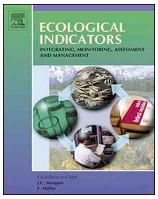
Ecological Indicators 97 (2019) 89–99

Contents lists available at ScienceDirect

Ecological Indicators

journal homepage: www.elsevier.com/locate/ecolind



Changes in forest structure along a chronosequence in the black spruce boreal forest: Identifying structures to be reproduced through silvicultural practices

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ARTICLE INFO

Keywords:
Picea mariana
Diameter structure
Time since last fire
Surficial deposits
Successional pathway
Sustainable management

ABSTRACT

In managed boreal forests, partial harvesting has been proposed to promote forest structural complexity and to therefore maintain associated biodiversity. However, there have been few studies identifying forest structures that should be maintained within the forest matrix, and fewer still on changes in these structures during succession. Consequently, there is no tool to identify these different structures in the field or their sequence along natural succession. This study proposes a key that can be used in the field and allows for the identification of different forest diameter structures along a successional sequence in the black spruce boreal forest. The specific objectives of this study were (1) to classify the types of forest structures encountered in natural black spruce boreal forest based on their diameter distribution, and (2) to link this classification to time since last fire and its spatial homogeneity at the stand level. This study shows that the forest stand structure, in black spruce forests, is varied and that this structural variety is mainly controlled by time since last fire. It also shows that the timing of stand structural maturation varies with severity of the last fire and surficial deposit. The identification key suggests that based on tree diameter distribution it is possible to discriminate among young, mature and old forest structures, which could help forest managers select stands to be harvested according to different objectives and hence maintain the variety of black spruce forest structures at the landscape scale.

1. Introduction

During forest management the preservation of ecosystem services provided by forests is an important challenge for the international community (MEA, 2005). In the boreal forest, the use of a short rotation period leads to the rejuvenation of forest age structure and reduction of the proportion of old-growth forest across the landscape (Bergeron et al., 2007; Cyr et al., 2009). In managed boreal forests, maintaining a structural variability comparable to that encountered in natural forests should maintain biodiversity and essential ecological functions (Franklin, 1993; Gauthier et al., 1996). To ensure the preservation of its forests and its socio-economic services, Canada now encourages ecosystem-based forest management, which promotes the diversification of silvicultural practices and the maintenance of forest stands of various structures (Gauthier et al., 2008). In this context, partial harvesting has appeared, over the last fifteen years as an alternative to clearcutting in order to reduce the differences at the stand and landscape scale between natural and managed forests (Franklin et al., 1997; Beese et al., 2003). Partial harvesting is applied with the objective to promote forest continuity and heterogeneity of habitats that can maintain both the structural complexity and biodiversity associated with old-growth forests (Rosenvald and Lohmus, 2008).

However, boreal forest stands are complex systems in which many factors and processes may influence both stand composition and structure over time (Lecomte and Bergeron, 2005; Lecomte et al., 2005; Taylor and Chen, 2011; Puettmann et al., 2012). Nevertheless, as fire is an integral part of the boreal forest dynamics (Payette, 1992; Hunter, 1993; Bergeron et al., 1998), time since last fire (TSF) is generally the most frequently stated factor in the literature to explain changes in both forest structure and composition. From a compositional standpoint, in the boreal forest changes in both forest structure and composition after fire result in the recolonization of the burned matrix by early-successional species pre-adapted to open post-fire conditions (e.g. increased light availability), i.e., trembling aspen (*Populus tremuloides* Michx.),

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https://doi.org/10.1016/j.ecolind.2018.09.059
Received 6 November 2017; Received in revised form 6 April 2018; Accepted 30 September 2018

white birch (*Betula papyrifera* Marsh.), jack pine (*Pinus banksiana* Lamb.) and black spruce (*Picea mariana* [Mill.] BSP) (Bergeron, 2000). With time, most of these species are gradually replaced by shade-tolerant and more competitive late-successional species such as balsam fir (*Abies balsamea* (L.) Miller) (Larson and Oliver, 1996; Lecomte et al., 2005). While this multispecies succession is much studied, there has been little attention given to monospecific succession.

In the case of the generally monospecific boreal black spruce forest, changes that occur over time are structural rather than compositional. With respect to diameter structure, an unimodal regular diameter structure is often associated with young stands, whereas irregular and complex diameter structures are associated with mature stands (Smith et al., 1997; Boucher et al., 2003). Although this structural complexity has been recognized in the literature (Kuuluvainen et al., 1996; Franklin and Van Pelt, 2004), little attention has been given to the classification of stands with respect to their diameter structure. With the exception of Chaieb et al. (2015) and Moussaoui et al. (2016a) (who studied the structure of post-fire and post-harvest residual black spruce patches in the context of sustainable forest management), and Boucher et al. (2003) (who compared the diameter structure of eastern and western black spruce stands and characterized them into three classes i.e. regular, irregular and inverted J distribution structures), there is no such reference structural classification of black spruce stands permitting their identification.

Nevertheless, it has been proposed that in the Canadian boreal forest multi-cohort management could maintain structural diversity as well as respect the successional development that follows natural disturbances, which have been well described (Bergeron et al., 1999; Fenton et al., 2013). Paludification is a phenomenon that can via the accumulation of a thick organic layer transform a forest stand on mineral soil into a forested peatland (Payette and Rochefort, 2001; Fenton et al., 2009). In paludified black spruce forest, severity or depth of burn of the organic layer of the forest floor has significant consequences for forest structure and productivity (Lecomte et al., 2006a,b; Simard et al., 2007; Lafleur et al., 2016). High-severity fires that consume most of the organic layer promote the establishment of productive stands on mineral soil (Dyrness and Norum, 1983; Greene et al., 2005; Simard et al., 2007). In contrast, low-severity fires that leave the organic layer almost intact, stimulate the development of very thick organic layers that may develop into peatlands (Fenton et al., 2005; Simard et al., 2007). Following a high severity fire, a first structural cohort composed of trees of similar size (creating a closed stand with a regular or even-aged structure) establishes. When trees of the first cohort start to dieback and fall on the ground (gap dynamics according to Larson and Oliver (1996)), small-sized trees growing under the tree cover take over the canopy. This second structural cohort displays a wider stem diameter distribution. Tree mortality within this 2nd cohort leads to a loss of density and further opening of the stand (Bergeron et al., 1999; Fenton et al., 2013). A third cohort of trees originated mainly from layering then dominates the canopy and this cohort tends to show a classic inverse-J distribution (Bergeron and Harvey, 1997). In contrast, following a low severity fire, the residual post-fire thick organic layers (> 40 cm) over mineral soil (Fenton et al., 2005) limits establishment and growth of black spruce regeneration leading to less dense and less productive stands, i.e., stands with an irregular open structure (Lecomte et al., 2009).

It is generally suggested that the use of selection harvest approaches within partial harvesting could reproduce the structural complexity of these different types of structural cohorts and emulate natural gap dynamics typical of old-growth stands (Etheridge and Kayahara, 2013). To date there is no tool to identify these different structures in the field or their sequence along the natural chronosequence. In forest management, the structural issues have always been addressed in generic terms such as total density, basal area, and deadwood volume that give few indications on specific target structures to be reproduced. In this context, the ability of partial harvesting to reproduce forest habitat conditions favorable to maintaining biodiversity and structural complexity remains to be validated. If partial harvesting is to favor the conservation of old-growth forest structures, it is necessary to propose a user-friendly method to identify young, mature and old structures, and which can help forest managers to select stands to be harvested according to different objectives.

This study aims to propose a key to facilitate the identification of different diameter structures along a chronosequence in the boreal black spruce forest. Our objectives are to (1) conduct a classification of stand structural types encountered in natural boreal black spruce forests based on their diameter distribution, and (2) to validate this classification by establishing a link with time since the last fire and verify the spatial homogeneity of the structural classification at the stand level. In order to determine whether the differences among identified structural types were controlled by other explanatory variables, we also considered the influence of soil drainage, the importance of companion species such as white birch and trembling aspen, the presence or absence of balsam fir, and the density of black spruce saplings. Finally, an identification key for these structural types was developed. To achieve this, we used an extensive database of over two thousand forest inventory plots collected by the Quebec Ministry of Natural Resources (QMNR), and for time since fire data was available.

2. Methods

2.1. Forest inventory data and study area

Data were retrieved from the 400-m^2 forest inventory plots established by the QMNR between 1985 and 1997, for which time since last fire data was available from a fire map developed by Bergeron et al. (2004). They used the age of the trees established after the last fire or dating fire scars on surviving trees for fires that occurred prior to 1880 using historical record and aerial photographs (Belleau et al., 2012). In this study, we used 2100 400-m^2 plots of the forest inventory, which are located in the western section of the boreal forest of Quebec (Matagami Lowland), at the border between Quebec and Ontario (Bergeron et al., 2004). The study area (from 78°30′ to 79°30′ W and from 49°00′ to 50°00′ N) belongs to the black spruce-moss bioclimatic domain referred as coniferous region (Robitaille and Saucier, 1998) (Fig. 1).

The study area is dominated by black spruce in addition to companion species such as jack pine, trembling aspen, balsam fir and white birch. The climate is continental with cold winters and warm summers, and according to the nearest weather station (1981–2010), Lebel-Sur-Quévillon, Quebec, mean annual temperature is 1 °C and mean annual precipitation is 928 mm (Environment Canada, 2015). The topography of this area forms an undulating plain. In the northern part of the study area, the surficial deposit was affected during the last glaciation by late southward glacial surges that restructured the glaciolacustrine fine clay deposits; these soils are known as the Cochrane Till (Robitaille and Saucier, 1998). In this region, stand-replacing fires are the main drivers of natural forest dynamic. Since 1920, the fire cycle is estimated at over 400 years and average stand age is over 150 years (Bergeron et al., 2004). Nevertheless, in the last 30 years, the landscape mosaic is as likely to have been shaped by harvest as by fire (Bergeron et al., 1998; Imbeau et al., 2015).

The forest inventory plots were established along transects that generally extended from 500 to 1500 m in length; with each transect usually comprising between four and seven plots. Transect locations were selected using a stratified sampling design that aimed to characterize the different stand structures of the region. In each forest inventory plot, diameter at breast height (DBH) of all commercial stems of all trees (DBH ≥ 9 cm) and saplings (DBH < 9 cm) was measured, identified to species, and average height measured using a clinometer. Surficial deposit was also identified and then grouped into two types: well-drained soil (clay) and poorly drained soil (organic, Cochrane till). In well-drained soil, deposits show generally a moderate drainage where water infiltrates at a medium rate whereas poorly drained soils present a high sensitivity to paludification (Veillette and Thibaudeau, 2007).

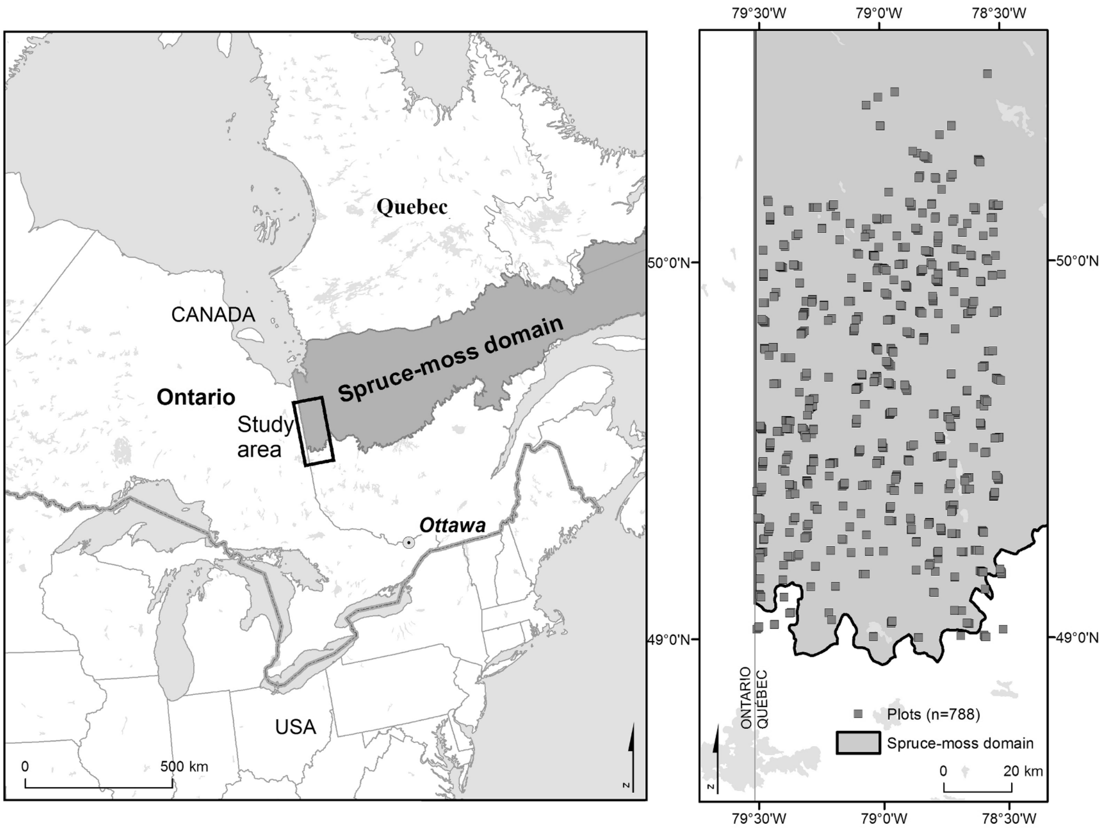

Fig. 1. Location of the study area in the spruce-moss bioclimatic domain. The forest inventory is located in the western section of the boreal forest of Quebec at the border between Quebec and Ontario. The gray dots represent the sampling sites.

For this study, only plots where black spruce basal area was > 75% of the total basal area and where total commercial volume was > 60 $m^3 ha^{-1}$ were selected to eliminate unproductive and very old stands (in Quebec, stands where volumes are lower than 60 $m^3 ha^{-1}$ are not harvested (Moussaoui et al., 2016b)). Thus, a total of 788 plots of the original 2100 forest inventory plots were considered in the analyses. For each plot, other structural characteristics were computed, i.e., percentage of basal area of intolerant companion species and balsam fir (a competitive species of black spruce species), sapling density (a characteristic of productive stands), and volume of merchantable trees (Table 1).

2.2. Stand structural diameter

A structural classification of the 788 forest plots was developed based on DBH class data, following a method proposed by Moussaoui et al. (2016a). More specifically, the method is as follows: (1) for each site, create from the DBH data, diameter classes of 2 cm, starting at 9.1 cm (10 cm class) and finishing at the class with the largest DBH (32 cm), in which living trees are distributed; (2) build a matrix containing the basal area ($m^2 h^{-1}$) and the density (number of trees ha^{-1}) of living trees per DBH class for each site; (3) transform the absolute matrices of tree density and basal area into inverse cumulative matrices for each DBH class. Trees were cumulated to reduce the number of zeros and to make diameter distributions insensible to the width of classes starting from the largest class to the smallest. In this study, the cumulative data was not transformed to a percentage (relative scale) in order to take into account, the variations in density and basal area.

Afterward, using the two inverse cumulative matrices of tree density and basal area, structural types were determined using a k-means clustering algorithm (Nock and Nielsen, 2006). K-means clustering is a heuristic technique used to minimize intra-class distance by partitioning observations into a limited number of classes (Nock and Nielsen, 2006; Borcard et al., 2011; Brock et al., 2011). The optimal number of clusters was evaluated following exploratory tests using the clValid function in R, a function that integrates three validation criteria, i.e. connectivity, width and Silhouette Dunn index, which measure, respectively, the connection, compactness and separation of different numbers of clusters. The classification was finally verified by visually comparing the diameter distributions of the different structural types identified.

Finally, in order to illustrate whether identified structural types differed or were influenced by other ancillary variables, a principal component analysis PCA was performed using the R package “vegan”. In the PCA, structural types (K-mean cluster groups) were overlaid on a sample scores plan generated by ancillary variables such as the proportion in basal area of black spruce, balsam fir, and companion species; total tree density (corresponding to cumulative basal area of all tree diameter classes); sapling density; time since last fire; and four cumulative diameter classes of basal area and density used in K-means analysis (Tables 1 and 2), i.e., D10: total tree density (trees/ha) corresponding to the cumulative density of all tree diameter classes; BA10: total stand basal area ($m^2 ha^{-1}$) corresponding to the cumulative basal area of all tree diameter classes; BA12: cumulative basal area of all diameter classes except for the smallest class ($m^2 ha^{-1}$; trees > 11 cm of diameter); BA14: cumulative basal area of all diameter classes except for two smallest classes ($m^2 ha^{-1}$; trees > 13 cm). PCA allowed us to visualize the proximity between the different structural types in the factorial spaces generated by ancillary variables and cumulative diameter classes used in cluster analysis.

2.3. Influence of TSF on structural changes

In order to examine the links between TSF (Time since last fire), which corresponds to the age of the forest, and the different structural types encountered in the natural unmanaged forests, we compared the frequency of structural types occurring in each TSF class, which are C1: < 100 years since last fire, C2: 100–150, C3: 150–200, C4: 200–250 and C5: > =250 in a 5 age classes × n structural types contingency table. The relationship between the two categorical variables TSF classes and structural types was analyzed in R, with the Fisher-exact test (adapted to small theoretical values < 5). We tested the null hypothesis that each structural type could have any age, i.e., the diameter structure is independently distributed among the forest age classes. When the p-value was less than the critical p-value of 0.05, the null hypothesis was rejected, i.e., TSF classes by structural types tables of frequencies shows heterogeneity. Then, to determine where the TSF classes and stand structural types were associated, we calculate the deviate. Deviate is the relative difference between observed (O) and expected (E) frequencies reported on expected value (E) (Legendre and Legendre, 1998).

Deviate = (O−E)/E.

A positive value of deviate indicates an overrepresented in a particular structural type in a specific TSF class. In contrast, a negative value of deviate indicates that a structural class is underrepresented in an age class. It is usually recommended to give ecological significance only to contingency cases having more than 5 observations since deviate is very sensitive to weak observed frequency situations (Legendre and Legendre, 1998). Hence, positive values are usually more interpretative than negative ones.

Finally, to determine whether soil drainage type influenced the link between TSF and structural type, two others deviate tables were elaborated for each surficial deposit type, i.e. poorly and well-drained soil.

2.4. An operational identification key for stand structures

To elaborate an operational identification key for stand structures, a multivariate regression tree was used (De'Ath, 2002; Larsen and Speckman, 2004) on the same data set used by K-means clustering analysis. This method allows the analysis of all structural types (response variables) along multiple explanatory variables within one model or tree. This analysis is a type of repeated regression analysis where the data are recursively partitioned to maximize the homogeneity within the resulting groups using different levels of the explanatory variables. In the single node at the top of the tree, all the data set are represented by the most influential variable. Then the tree is grown by repeated binary splitting of the data set of the preceding node. Each split is defined by a simple rule, usually based on a single explanatory variable cut off, and forms two nodes.

In order to validate the tree, we use the “printcp” and “plotcp” functions in R, where ‘cp’ stands for complexity parameter of the tree. The syntax: printcp is a function that provides the optimal pruning based on the cp value. We pruned the tree to avoid any overfitting of the data or the risk of falling on a non-optimal solution. The convention was to have a small regression tree and the one with least cross validated error given by printcp function.

Explanatory variables considered were summarized in the Table 1.

2.5. Validation of the identification key for structural types and identification of structural types occurring at the stand scale

In order to validate the identification key elaborated in the preceding section, we compared the original classification given by the K-means clustering to the classification obtained with the regression tree. A confusion table comparing both classifications was developed. This confusion table calculates an error rate by structural type and identifies in which structural type confusions occur. An error rate by structural stand type was calculated as the difference between 1 (100% overall success) and the success rate (the number of sites well classified over the total number of the sites).

In order to show the spatial homogeneity of structural types at the stand level, we characterized, according to the identification key, the

Table 1

Summary statistics for each structural stand type (T1–T8). Number outside bracket is mean variable and numbers inside bracket are, respectively, the observed 1st and 3rd quartiles. EPN: proportion in basal area *of P. mariana* (%); PPS: the proportion in basal area of companion species (%); SAB: proportion in basal area of *A. balsamea* (%); D10: total tree density (trees/ha) corresponding to the cumulative density of all tree diameter classes; SD: sapling density (saplings/ha); TSF: time since last fire (years); BA10: total stand basal area ($m^2 ha^{-1}$) corresponding to the cumulative basal area of all tree diameter classes; BA12: cumulative basal area of all diameter classes except for the smallest class ($m^2 ha^{-1}$; trees > 11 cm of diameter); BA14: cumulative basal area of all diameter classes except for two smallest classes ($m^2 ha^{-1}$; trees > 13 cm); VOL: total tree volume ($m^3 ha^{-1}$).

Variable	Structural stand type							
	T1 (n = 89)	T2 (n = 115)	T3 (n = 89)	T4 (n = 124)	T5 (n = 154)	T6 (n = 57)	T7 (n = 67)	T8 (n = 93)
EPN	95.8 (93.6, 100)	95.3 (93, 100)	83.8 (75.5, 97.2)	94.8 (93.1, 100)	96.7 (96.5, 100)	95.2 (92.1, 99.8)	95.2 (92.6, 99.9)	92.4 (87.7, 98.6)
PPS	3.7 (0, 3.5)	2.8 (0, 2.7)	6.7 (0, 9.9)	2.5 (0, 3)	2.2 (0, 1.3)	4.2 (0, 6.2)	3.5 (0, 5.3)	3.2 (0, 4.6)
SAB	0.5 (0, 0)	1.8 (0, 1.5)	9.5 (0, 19.8)	2.6 (0, 1.8)	1 (0, 0.3)	0.5 (0, 0)	1.3 (0, 0.6)	4.3 (0, 7.2)
D10	1984 (1825, 2125)	1396 (1250, 1538)	554.8 (450, 675)	947.4 (850, 1031)	1354 (1250, 1450)	2172 (1975, 2375)	1514 (1400, 1650)	990.9 (875, 1100)
SD	3430 (1750, 4500)	1576 (750, 2250)	1419 (250, 1750)	2482 (1438, 3500)	3101 (2000, 3750)	1175 (500, 1500)	526.1 (0, 750)	1132 (500, 1750)
TSF	133.3 (80, 164)	163.3 (116, 212)	151.7 (112, 189)	167.1 (112, 212)	165 (112, 212)	112.6 (69, 162)	132.3 (80, 162)	159.1 (112, 212)
BA10	23.7 (21.9, 25.2)	22.7 (20.9, 24.6)	14.6 (12.2, 17)	15.4 (13.7, 16.8)	17.1 (16, 18.3)	32.5 (29.5, 34.4)	32.5 (28.8, 35)	23.5 (21, 25.5)
BA12	17.6 (15, 20.2)	20.5 (18.5, 22.3)	14.1 (13.2, 19.6)	13.6 (11.8, 15.2)	13.2 (12, 15)	28.9 (26, 30.4)	31.3 (27.6, 34.1)	22.6 (19.9, 24.7)
BA14	10.5 (7.4, 13.4)	16.8 (14.5, 18.9)	13.3 (10.7, 16.1)	11.2 (9.3, 13.1)	8.7 (7.1, 10.5)	22.5 (19, 25.2)	28.9 (25, 31.6)	21.3 (18.5, 23.5)
VOL	105.2 (87.6, 117.9)	122.8 (89.8, 134.6)	106.4 (79.9, 127.1)	84.5 (70.1, 94.3)	76.1 (66.8, 84.1)	172.2 (147.4, 192.8)	207.8 (171.2, 237.6)	157.1 (135.5, 168.7)

Table 2
Factor loadings for structural factors produced by PCA in 788 sites. Elements in bold indicate with which factors the first and the second principal components (PC 1, PC2) are strongly correlated.

Factors	PC 1	PC 2
Cumulative diameter classes of basal area trees:BA10	0.720777	0.633998
BA14	**0.932622**	0.257695
BA18	0.907669	−0.10262
BA22	0.783764	−0.31128
Volume of merchantable trees	**0.949972**	0.243142
Proportion of *P. mariana* basal area	−0.31261	0.783184
Proportion of companion species basal area	0.238166	−0.41161
Proportion of *A. balsamea* basal area	0.203172	**−0.69336**
Total tree Density	−0.01275	**0.801615**
Sapling density	**−0.62767**	0.181737
Time since last fire	−0.20289	−0.08311
Percentage variance explained	39.64%	23.48%

diameter structure of several 400-m^2 plots grouped in four 50 ha forest blocks (experimental sites) located in the black spruce forest. These uncut forest blocks were preserved in 1998 in order to evaluate over both the short and medium terms the effects of partial harvesting on biodiversity and its potential as a silvicultural treatment in managed boreal black spruce forest. The data set is comprised of 52 control plots of 400-m^2 black spruce basal area > 75% and where total commercial volume was > 60 m^3 ha^{-1}, and distributed over four experimental sites, i.e. 12 plots in Cramolet (CRA, 155 years TSF), 14 in Fenelon (FEN, TSF = 183 years), 11 in Gaudet (GAU, 283 years since last fire), and 15 in Puiseau (PUI, TSF = 183 years). In order to illustrate their structural similarity, these control plots have been positioned in the two-dimensional factorial space of the PCA developed in Section 2. As forest blocks size is 50 ha, the distribution of these structural types among the plots makes it possible to verify the homogeneity of the stands at the block level.

3. Results

3.1. Stand structural classification and differences among forest structural types

K-means analysis classified the 788 black spruce plots into eight structural types (Table 1). Average absolute basal area and stem density by DBH class of these structural types are presented in Fig. 2. Types 1 and 5 had an inverted-J structure dominated by small DBH classes varying between 9.1 and 14.0 cm. Types 2 and 6 had a truncated unimodal structure with regular diameter structures, dominated by trees of small and intermediate DBH classes (10–18 cm). Types 3 and 4 had an irregular structure, with a wide range of diameters. Finally, types 7 and 8 had a bell-shaped structure, dominated by trees of intermediate and relatively large DBH classes.

The variation in the density of saplings per hectare among the eight structural types is illustrated in the Fig. 3. Types 1, 4 and 5 had more saplings (DBH < 9 cm) than other structural types. They had respectively, 3430, 2482, and 3101 saplings/ha. Type 7 seemed to have a lower sapling density, while types 2, 3, 6 and 8 were characterized by an intermediate sapling density.

The first and the second axes derived from the PCA of the 11 structural factors accounted for 39.64 and 23.48% of the variation in the data, respectively (Table 2). The first principal component (PC 1) was strongly and positively correlated with merchantable volume, and negatively correlated with sapling density. The second principal component (PC 2) was positively correlated with tree density, and negatively correlated with percentage of stand basal area occupied by balsam fir. PCA showed that although the extent of the structural types overlaps, they occupy distinct portions of the ordination plan (Fig. 4). The plots in the structural types 3 and 4 had low tree volume and density, whereas those of type 5 had low tree volume and intermediate density. Plots in the structural types 7 and 8 were characterized by intermediate tree density and volume. Type 1 stands had high tree density with low tree volume and 6 stands had high tree density with high tree volume. Stands in the type 2 were, generally intermediate in terms of trees density and volume.

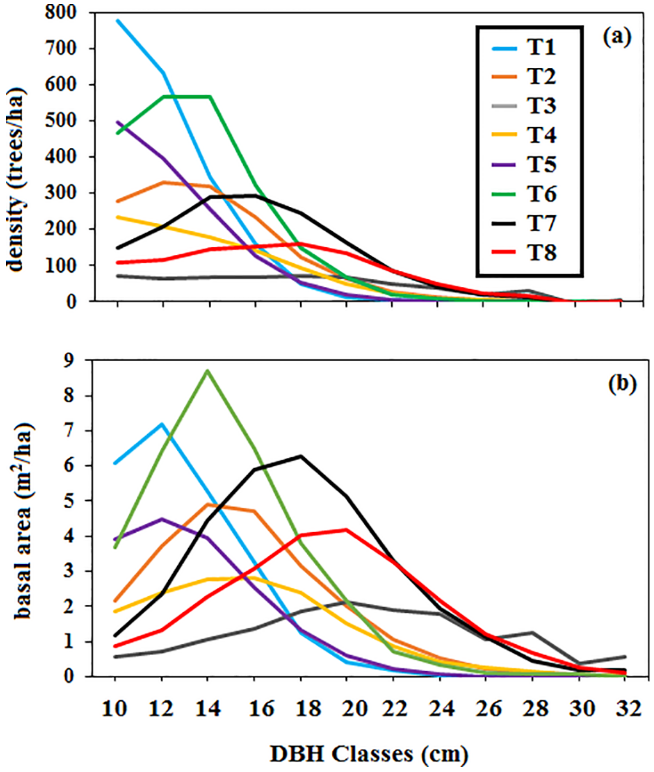

Fig. 2. Representation of the eight structural types (T1–T8) present in natural black spruce forest stands (k-means structural types) with the distribution of the average tree (a) density and (b) basal area plotted by DBH class. T: Structural type.

3.2. Time since last fire influence on structure

The analyses of the relationship between stand structural types (T1, T2, T3, T4, T5, T6, T7, T8) and the time since last fire TSF (i.e. C1, C2, C3, C4, C5) showed that TSF classes and structural types were associated (Fisher's exact test, p-value = 0.0005; Fig. 5). Individual

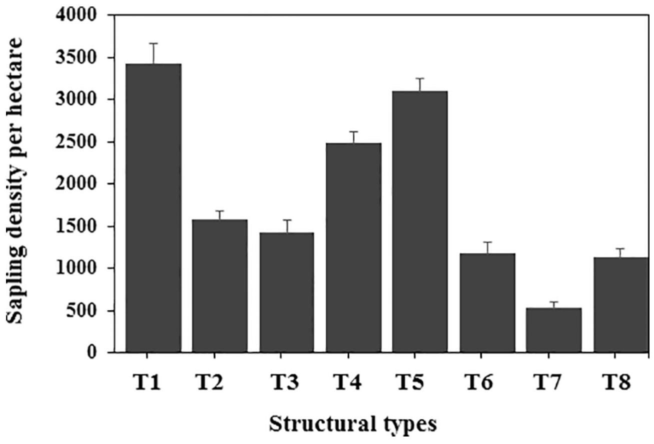

Fig. 3. Bar charts showing the density of the saplings per structural stand types (T1–T8). T: Structural type.

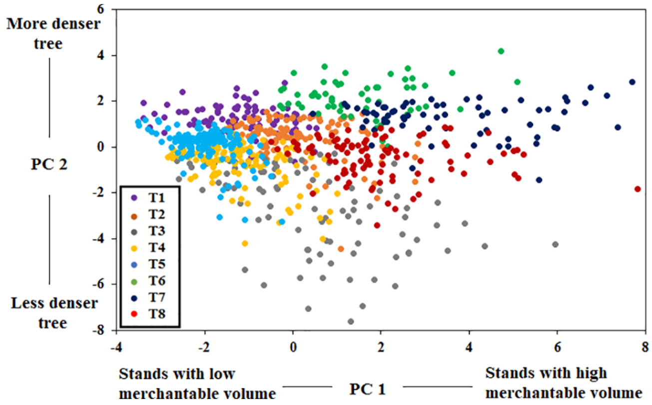

Fig. 4. Two-dimensional scatter diagram of the principal components analysis PCA of eight structural types (T1–T8) from 788 study black spruce forest stands. T: Structural type. PC 1 and PC 2 explained, respectively, 39.64% and 23.48% of the percentage variance. See Table 2 for factor loadings for different factors produced by PCA in 788 sites.

structural types were significantly associated with TSF classes. Structural type 1 was more frequent (46%) in younger stands (C1, TSF $<$ 100 years), whereas structural types 4 and 5 were more abundant in older than 200 years (C4 and C5). Structural types 8 and 2 were more common in mature and old stands (C3 and C4). Structural types 6 and 7 were absent form the oldest stands ($>$ 250 years; C5), but were generally associated to young (TSF $<$ 100 years; C1) or mature (150 $>$ TSF $>$ 200 years; C3) stands. Finally, structural type 3 was showed no association with forest age class. There seems to be a structural stand evolution with time since last fire in the black spruce boreal forest stands which can be ordered, from youngest to oldest as follows: type 1 and 6, followed by types 7, and 8 or 2, and finally by types 5 and 4 (Fig. 5a).

When considering soil drainage, on well-drained soils (clay deposit), structural types 6, 7 and 8 were associated to young (TSF $<$ 100 years) or intermediate stands (from 100 to 150 years TSF), while structural types 2, 4 and 5 were more common in old stands (from 200 to 250 years TSF). In contrast, on poorly drained soils (mostly Cochrane till deposit), the structural stands T6, T7 and T8 persist longer after the last fire (C2, C3) and the structural stands T3, T4 and T5 occur later (TSF $>$ 250 years; Fig. 5c). Usually one age class (50 years) in structural maturation time distinguishes between poorly and well-drained soil (Fig. 5b and c).

3.3. Classification key for management practices in boreal forests

The proposed operational identification key for stand structure elaborated by a multivariate regression tree approach is presented in Fig. 6. The regression tree used a combination of basal area and tree density of the cumulated diameter classes to partition the data into homogeneous groups (Fig. 6). From top to bottom of the tree, the first node (a) separates the plots based on BA10 ($20\,\mathrm{m}^2\,\mathrm{h}^{-1}$), which corresponds to the total basal area per hectare and a cumulative basal area of all tree diameter classes. The single split at the top (a) splits between open, i.e., BA10 $<$ $20\,\mathrm{m}^2\,\mathrm{h}^{-1}$ (47%; types 3, 4 and 5) and closed, i.e., BA10 $>$ $20\,\mathrm{m}^2\,\mathrm{h}^{-1}$ (53%; types 1–2 and 6, 7–8) stands.

In open stands (BA10 $<$ $20\,\mathrm{m}^2\,\mathrm{h}^{-1}$), the first node (b) separates the plots based on total tree density. In the first case, i.e., when total tree density (D10) $> =$1138 trees ha^{-1}, $<$ open stands have a type 5 structure (20% of the plots). In the second case (i.e. tree density $< =$1138 trees ha^{-1}), node c separates structural types 4 (16% of the plots) and 3 (11% of the plots) (Fig. 6).

In the closed stands (BA10 $> =$ $20\,\mathrm{m}^2\,\mathrm{h}^{-1}$), the first node (d) also separates the plots according to total density. In dense stands (i.e. D10 $> =$ 1662 trees ha^{-1}), node e separates closed (type 6) and less closed stands (structural type 1) by BA12, corresponding to the basal area of all the stems except the small stems (9.1 $<$ DBH $<$ 11 cm). In the second case (i.e., D10 $<$ 1662 trees ha^{-1}), the node f divided the stands again in terms of tree density to structural type 8, i.e. stands having $<$ 1212 trees ha^{-1} (13%). When the D10 is between 1212 and 1662 stems per hectare, the node g separates stands to those of type 2 (14%) if BA12 $>$ $26\,\mathrm{m}^2\,\mathrm{h}^{-1}$, and type 7 (6%) if BA12 $< =$ $26\,\mathrm{m}^2\,\mathrm{h}^{-1}$ (Fig. 6).

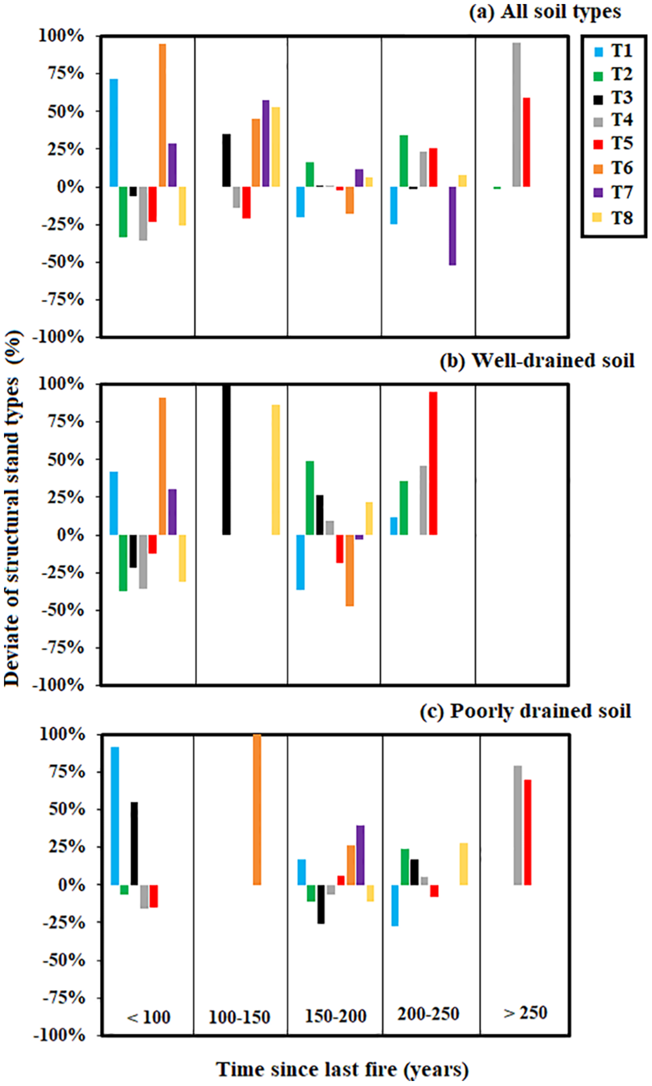

Fig. 5. Clustered column representing the proportion of structural stand types ordered in time (T1–T8) in each TSF class: (a) in all soil types; (b) in well-drained soil; (c) in poorly drained soil. T: Structural type. When there are fewer than five observations by structural stand type, the deviate is not represented in these figures.

The confusion table comparing both classification given by K-means with that obtained by the regression tree shows that the suggested identification key can distinguish the eight structural stand types given by K-means with an overall success of 88.7% (Table 3). Error rate (1 – success rate) by structural type appears relatively low except for type 7, which can be confused with type 6 (Table 3).

3.4. Validation of the identification key: identification of the structural types at plot and stand scales

Using the identification-key, the structural classification of the 52 control plots of the partial harvesting network (Fig. 7a, b) located in the black spruce forest in northwestern Quebec, showed that these plots

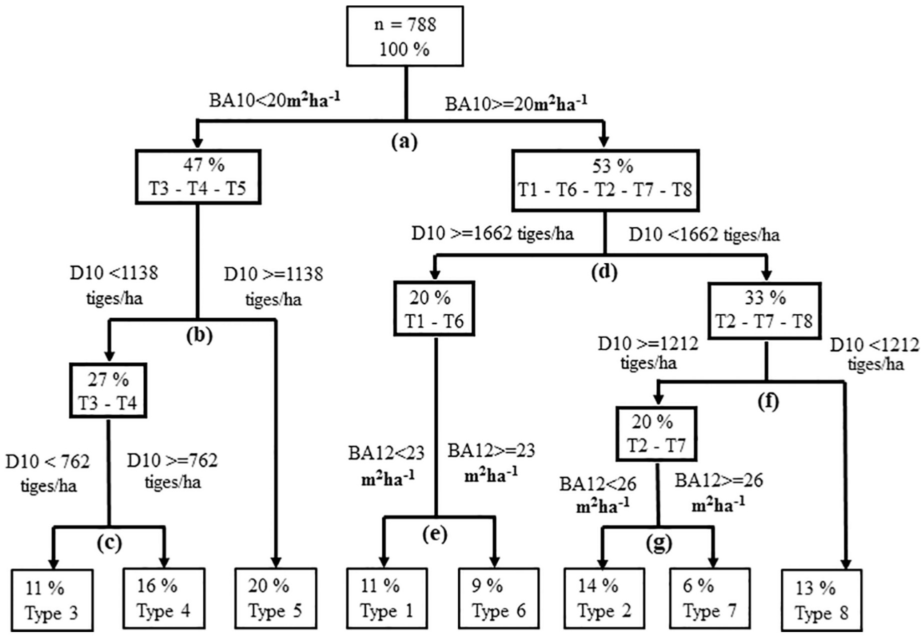

Fig. 6. Regression tree showing the proposed identification key of the structure of forest stands in black spruce boreal forest according to explanatory variables (For acronyms see Table 1). The percentages in the boxes present the proportion of plots classified by the regression tree. The structural type in last boxes corresponding to the dominant forest structural types classified by kmeans. The Table 3 presents all structural types combined with their frequency. The letters a, b, c, d, e, f and g identify each of the nodes.

were generally classified in structural types 4 (n = 9), 5 (n = 10), 7 (n = 5) and 8 (n = 9), which are typical of older stands (T4 and T5) or stands of intermediate age (T7 and T8). At the plot scale (400 m^2) we found a great deal of structural variability (Fig. 7b). At the level of the experimental site (GAU, FEN, CRA and PUI) although the extent of the sites may seem great, they still occupy different portions of the ordination which is in accord with their age (Fig. 7a, b; Table 4). Cramolet was the youngest site (TSF = 155 years) and had a structure characteristic of young stands (types 6 and 7), and lacked mature and older stands (types 4 and 5). The three other sites were older (TSF > = 183 years) and were dominated by types 4 and 5. At the plot scale (400 m^2), although Gaudet was the oldest site (TSF = 283), it nonetheless featured some structures of type 1 stands (TSF < 100 years; Fig. 7a, b).

4. Discussion

This study shows that stand structure in black spruce forests is varied and is mainly controlled by the time since last fire. It also shows that the time of stand structural maturation vary depending on surficial deposit. In this study, we propose an identification key to discriminate among young, mature and old structures, which can help forest managers to select stands to be harvested according to different objectives.

4.1. Successional pathways: structural and temporal proximities along structural stand types

Our structural classification approach, based on tree size distribution, suggested that there are eight distinct structural types characterizing black spruce forest stands. The analysis of the structural proximity along these eight structural stand types indicates that high density stands dominated by small trees and showing a trunked-unimodal structure are grouped within the type 1. Stands with unimodal and regular diameter structure, characterized by a high tree density and basal area and an occurrence of large stems are found in both structural types 6 and 7. As suggested by Moussaoui et al. (2016a), the gradual recruitment of large stems suggests a structural evolution in this study from structural type 1 to 6, and then 7 (according to the tree size distribution in Fig. 2b). In comparison, stands having a flattened unimodal diameter structure (intermediate tree size) with a lower basal area are grouped into types 3 and 8. Finally, open stands with relatively irregular structure are represented by structural types 2, 4 and 5. These stands are characterized by a lower density of large stems with an increased importance of small stems (saplings). Knowing that the recruitment of large deadwood is one of the particularities of old-growth forests (Moussaoui et al., 2016b), this loss of large stems density accompanied by the recruitment of saplings, especially observed in both structural types 4 and 5, suggests that stands of these structures are

Table 3
The proportion (%) of the different structural stand types classified by the regression tree in the inside of the eight structural types classified by K-means with an overall success of 88. 7%. The total numbers are inside bracket.

Regression tree classification	The eight structural types classified by K-means							
	T1	T2	T3	T4	T5	T6	T7	T8
Key-T1	**93.3**	1.7	0	0	0	0	0	0
Key-T2	0	**79.1**	0	0	1.3	0	4.5	3.2
Key-T3	0	0.0	**89.9**	4.0	0.0	0	0.0	0.0
Key-T4	0	5.2	3.4	**91.9**	1.9	0	0.0	10.8
Key-T5	5.6	7.8	0	3.2	**96.8**	0	0.0	0.0
Key-T6	1.1	1	0	0	0	**100**	**22.4**	0.0
Key-T7	0	0	0	0	0	0	**68.7**	1.1
Key-T8	0	5.2	6.7	0.8	0	0	4.5	**84.9**
Total (N = 788)	100 (89)	100 (115)	100 (89)	100 (124)	100 (154)	100 (57)	100 (67)	100 (93)

Elements in bold indicate with which structural types classified by K-means and regression tree classification arestrongly correlated.

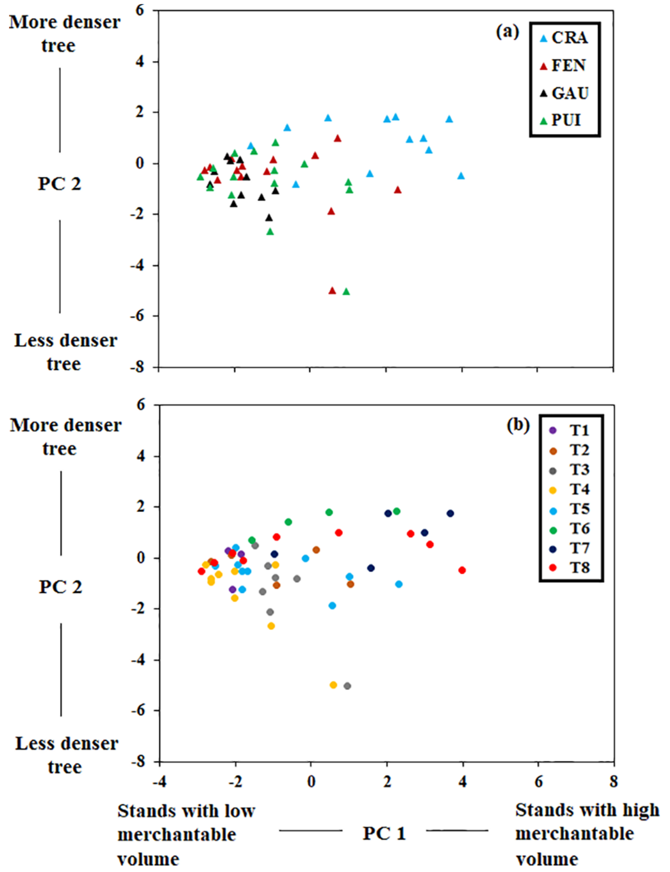

Fig. 7. The position of 52 control sites in the two-dimensional scatter diagram of the principal components analysis PCA, presented in: (a) by the names of the four experimental partial sections; (b) by their structural types (T1–T8). PC 1 and PC 2 explained, respectively, 39.64% and 23.48% of the percentage variance. CRA: Cramolet (155 years); FEN: Fenelon (183 years); GAU: Gaudet (283 years); PUI: Puiseau (183 years).

Table 4
The proportion (%) of the different structural stand types classified by the regression tree within experimental partial harvesting sites. The total numbers are inside bracket. Elements in bold indicate that the proportion of the structural stand type is important.

Structural stand types	CRA (155 yrs)	FEN (183 yrs)	PUI (183 yrs)	GAU (283 yrs)	Total
T1	0	0	6.7 (1)	18.2 (2)	5.8
T2	0	14.3 (2)	6.7 (1)	18.2 (2)	9.6
T3	8.3 (1)	7.1 (1)	20 (3)	18.2 (2)	13.5
T4	0	**21.4 (3)**	**26.7 (4)**	18.2 (2)	17.3
T5	0	**28.6 (4)**	**20 (3)**	**27.3 (3)**	19.2
T6	**33.3 (4)**	0	0	0	7.7
T7	**33.3 (4)**	7.1 (1)	0	0	9.6
T8	25 (3)	21.4 (3)	20 (3)	0	17.3
Total	100 (12)	100 (14)	100 (15)	100 (11)	100 (52)

typical of the later portion of the chronosequence.

The analysis of age class deviate indicates an overrepresentation of structural types within certain age classes, and, confirms the temporal sequence of the structural type evolution. Fig. 8 illustrates schematically this sequence and proposes two successional pathways depending on tree density at establishment. Specifically, depending on the age class, i.e., time since last fire, our results suggest that probably after a severe fire, the young forest stands develop a high density of small stems (type 1; 50–100 years age class) as reported by several studies in the same region (Boudreault et al., 2002; Harper et al., 2002; Lecomte and Bergeron, 2005). Then, types 6 and 7 stands are overrepresented in the 50–100 and 100–150 age classes, a period during which these stands develop important merchantable volume without losing too much density. As forests age, stand volume starts to decline thus opening the canopy which begins ca. 150 years after last fire probably because of a phase of large-tree collapse (Chen and Popadiouk, 2002). It results in forest stands having an irregular structure with a wide range of diameters, i.e., stems from the first cohort and small stems grown under the canopy of the 2nd cohort. Later, around 200–250 years since fire, the loss of large stems from the 1st and 2nd cohorts, is accentuated, stands open up, permitting the recruitment of small stems (Types 4 and 5). This supports previous studies suggesting that structural maturity depends on the time since last fire (Groot and Horton, 1994; Smith et al., 1997; Boucher et al., 2006; Brassard and Chen, 2006; Taylor and Chen, 2011; Moussaoui et al., 2016a). Initially, the young forest stands develop an important merchantable volume until stand break-up, and then, as trees senesce, this volume will decrease to produce an uneven stand structure (Smyth et al., 2005; Brassard et al., 2008).

However, the conceptual successional pathways that include dense and high-tree volume structural types with (i.e., types 1, 6, 7 and 8) cannot be used to describe structural succession following low severity fires that, usually, generates low density stands (Lecomte et al., 2005, 2006b). In this case, we suggest another structural maturation sequence which only uses structural types having low tree density, i.e., types 2, 4, and 5 (Fig. 8), because following a low severity fire, the post-fire thick organic layers over mineral soil (Fenton et al., 2005) limits the establishment and growth of black spruce regeneration leading to less dense and less productive stands (Lecomte et al., 2009). As a sequence occurring after a low severity fire, we suggest a sequence that originates at type 2 to type 4 via type 5 (Fig. 8). The structural type 3 appears to occur very early between 100 and 150 years since last fire, but, its low tree density compared to the other structural types, places it in the margin of all chronosequence. Therefore, this structural type would likely occur immediately after fire and to remain over time, as suggested by the absence of negative deviate for stands > 200 years-old.

Moreover, although the oldest forests are associated with structural type 4 and 5, their diameter structure is similar to that of the young forests of type 1. While stands with high volume are generally those that contain the lowest density of saplings, old forest stands (types 4 and 5) are characterized, by a relatively important density of saplings. This suggests recruitment following the opening up of the stand leading to cohort 3. The PCA ordination shows that structural type 5 characterizing the old forest stands are similar to that of type 1 typical of young stands. While these two types, 5 and 1, of different age occupy similar positions in the PCA, our identification key indicates that it should be possible to distinguish between stands of structural types 5 and 1 using tree density and basal area. Indeed, forest stand structures can be identified by only referring to two criteria, i.e. total basal area and tree density, which are easily assessed in the field. Like young forests, old forests have low timber volume because of the loss of their larges stems, changes that globally can be associated with secondary disturbances (gap dynamics or senescence) (Kneeshaw and Bergeron, 1998; Grandpré et al., 2000; McCarthy, 2001) or windthrow (Ruel, 2000), which favor the recruitment of small stems mainly by layering (in case of black spruce) (Lecomte et al., 2006b). It has recently been shown that the opening of the black spruce stand can also be due to a degradation of growth conditions rather than weak recruitment of saplings (St-Denis et al., 2010).

4.2. Robustness of structural classification at the forest stand level

The spatial heterogeneity analysis of structural type at the scale of 50 ha blocks shows a good coherence with the age of the blocks. The Fenelon and Puiseau sites are between 150 and 200 years old and are dominated by cohort 3 stands (i.e. types 4 and 5), and co-dominated by cohort 2 stands (i.e. type 2 and 8). At 283 years old, the Gaudet site is mostly dominated by cohort 3 stands, stands of the second cohort being

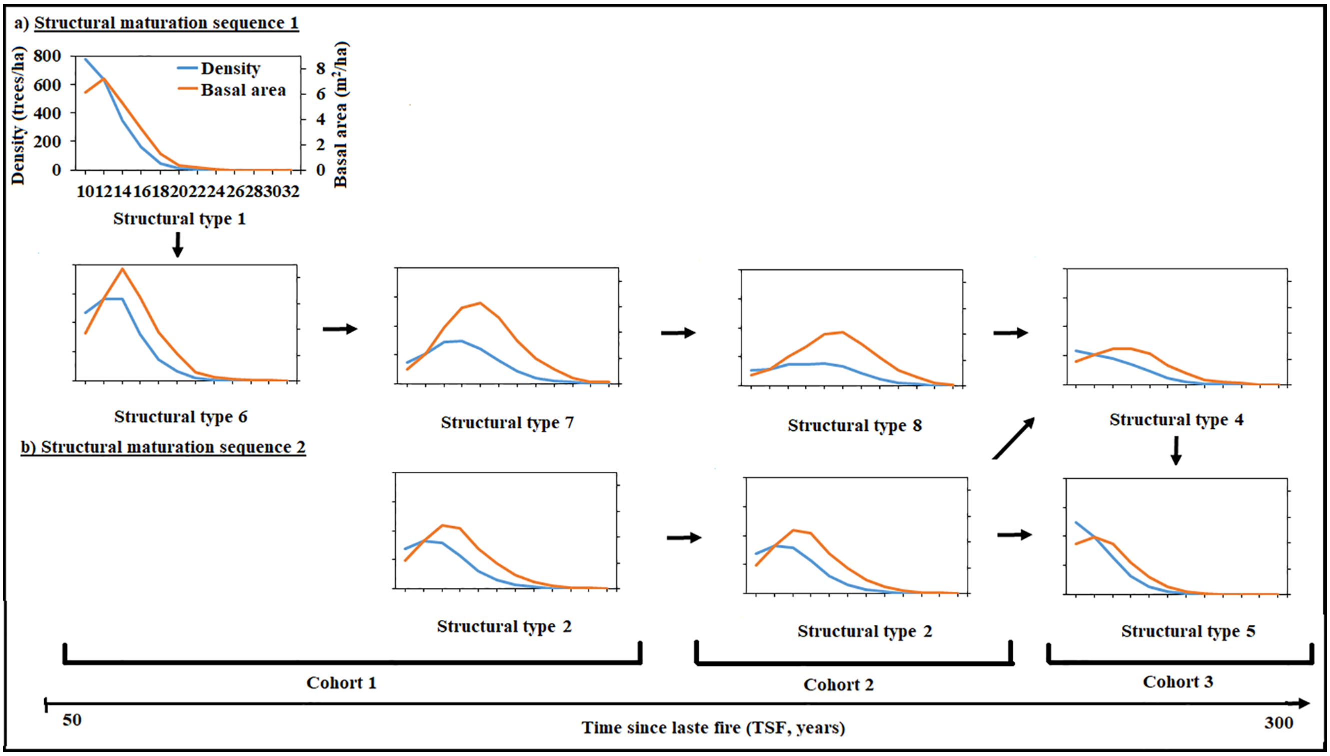

Fig. 8. Two successional pathways (temporal sequence of structural types evolution) proposed by this study according to the tree establishment density.

virtually absent. On the other hand, the Cramolet site is ca. 155 years old and includes no stands belonging to cohort 3, and is dominated by structural types 6 and 7, which are characteristic of cohort 1. However, even if stand structural variety is consistent with the age of forest stands, it is nonetheless variable at the 50 ha block scale. For example, it is noted that structural type 3 characterizing open stands can be observed in all blocks. Although 400 m^2 inventory plots are considered large enough to estimate the stand volume in the black spruce forest (as suggested by Boucher et al. (2003)), the probability that the inventory plot is unable to sample large stems is relatively high, especially when the stand is not very dense. However, since the forest inventory used in this study was based on at least five plots per 50 ha, the structural variety observed at the 50 ha block scale may be due to other site characteristics such as site productivity or secondary disturbances occurring at smaller spatial scales (Boucher et al., 2006; Moussaoui et al., 2016a).

4.3. Influence of surficial deposit on the structural maturation rate

The comparison of age-class deviate profiles between well and poorly drained sites suggests a shift (distinguish peak of abundance of a specific structural type on well-drained vs poorly drained soils) of one age class, approximately of 50 years in structural maturation time. This shift is particularly observed in stands within structural types 6, 7 and 8, for which maximum positive deviates occur later on poorly drained soils (from 150 to 200 or 200–250 years since last fire). On well-drained soils, closed stands (types 6, 7 and 8) persist less, and open stands (types 3, 4 and 5) appear earlier. In contrast, on poorly drained soils, closed stands persist for a longer time, whereas open stands appear later since fire. In fact, in addition to time since fire, site productivity has often been cited as an important factor influencing the structural maturation of the coniferous boreal forest (Harper et al., 2005; Simard et al., 2007, 2009; Brassard et al., 2008; Laamrani et al., 2014) or, as a process that drives the post-fire successional pathways dynamics (Harper et al., 2002; Fenton et al., 2005; Lecomte and Bergeron, 2005; Fenton and Bergeron, 2006; Belleau et al., 2012).

In boreal forests, one of the natural causes of loss of forest productivity is paludification. It is a phenomenon that transforms a forest stand on mineral soil into a forest peatland via the accumulation of organic layer (Payette and Rochefort, 2001; Fenton et al., 2009). This gradual transformation over time leads to the deterioration of growth microsites at the tree scale, which leads to the loss of stand productivity (Lafleur et al., 2010). Moreover, since the opening of forest stands does not take place homogeneously at the landscape scale, paludification will not occur homogenously; some stands open faster than others. This supports the idea that due to the interaction with the site productivity (soil drainage), a higher growth rate in productive stands is likely to induce an accelerated transition to an irregular structure (Boucher et al., 2006). This suggests that successional paludification should occur faster because of the opening of stands on well-drained and clay-soils. Consequently, our results support the idea that the structural maturation sequence can proceed more or less quickly depending on the different surficial deposit types (Belleau et al., 2012).

4.4. Limitations of the identification key application and guidelines

Faced with increasing industrial pressure on boreal forests, there is a growing need for the development of novel forest management tools to help forest managers select stands to be harvested in accordance with their different objectives. Although we are convinced that the proposed key for field identification of forest diameter structure is a promising diagnostic tool, we acknowledge the potential limitations to its application and that these need to be considered and addressed. First, the identification key was developed using black spruce stands, and therefore it is intended to be used in forest landscapes dominated by black spruce stands. However, our structural classification approach permitting the development of an identification key of forest diameter structures could be used in others forest regions if additional structural types typical of these forest regions are explicitly considered; i.e., for example in some cases, compositional changes could influence forest structural dynamics. Second, although both time since fire (Payette, 1992; Hunter, 1993; Bergeron et al., 1998) and site productivity (Harper et al., 2005; Brassard et al., 2008; Simard et al., 2009;

Laamrani et al., 2014) have often been cited as important factors influencing the structural maturation of the coniferous boreal forest, there is a need to considered other factors, particularly windthrow and insects outbreaks (Harper et al., 2002; Boucher et al., 2006; Moussaoui et al., 2016a).

5. Conclusions and implications for forestry management

This study shows that in black spruce forests, stands can be divided into a few structural types easily recognizable in the field. The second and third cohort stands appear usually 150 years after fire, whereas in a Canadian managed boreal forest harvest rotation is relatively short at 70–100 years (Gauthier et al., 1996; Bergeron et al., 2002). In this context, we expect that only even-aged structural types 1 and 6 (with some stands of structural type 7) that are maintained in managed landscape. Therefore, the frequency of all other structural types, namely types 2, 3, 4, 5 and 8, are likely to decline with traditional forest management approaches. But, since structural types 2, 4 and 5 are fairly open, they may be partly spared because of their low economic value. Otherwise, intermediate forest stands having a relatively irregular structure (types 2 and 8) could completely disappear from managed landscapes due to their high economic value. According to our results (Fig. 5), these stands occur generally after 100 or even 150 years since fire. We therefore believe that it is these structural types of forests that are more threatened in the current management context, and that we should try to maintain them with partial harvesting in order to prevent them from disappearing from the managed landscape.

To retain a variety of natural black spruce forest structures in managed context, the identification key suggested in this study makes it possible to discriminate in the field structures typical of young, mature and old forests, and thus, facilitate their selection according to the different silvicultural objectives. However, through studies on partial harvesting have mainly addressed issues related to the conservation of biodiversity whereas few have addressed their silvicultural potential. In unpaludified stands adapted partial harvesting practices could allow for the creation of complex and uneven forest structures similar to those of natural forests. As several forest species are partially or totally dependent on the recruitment of snags and fallen deadwood, one of the particularities that could distinguish old-growth forests from unproductive stands (Moussaoui et al., 2016b), the old-growth decline is likely to influence both fauna and flora (Franklin et al., 1997; Drapeau et al., 2002). In this case, we believe only their integral preservation would make it possible to preserve these structural variety important to maintaining biodiversity (Hunter, 1990; Beese et al., 2003). On the other hand, in paludified forest stands, the development of silvicultural practices that recreate the complex structures typical of young stands seems necessary.

Thus, to retain a variety of natural black spruce forest structures in a managed context, the identification diagnostic key suggested in this study could help forest managers to select stands to be harvested according to their different objectives. However, the ability to maintain this structural diversity at the managed landscape scale remains to be demonstrated.

Acknowledgements

This work would not have been possible without the financial support of the Mitacs accelerate fellowship program. We think Annie Belleau and Dominique Boucher for their helpful comments. We are also grateful to Mélanie Desrochers for helping us with the Fig. 1 (map).

Appendix

See Table A1.

Table A1
La matrice de distance moyenne entre les clusters en termes de densité et de surface terrière à l'hectare.

	T1	T2	T3	T4	T5	T6	T7	T8
T1								
T2	1454.5							
T3	3151.7	2361.8						
T4	1935.9	**1371.0**	**1215.9**					
T5	**1142.4**	**1195.9**	2063.6	**929.3**				
T6	1885.4	1872.5	4206.5	3199.4	2985.8			
T7	2936.3	**1900.4**	3595.9	3269.6	3096.3	**2107.4**		
T8	2890.4	**1481.6**	1809.5	1525.4	2077.9	3119.0	**1806.3**	
T1								
T2	28.6							
T3	58.5	42.5						
T4	25.4	**25.9**	**34.0**					
T5	**14.0**	39.2	50.7	**16.7**				
T6	50.4	**27.8**	69.3	51.8	63.1			
T7	102.3	75.8	79.1	101.7	115.0	**52.1**		
T8	70.5	43.5	44.4	69.3	82.6	52.7	**35.8**	

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