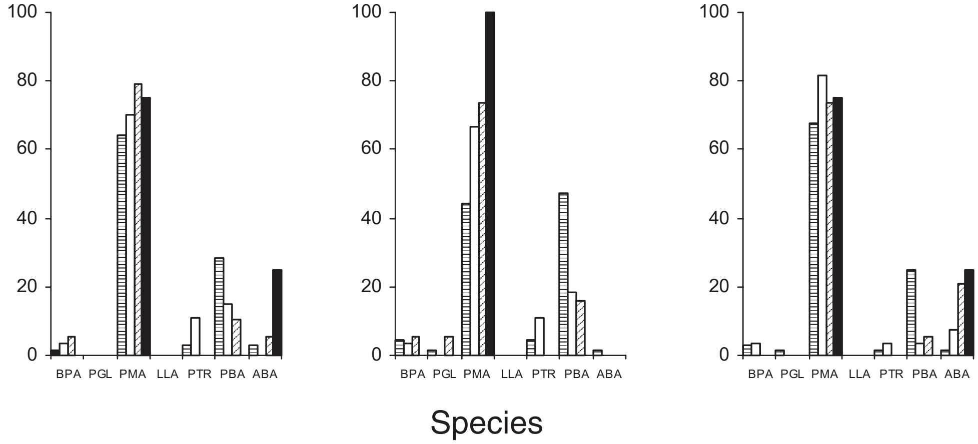
(a) Organic



(b) Fine-textured



(c) Coarse-textured



On organic and fine-textured soils the frequencies of small *P. mariana* and *L. laricina* stems increase as the TSF increases, whereas the frequency of small *A. balsamea* stems appears to decrease or stabilize (Table 2). On coarse-textured deposits, only small *A. balsamea* and *P. mariana* stems are present in the prolonged absence of fire, and the frequencies of small stems of these species increases as the TSF increases (Table 2). Small *Populus tremuloides* and *P. glauca* stems were encountered, respectively, in only two and one stand older than 100 years (data not shown).

Table 2. Proportion of small stems (DBH < 9 cm) of *Picea mariana*, *Abies balsamea*, and *Larix laricina* per surficial deposit (organic, fine, and coarse) and 50-year time since fire (TSF) age-classes older than 100 years.

	TSF (years)								
	Organic			Fine			Coarse		
Species	100	100–150	>200	100	100–150	>200	100	100–150	>200
P. mariana	100.0	90.8	98.6	86.3	96.4	97.8	80.0	88.2	100.0
A. balsamea	12.5	6.2	8.2	21.6	24.1	17.8	20.0	35.3	37.5
L. laricina	0.0	23.1	19.2	2.0	8.9	12.4	0.0	0.0	0.0

Table 3. Canopy advanced regeneration relationships showing the frequency of stands (in parentheses) where the different species or group of species is present and dominating the advanced regeneration, depending on surficial deposit and the species that dominates in the canopy.

	Populus tremuloides, *Betula papyrifera*			*Pinus banksiana*			*Picea mariana*		
	Organic (0)	Fine (46)	Coarse (10)	Organic (0)	Fine (22)	Coarse (41)	Organic (154)	Fine (432)	Coarse (71)
Species present in the advanced regeneration									
Populus tremuloides, *Betula papyrifera*	—	80	100	—	32	15	1	6	12
Pinus banksiana	—	22	10	—	95	93	1	1	24
Picea mariana	—	78	70	—	95	95	100	100	98
Picea glauca, *Abies balsamea*	—	30	60	—	14	5	17	25	23
Larix laricina	—	4	—	—	5	—	14	5	—
Species dominating the advanced regeneration									
Populus tremuloides, *Betula papyrifera*	—	24	60	—	—	—	—	—	—
Pinus banksiana	—	—	—	—	50	40	—	—	4
Picea mariana	—	67	10	—	45	60	99	99	98
Picea glauca, *Abies balsamea*	—	9	30	—	—	—	—	—	7
Larix laricina	—	—	—	—	5	—	<1	<1	—

Within-stand canopy advanced regeneration trends

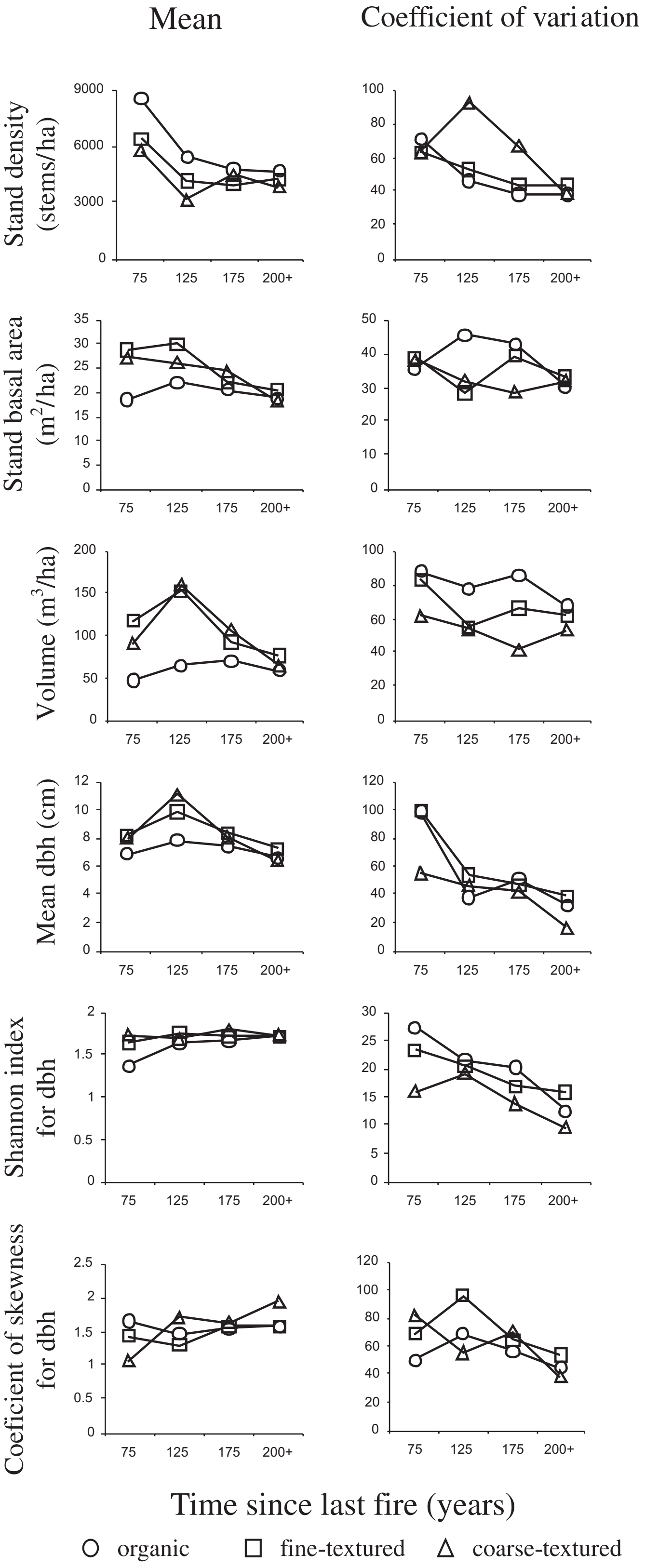
When *P. mariana* dominates the canopy, numerous species can be present in the advanced regeneration; however, conspecific stems or occasionally *A. balsamea* – *P. glauca* on coarse-textured deposits and *L. laricina* on fine-textured and organic deposits, dominate the advanced regeneration (Table 3). When deciduous species (*Populus tremuloides* and *B. papyrifera*) dominate in the canopy the advanced regeneration is mainly composed of conspecific, *P. mariana* or *A. balsamea* – *P. glauca* stems. Whereas conspecific or *P. mariana* stems tend to dominate the advanced regeneration in the youngest age-class, the older age-classes on fine-textured deposits are almost exclusively dominated by *P. mariana*, with a few stands dominated by *A. balsamea* – *P. glauca* (Fig. 2, Table 3). On coarse-textured soils the older deciduous-dominated canopies tend to be preferentially dominated by *A. balsamea* – *P. glauca* than by *P. mariana*. When *Pinus banksiana* dominates the canopy, in the youngest age-class the advanced regeneration is either dominated by conspecific stems or more commonly by *P. mariana* stems, and in the older age-classes almost exclusively by *P. mariana* (Fig. 2, Table 3).

Successional trends in stand structure for the main surficial deposits

Apart from a decrease in stand density, few structural changes were observed on organic soils (Fig. 3). On coarse- and fine-textured deposits the six stand structural attributes varied as follows. Stand density decreased after 100 years and remained relatively constant afterwards. Stand basal area remained constant between 50 and 150 years since the last fire and decreased afterwards. Stand volume and mean diameter increased to 150 years since the last fire and eventually decreased after 150 years. The diversity of diameter classes remained relatively constant through time. Stand coefficient of skewness for diameter remained relatively low for the first 150 years and subsequently increased (Fig. 3). The same trends in structural attributes were apparent when we isolated stands where *P. mariana* dominated the canopy and advanced regeneration basal area (data not shown).

Although our date set comprises more old stands than young stands (Appendix A), on all deposits, the within age-class coefficients of variation for the six structural attributes tended to be higher in stands younger than 150 years as compared to stands older than 150 years (Fig. 4). This higher structural variability among stands in the youngest age-class was also observed when we looked solely at *P. mariana* dominated stands and when we compared the structural development of *P. mariana* dominated stands on fine-textured deposits on the two main slope classes (Fig. 4). Similarly, on coarse- and fine-textured deposits, while about 40% of the stands in the youngest age-classes have closed canopies (>60% cover), over 90% of the canopies of older stands are open

Fig. 3. Mean and associated coefficient of variation values obtained for the six structural attributes (stand density, basal area, volume, mean diameter, coefficient of skewness, and Shannon's diversity index for dbh) per 50-year age-class and per surficial deposit.



(<60% cover) (Table 4). Few changes in canopy closure were observed on organic deposits, with over 90% of stands exhibiting less than 60% cover (Table 4).

Discussion

Successional pathways within the study area on different surficial deposits

Within the study area, as *Populus tremuloides*, *B. papyrifera*, *P. mariana*, and *Pinus banksiana* may be the dominant species following fire, numerous successional pathways co-occur under similar abiotic conditions. However, the comparison of successional pathways on the different surficial deposits revealed significant differences in the relative abundance of the respective pathways and different trajectories of the postfire stands (Fig. 5).

While *P. mariana* dominates on organic deposits, the other successional pathways are encountered on coarse- and fine-textured deposits. The relative abundance of the *Pinus banksiana* and *B. papyrifera* successional pathways are more abundant on coarse-textured deposits, while the *P. mariana* and *Populus tremuloides* pathways are more abundant on fine-textured deposits. The difference in relative importance of the successional pathways occurring on the deposits might be due to different disturbance regimes among the surficial deposits types. Paleoecological studies south of the study area have demonstrated that high fire frequencies favour *Pinus banksiana* and *B. papyrifera* over *P. mariana* (Larocque et al. 2000). While Bergeron et al. (2004*b*) found that fire frequencies were lower on organic soils than on fine- and coarse-textured deposits, no significant difference in fire interval length was observed between these two latter deposit types (Appendix A). Nonetheless, recent radiocarbon datings of forest-floor humus accumulated just above the uppermost charcoal in stands on fine-textured deposits revealed that the dendroecological dates obtained for sites older than 200 years significantly underestimated the age of some stands (Cyr et al. 2005). This suggests that fire frequency on fine-textured deposits may in fact be lower than that on coarse-textured deposits, which may explain the different relative abundance of successional pathways occurring on fine- and coarse-textured deposits.

Alternatively, the differing paludification potentials of the surficial deposits may influence fire severity, which in turn may influence the relative abundance of the successional pathways. For a given fire interval and stand composition, stands on fine-textured deposits will tend to have more organic matter accumulated on the ground as compared to those on coarse-textured deposits. Given a fire of equal intensity, this fire is more likely to not fully remove the organic matter accumulated above the fine-textured deposits. Low-severity fires that do not remove all the organic matter would favour species that do not require an exposed mineral seedbed to germinate, such as *P. mariana* (Jeglum et al. 1979) and unlike *Pinus banksiana* (Lavoie and Sirois 1998). Furthermore, it has been argued that the fire-resistant reproductive organs of the two dominant deciduous species may differ as to their capacity to survive fires of differing severity. It has been postulated that *B. papyrifera*, which resprouts from the stem collar, would be more resistant to high-severity fires than *Populus tremuloides*, which resprouts from roots

Fig. 4. Mean coefficient of variation for within age-class values obtained for the six structural attributes used in our study (stand density, basal area, volume, mean diameter, coefficient of skewness, and Shannon's diversity index for dbh) per 50-year age-class and per surficial deposit for (*a*) all stands, (*b*) stands where *Picea mariana* dominates the canopy and advanced regeneration basal area, and (*c*) *P. mariana* dominated stands on fine-textured deposits on the two main slope classes (slope 1: 0%–3% and slope 2: 3%–8%).

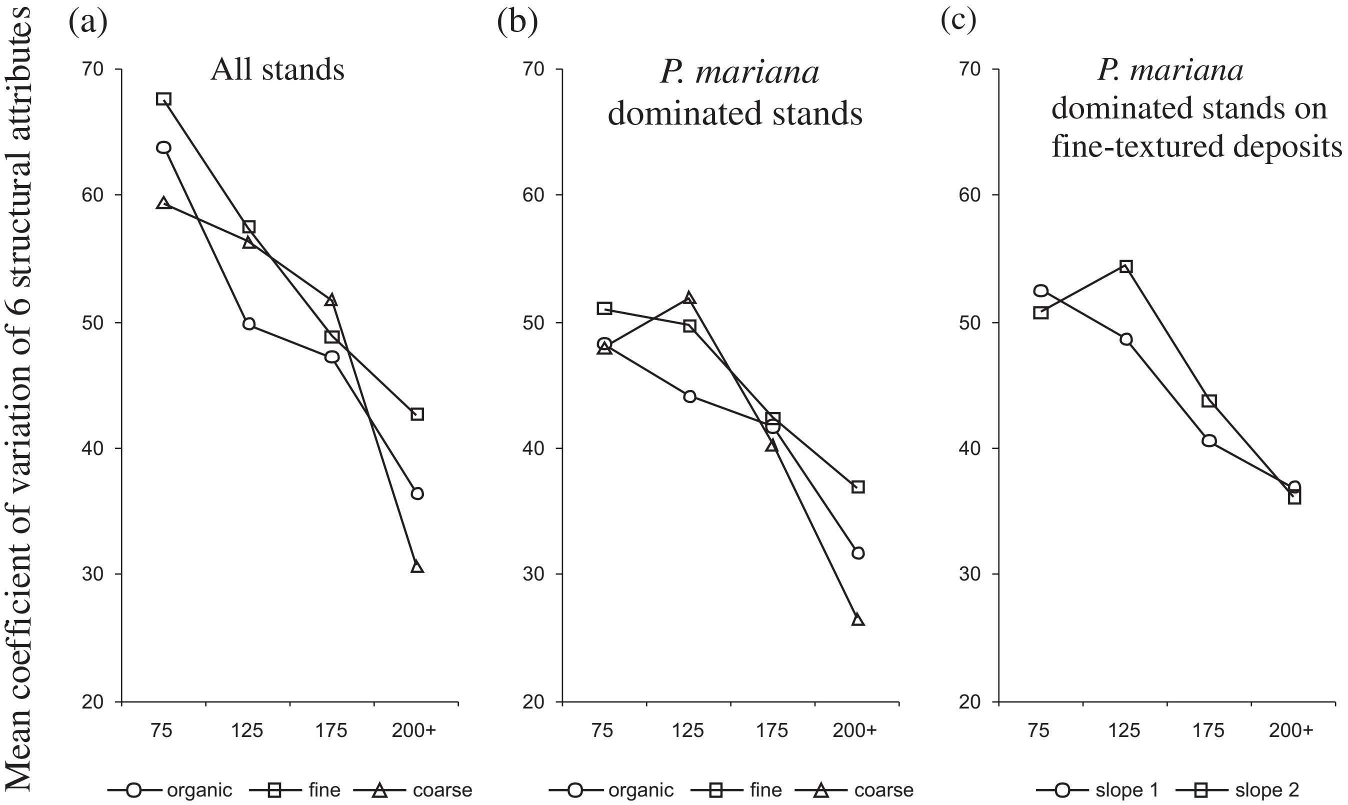


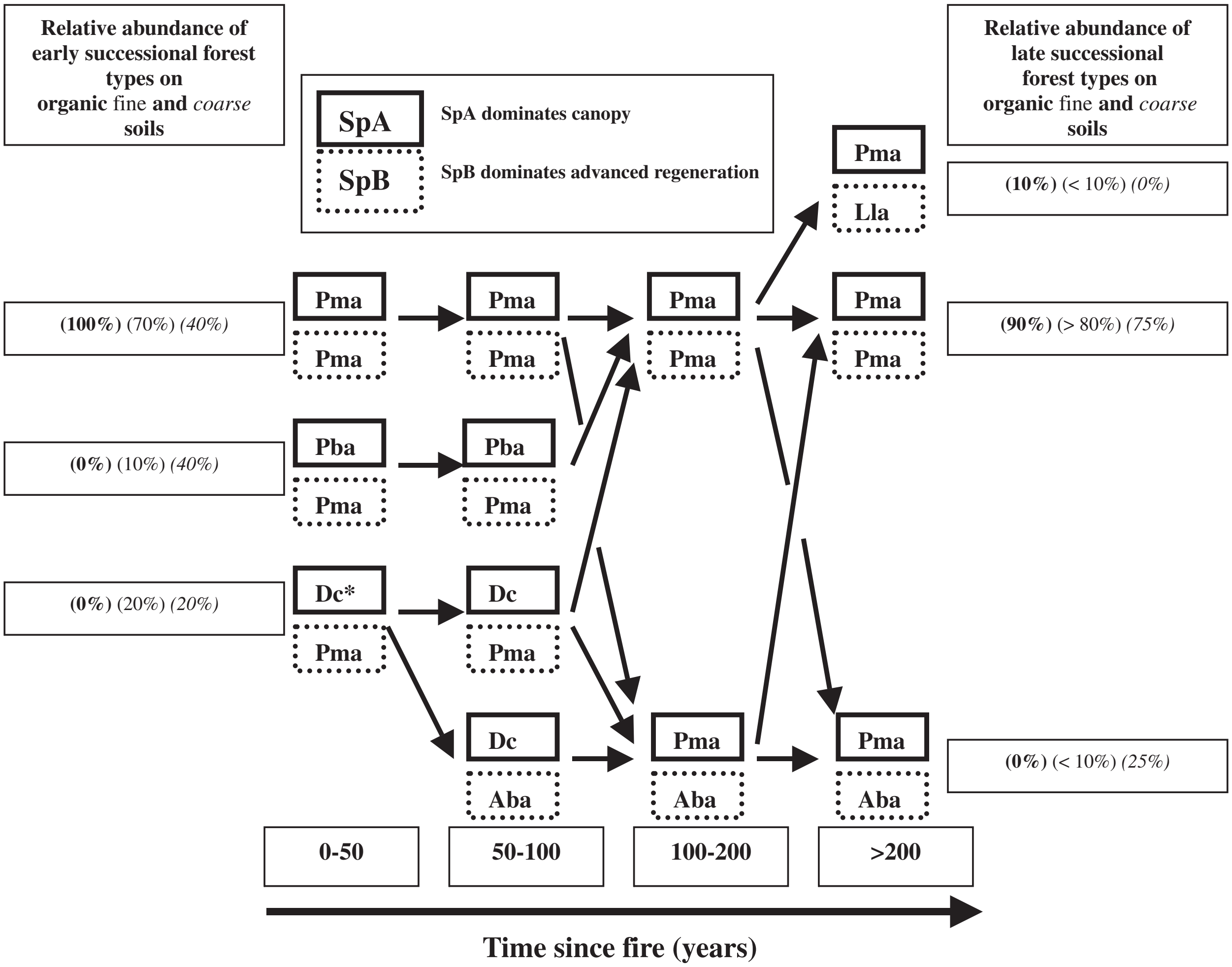
Table 4. Relative importance of open and closed stands with respect to surficial deposit (organic, fine, and coarse) and time since fire (T1, <100 years; T2,100–200 years; T3, 200+ years) with all stands and *Picea mariana* dominated stands.

	Organic			Fine			Coarse		
Stand canopy type	T1	T2	T3	T1	T2	T3	T1	T2	T3
All stands									
Closed (density >60%)	0	14	4	50	36	10	38	15	0
Open (density <60%)	100	86	96	50	64	90	62	85	100
***Picea mariana* dominated stands**									
Closed (density >60%)	0	14	4	39	35	10	39	9	0
Open (density <60%)	100	86	96	61	65	90	61	91	100

(Viereck 1983). Therefore, a fire regime at the scale of the Holocene composed of more frequent fires and (or) fires of greater severity on coarse-textured soils as opposed to fine-textured deposits may explain the different relative importance of the successional pathways on these deposits.

As *P. mariana* dominated all old stands and the advanced regeneration of most stands, succession in this landscape appears to be driven by the shade tolerance of the species. Shade-tolerant species in the absence of fire would be able to progressively invade and survive in the understory and would be at a competitive advantage when the fire cohort is dismissed by secondary disturbances (Frelich and Reich 1995; Bergeron 2000). However, since the frequencies of *A. balsamea* and *L. laricina* in later stages on the three surficial deposits were, respectively, negatively and positively correlated to the paludification potential of these deposits, the species tolerance to paludification appears be an important factor driving succession in the coniferous boreal forest. On coarse-textured deposits, *P. mariana* stands and the deciduous-dominated stands are more likely to evolve towards *A. balsamea* codominated stands as compared to stands on fine-textured deposits (Fig. 5). On organic and fine-textured deposits, *P. mariana* stands are more likely to be invaded by *L. laricina* than stands on coarse-textured deposits. We propose that the higher paludification potential of fine-textured and organic deposits favours *L. laricina*, which is known to tolerate nutrient-poor conditions (Heinselman 1981; Van Cleve and Viereck 1981; Giroux et al. 2001). Contrarily, we suggest that the low

Fig. 5. Successional pathways in the coniferous boreal forest of northwestern Québec on different surficial deposits as inferred by this study. Proportion of each forest type after fire and in the extended absence of fire are also shown. Aba, *Abies balsamea*; Lla, *Larix laricina*; Pma, *Picea mariana*; *, deciduous species (*Populus tremuloides* and *Betula papyrifera*).



paludification potential of coarse-textured deposits as compared to finer textured deposits favours *A. balsamea* over *P. mariana*. This hypothesis is supported by studies that have shown that on coarse-textured deposits no significant difference in the growth rates of *A. balsamea* and *P. mariana* regeneration was observed 10 years after the removal of canopy trees (Doucet and Boily 1995), while on more paludified sites *P. mariana* had significantly better growth rates than *A. balsamea* (Brumelis and Carleton 1988).

Structural development pathways

Stand structural development coincided with changes in species composition; however, the same structural development pathways were apparent when comparing young and old *P. mariana* dominated stands. Stand structural development in our study area, at first glance, appears to mirror that of the biomass accumulation model and the stand development stages of, respectively, Bormann and Likens (1979) and Oliver and Larson (1996). Early stages are dense and of low volume, intermediate stands are of lower density and higher volume, while older stands are characterized by lower volume, as the fire-origin cohort is replaced by understory trees. Paludification appears to be prevalent within our study area, as old stands tend to be characterized by low volume, open canopies, and a high within-stand coefficient of skewness for diameter. As stands become paludified and the fire-origin cohort is dismissed, the variability in microtopography is likely to increase with the formation of a hummock and hollow pattern that will gradually characterize old stands. Heterogeneity of microsites has a major influence on growth variation and hence size inequality in *P. mariana* stands (Macdonald and Yin 1999). Furthermore, since older stands tend to be more open than young stands and there exists a positive correlation between the openness of a stand and the potential windthrow risk hazard (Smith et al. 1987), the openness of the canopy may also be maintained by a high rate of windthrow-induced gap formation. Regardless of the causes, the low variability among stands within the oldest age-class suggests that as succession proceeds, canopy closure rate falls below the rate of canopy gap formation, which maintains the canopy openness of old stands.

Convergence of parallel structural development pathways

The higher variability among *P. mariana* stands within the younger age-classes as compared to older age-classes for the structural attributes studied suggests that multiple converging structural development pathways may be present within our study area, as has been noted for other North American fire-dominated landscapes (Kashian et al. 2005). While it has been generally accepted that postfire tree regeneration is high in the boreal forest, some have shown that stands exhibiting initial differences in tree densities have followed different recovery pathways (Arsenault 2001; Johnstone et al. 2004). Furthermore, some authors have described three natural disturbance histories that may lead to poor postfire tree regeneration in *P. mariana* stands. Some have indicated that a short fire interval may engender poor postfire tree regeneration (Lavoie and Sirois 1998; Larocque et al. 2000; Payette 1992). Others have demonstrated that regeneration may be low if a fire occurs in a *P. mariana* dominated stand having recently been affected by a spruce budworm outbreak (Payette et al. 2000). Finally, Foster (1985) suggested that a fire of low severity that does not fully consume the organic matter accumulated above the mineral soil may, by lowering the availability of adequate seedbeds, engender low postfire regeneration.

Although we cannot completely rule out other factors, given the low fire frequency in this landscape (Bergeron et al. 2004*a*) combined with the process of paludification (Boudreault et al. 2002), we propose that the variability in fire severity may be the chief process which explains the high variability in stand structure within young successional stages. This hypothesis necessitates further study; however, it is corroborated by two recent studies, which looked at the stratigraphy of the organic matter accumulated above the mineral soil. These studies found, in sparsely regenerated young stands (<100 years), charcoal horizons within the organic matter, as opposed to one horizon just above the mineral soil in similarly aged, densely regenerated stands (Cyr et al. 2005; N. Lecomte, unpublished data).

Management implications

The forest mosaic in this landscape is composed of a diversity of stand types, which can be partially explained by the absence of fire and the underlying surficial deposit. To maintain this diversity, forest management regimes should vary the relative abundance of successional series on the different surficial deposits and gradually adopt an uneven-aged management approach. Without abandoning clearcuts, this adoption may be attained by introducing the use of partial cuts that mimic successional changes occurring in the absence of fire. Furthermore, given the prevalence of paludification in this region, current sylvicultural interventions that by definition protect the organic matter accumulated above the mineral soil ("Coupe avec protection de la régénération et des sols") may be maladapted to the coniferous boreal forest on the Clay Belt. Inspired by the effects of severe fires, sylvicultural interventions that physically remove the accumulated organic matter (scarification, controlled burning, etc.) may be necessary, to not only counteract the detrimental effects of paludification on tree productivity but also maintain the diversity of stand structural types within this landscape.

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Appendix A

Appendix appears on the following page.

Table A1. Distribution of the 781 stands under study with respect to surficial deposit and time since fire (TSF) age-class and representative values of the 781 stands with respect to the relative abundance (% cover) of surficial deposits and mean stand age on each surficial deposit as compared to two previous landscape studies (Bergeron et al. 2004*b*; Harper et al. 2002).

	TSF (years)					% cover		Mean stand age (years)	
Surficial deposit	50–100	100–150	150–200	>200	Total	Our study	Harper et al. 2002	Our study	Bergeron et al. 2004*b*
Coarse	71	27	19	8	125	16	12	108	104
Fine	151	52	111	187	501	64	66	156	134–147
Organic	9	8	65	73	155	20	22	188	151
All	231	87	195	268	781	–	–	154	148