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Source: *Journal of Vegetation Science*, Vol. 11, No. 6 (Dec., 2000), pp. 791-800  
Published by: Blackwell Publishing  
Stable URL: <http://www.jstor.org/stable/3236549>  
Accessed: 20/10/2009 07:27

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## Long-term post-fire changes in the northeastern boreal forest of Quebec

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**Abstract.** Natural dynamics in the boreal forest is influenced by disturbances. Fire recurrence affects community development and landscape diversity. Forest development was studied in the northeastern boreal forest of Quebec. The objective was to describe succession following fire and to assess the factors related to the changes in forest composition and structure. The study area is located in northeastern Quebec, 50 km north of Baie-Comeau. We used the forest inventory data gathered by the Ministère des Ressources naturelles du Québec (MRNQ). In circular plots of 400 m<sup>2</sup>, the diameter at breast height (DBH) of all stems of tree species greater than 10 cm were recorded and in 40 m<sup>2</sup> subplots, stems smaller than 10 cm were measured. A total of 380 plots were sampled in an area of 6000 km<sup>2</sup>. The fire history reconstruction was done based on historical maps, old aerial photographs and field sampling. A time-since-fire class, a deposit type, slope, slope aspect and altitude were attributed to each plot. Each plot was also described according to species richness and size structure characteristics. Traces of recent disturbance were also recorded in each plot. Changes in forest composition were described using ordination analyses (NMDS and CCA) and correlated with the explanatory variables. Two successional pathways were observed in the area and characterized by the early dominance of intolerant hardwood species or *Picea mariana*. With time elapsed since the last fire, composition converged towards either *Picea mariana*, *Abies balsamea* or a mixture of both species and the size structure of the coniferous dominated stands got more irregular. The environmental conditions varied between stands and explained part of the variability in composition. Their effect tended to decrease with increasing time elapsed since fire, as canopy composition was getting more similar. Gaps may be important to control forest dynamics in old successional communities.

**Keywords:** *Abies balsamea*; Disturbance; *Picea mariana*; Succession; Species replacement; Windthrow.

**Abbreviations:** CCA = Canonical Correspondence Analysis; NMDS = Non-metric Multidimensional Scaling.

### Introduction

It is widely recognized that disturbances are the driving ecological forces of ecosystems (Shugart et al. 1992; Pickett & White 1985; Bergeron et al. 1998). Fire is a major force that structures the vegetation mosaic in

the boreal forest (Pickett & White 1985; Heinselman 1981; White 1979) and landscape diversity, to some extent, reflects the disturbance regime of a particular region (Romme 1982; Romme & Knight 1982; Bergeron 1991; Gauthier et al. 1996; Johnson et al. 1998).

Studies in *Picea mariana* forest have shown that vegetation development after fire involves very few changes in species composition (Morneau & Payette 1989; Foster 1985; Cogbill 1985; Carleton & Maycock 1978; Dix & Swan 1971). This absence of successional changes is closely associated with a short fire recurrence, precluding major changes in forest composition (Johnson 1992). However, fire is not the only disturbance element influencing boreal forest dynamics. In boreal regions where fires are rare, gap dynamics control establishment, growth and mortality (Lässig & Mocalov 2000; Drobyshev 1999; Kneeshaw & Bergeron 1998). In the mixed-wood boreal zone, vegetation development involves species replacement in the canopy (Gauthier et al. 1996; Bergeron & Charron 1994; Bergeron & Dubuc 1989; Foster & King 1986). In some of these forests, gap dynamics has a significant impact on community development (Kneeshaw & Bergeron 1998).

The Quebec North Shore is a vast, forested region of the boreal *Picea mariana* domain (Rowe 1972). Although *P. mariana* is dominant in these forests, *Abies balsamea* is also frequently observed and can be dominant in some areas, particularly along a northeastern narrow band following the St. Lawrence River. Little is known about the disturbance regime characteristics of the area but climatic data and the high occurrence of *Abies balsamea* suggest that fire may not be a major element contributing to forest dynamics. Spruce budworm outbreaks have been recorded in the region (Blais 1983) and windthrow is also a common disturbance in the area.

The objective of this study was to describe the changes in species composition and structure following fire using a chronosequence approach and to assess some of the factors related to such changes. We hypothesized that species and individual replacement in the canopy can occur in this part of the boreal forest and that gaps are important elements controlling natural dynamics.

As the stands grow older and become increasingly dominated by coniferous species, their dynamics will be more controlled by disturbances other than fire, mainly spruce budworm outbreaks and windthrow. As a result of these disturbances and natural mortality, stands will develop an irregular size distribution characteristic of multi-cohort stands (Oliver & Larson 1996).

The interpretations of the results of a chronosequence have to consider that the differences in forest composition between sites may not be only related to time elapsed since last fire. Historical, environmental and physical factors specific to each site may confound temporal changes in species composition. However, chronosequence studies in the boreal forest have recently been supported by site history reconstruction studies (Bergeron 2000). Furthermore, preliminary results from the analysis of the changes in canopy composition in the Quebec North Shore region, with the use of old and recent aerial photographs, also support the idea that changes in canopy dominance do occur in the absence of fire for long periods of time.

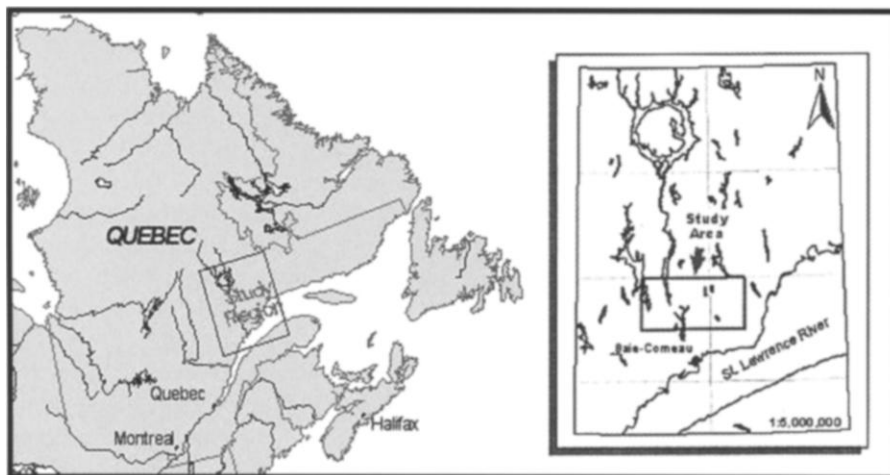
### Study area

The study was conducted in the Quebec North Shore region (49° 30' - 50° 00' N; 67° 30' - 69° 00' W) (Fig. 1). The study area covers 6000 km<sup>2</sup> and its topography is characterized by hills of moderate slopes (16 - 30%) with flat or rounded summits that can reach 500 to 700 m. Rocky outcrops occupy close to 40% of the area and are present on the summits, close to bodies of water and on steep slopes. Undifferentiated glacial till deposits constitute the majority of the remaining surficial deposits and are found on gentle slopes and in depressions. Glacial fluvial sand deposits occupy the bottom of large valleys (Robitaille & Saucier 1998).

The closest meteorological station is located in Baie-Comeau, 50 km south of the study area. The climate can be classified as cold and maritime with a mean annual temperature of 1.4 °C and a mean annual precipitation of 1018 mm where 70% of this total is rainfall (Anon. 1996). The region is located in the boreal forest and is part of the Chibougamau-Natashquan boreal region (Rowe 1972), which is dominated by *Picea mariana*. The study area overlaps two bioclimatic domains. The *Abies balsamea*-*Betula papyrifera* domain characterizes the southern part of the area whereas the northern section is part of the *Picea mariana*-moss bioclimatic domain (Thibault & Hotte 1985). Overall, *P. mariana* and *A. balsamea* are the dominant species in the area. According to Robitaille & Saucier (1998), *A. balsamea* is dominant on mesic sites in the south along with *B. papyrifera* and *Populus tremuloides*. *P. mariana* becomes more frequent as the latitude increases. *Pinus banksiana* is found on sandy soils.

### Disturbance history

With the use of historical documents, it was possible to reconstruct the recent fire history of the study area. Major fires (over 2500 ha) have been mapped by the MRNQ since 1941. The use of aerial photographs from 1930 allowed us to map some older fires. Some of these areas were then visited and trees were cored to confirm the passage and the year of the fire. Four major fires affected the area during the last 100 yr (1955, 1941, 1923 and 1896) (Fig. 2). For the remainder of the territory, it was not possible to precisely map the passage of a fire. However, with the use of existing data from the MRNQ and some field sampling it was possible to give a minimum time since fire for most of the territory (Fig. 2). The 1930 aerial photographs did not cover the western part of the study area, which explains the lack of information on this portion of the map.



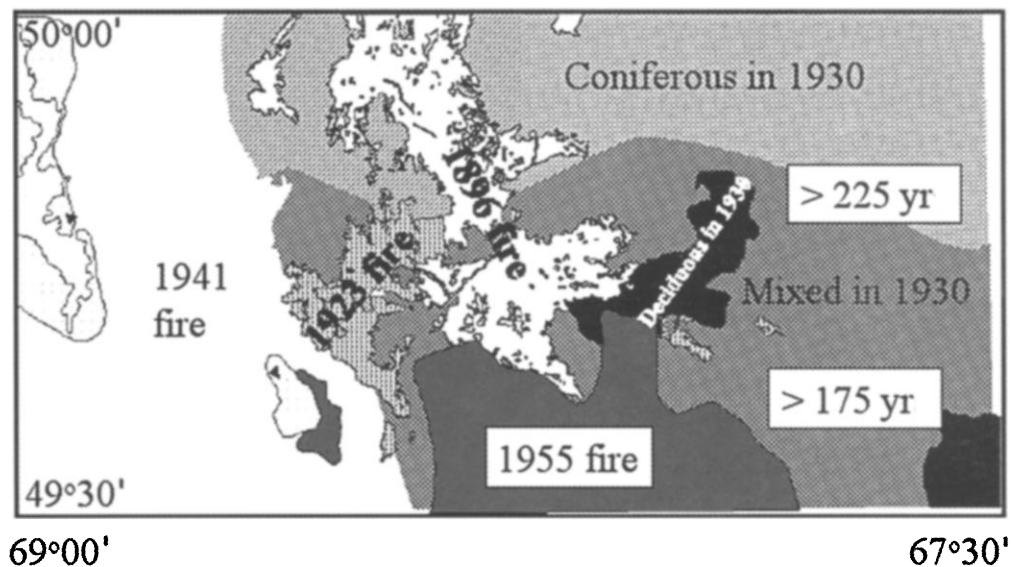
**Fig. 1.** Location of the study area in the Quebec North Shore region.

## Methods

The data used to describe the changes in forest composition through time elapsed since last fire were gathered by the MRNQ. Forest inventories are composed of data collected over the territory of Quebec. Since these plots are sampled for forestry purposes, the selected stands represented forests that could be harvested. For this reason, forest stands on slopes of more than 40% were not sampled. In the study area, 501 circular plots of 400 m<sup>2</sup> were sampled in 1988. The plots were sampled every 250 m along 1.5 km transects (five to seven plots per transect). In each 400 m<sup>2</sup>, the DBH of every tree of 10 cm and more was measured in 2-cm classes. Trees with a DBH less than 10 cm were measured in 2-cm classes in a subplot of 40 m<sup>2</sup> within the larger plot and sharing the same centre. In each plot, the height and age of three of the dominant trees were measured. A total of 380 plots were kept for further analyses as plots affected by logging were eliminated. For each plot, a surficial deposit type was attributed (rocky outcrop, tills on rock, tills and sand deposits) based on surficial deposit maps. With the use of a digital elevation model (DEM), altitude, slope and aspect were attributed to each plot. Any recent traces of disturbances that affected the stands were also noted (windthrow, spruce budworm outbreak or fire). Each plot was assigned a time-since-fire class (0 - 50 yr, 50 - 100 yr, > 175 yr and > 225 yr).

## Data analysis

For each species, four pseudo-species were created based on diameter classes (DBH measuring 1 - 5 cm, 5 - 10 cm, 10 - 15 cm and more than 15 cm). The basal area (m<sup>2</sup>/ha) in each diameter class was used to describe the species' importance in the stands. In order to evaluate the size structure of each stand, a simple index was computed. Two elements were considered in the size structure index. The number of DBH classes (2-cm classes) in each stand was divided by the total number of species, to obtain a measure of stand structure. This was done to reduce the effect of differential growth rates between species, which could have wrongly been interpreted as irregular size distributions. All these variables were used to interpret the changes in composition and structure. The Non-metric Multidimensional Scaling (NMDS) ordination method was used on the matrix of plots by species. This ordination technique was performed using the Sørensen distance measure and three axes. Additional axes did not provide more interpretable information. The ordination axes were then rotated to align axis 1 with strongest explanatory variables. Axes one and three are presented and discussed as they reflected most of the variability in species composition. The environmental variables were then correlated (Pearson correlation coefficients) with the ordination axes. Only the significant variables ( $p < 0.05$ ) are represented on the ordination diagram. Species were also



**Fig. 2.** Fire history map of the study area. Fires, which have occurred since 1896, were mapped precisely. The remaining part of the territory was given a minimal time since fire, based on field sampling in 1998 and with the use of the age of the trees sampled in each 400-m<sup>2</sup> plot by the MRNQ. Canopy cover has also been estimated based on the aerial photographs of 1930.

correlated to the ordination axes. The variables used in the correlation were: time elapsed since last fire, geographic location of each plot, surficial deposit type, elevation, slope, slope aspect, age of the oldest tree in each plot, presence and type of disturbance at the stand level, stand structure and species diversity.

As 'time elapsed since last fire' was the variable more strongly associated with the compositional gradient, separated ordinations were done on each of the time-since-fire classes (four time-since-fire classes: 0 - 50 yr, 50 - 100 yr, > 175 yr and > 225 yr). As NMDS did not allow us to eliminate the effect of covariables and to use nominal variables, partial Canonical Correspondence Analyses (CCA) were computed on the plots by species matrices (four analyses, one for each time-since-fire class). All of the analyses were constrained by the geographical location of each plot. Since *Pinus banksiana* was not present in all the age classes, the species was deleted, to focus only on compositional differences of the most frequent species and related to the environmental factors, to the stand structure and species richness. The forward selection option was used and only the significant variables were entered in the model ( $p < 0.05$ ).

**Table 1.** Correlation (Correlation coefficient) of pseudo-species with the ordination axes.

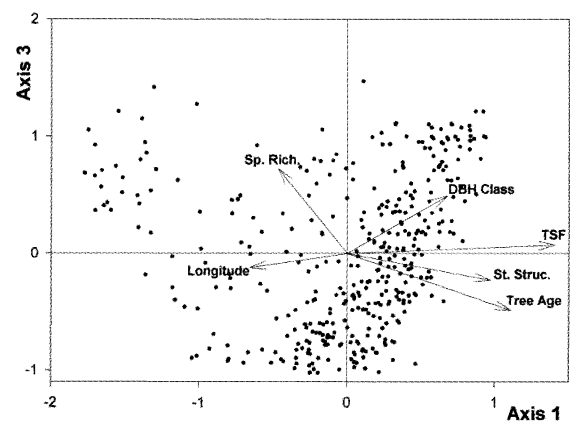
	$R^2 = 0.431$ Axis 1	$R^2 = 0.145$ Axis 2	$R^2 = 0.293$ Axis 3
<b>DBH &gt; 15 cm</b>			
<i>Abies balsamea</i> (Aba)	0.648	0.230	0.616
<i>Betula papyrifera</i> (Bpa)	0.142	0.375	0.290
<i>Picea glauca</i> (Pgl)	0.225	0.120	0.357
<i>Picea mariana</i> (Pma)	0.167	0.391	-0.701
<i>Pinus banksiana</i> (Pba)	-0.050	-0.367	-0.136
<i>Populus tremuloides</i> (Ptr)	-0.223	0.280	0.069
<b>10 cm &lt; DBH &gt; 15 cm</b>			
<i>Abies balsamea</i>	0.487	0.305	0.436
<i>Betula papyrifera</i>	-0.238	0.343	0.036
<i>Picea glauca</i>	-0.136	0.064	0.169
<i>Picea mariana</i>	-0.298	-0.103	-0.580
<i>Pinus banksiana</i>	-0.127	0.211	-0.086
<i>Populus tremuloides</i>	-0.570	0.056	0.202
<b>5 cm &lt; DBH &gt; 10 cm</b>			
<i>Abies balsamea</i>	0.143	0.156	0.255
<i>Betula papyrifera</i>	-0.423	0.017	0.079
<i>Picea glauca</i>	-0.195	-0.017	0.154
<i>Picea mariana</i>	-0.362	-0.327	-0.327
<i>Pinus banksiana</i>	-0.105	-0.163	0.040
<i>Populus tremuloides</i>	-0.426	-0.062	0.176
<b>1 cm &lt; DBH &gt; 5 cm</b>			
<i>Abies balsamea</i>	0.101	0.131	0.208
<i>Betula papyrifera</i>	-0.359	-0.102	0.180
<i>Picea glauca</i>	-0.194	0.027	0.196
<i>Picea mariana</i>	-0.259	-0.365	-0.233
<i>Populus tremuloides</i>	-0.421	-0.141	0.180

## Results

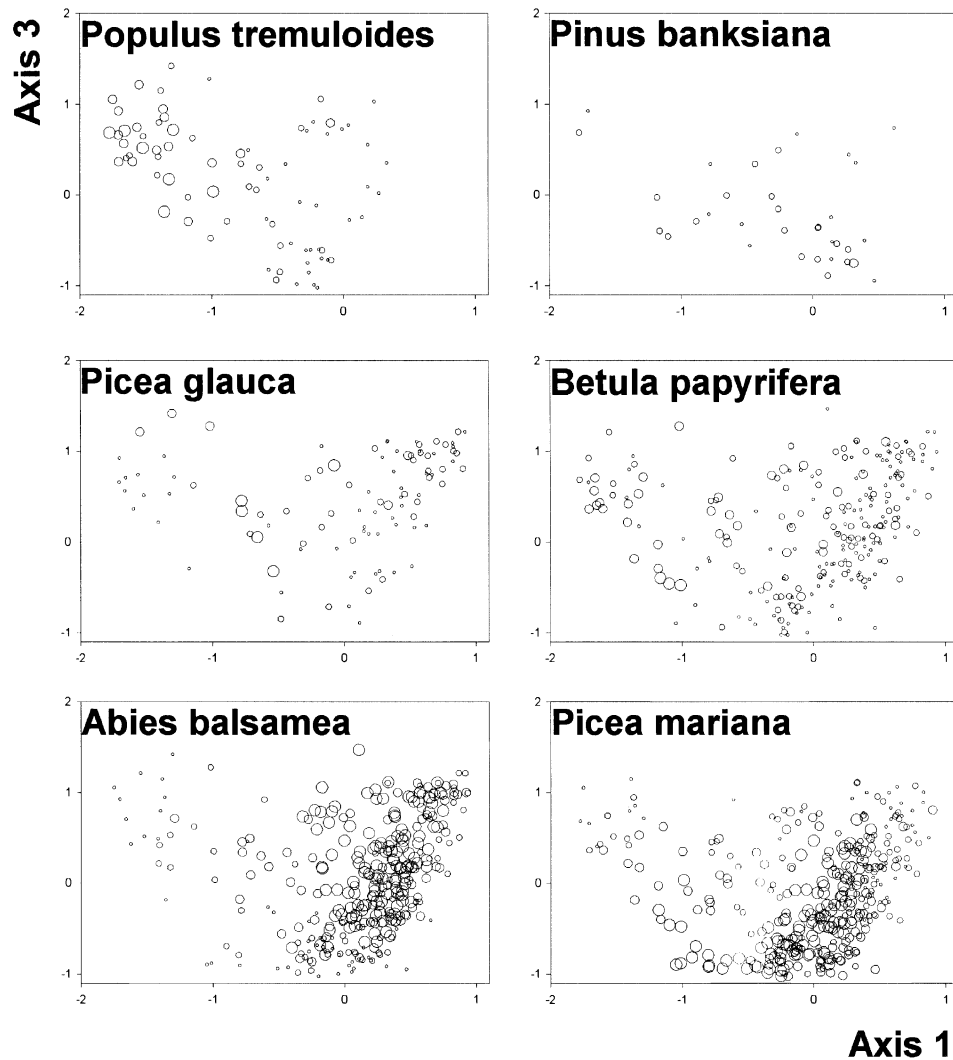
### Changes in forest composition through time elapsed since last fire

Axis 1 and axis 3 of the NMDS ordination explained respectively 43.1% and 29.3% of the variance in species composition (Table 1). Along axis 1, stands located on the right end portion were dominated by large diameter classes of *Abies balsamea*, with *Picea glauca* and *Picea mariana* (Fig. 3). The left portion of the first ordination axis was characterized by the dominance of smaller DBH classes of *Populus tremuloides*, *Betula papyrifera* and *Picea mariana*. Axis 3 mainly discriminated between stands dominated by *A. balsamea* (located in the upper part of the axis) and ones dominated by *P. mariana* (in the lower part of the axis) (Table 1, Fig. 3). The first ordination axis was positively correlated with the time elapsed since last fire, the age of the oldest trees in each plot, the stand structure, the richness in DBH classes and negatively associated with longitude and species richness (Fig. 3). Species richness and the number of DBH classes were positively associated with axis 3 (Fig. 3). Younger successional communities presented a higher species richness as did stands dominated by balsam fir, as opposed to stands dominated by *P. mariana*. *Pinus banksiana* was the only species not associated with either axis 1 or 3.

Along the chronosequence, changes in stand structure were analysed (Fig. 4). App. 1 presents a detailed description of stand composition along the chronosequence, which complement the results of Fig. 4. All DBH classes of *P. tremuloides* were found together in the youngest successional communities. As time since fire increased, *P. tremuloides* was only represented by



**Fig. 3.** Position of the 380 plots on axes 1 and 3 of the NMDS ordination. Vectors showing the influence of the significant explanatory variables are also shown on the diagram ( $p < 0.05$ ).



**Fig. 4.** Frequency of appearance of the pseudo-species on axes 1 and 3 of the Non-metric Multidimensional Scaling ordination diagram. The size of the circle corresponds to the number of pseudo-species by species present in the same stand.

one pseudo-species or absent from older stands (App. 1). For *P. banksiana*, all pseudo-species were never found in the same stand. *P. glauca* and *B. papyrifera* were present throughout the successional sequence but rarely characterized by all the pseudo-species (Fig. 4). The last two species, *P. mariana* and *A. balsamea*, showed similar behaviour in their DBH distribution

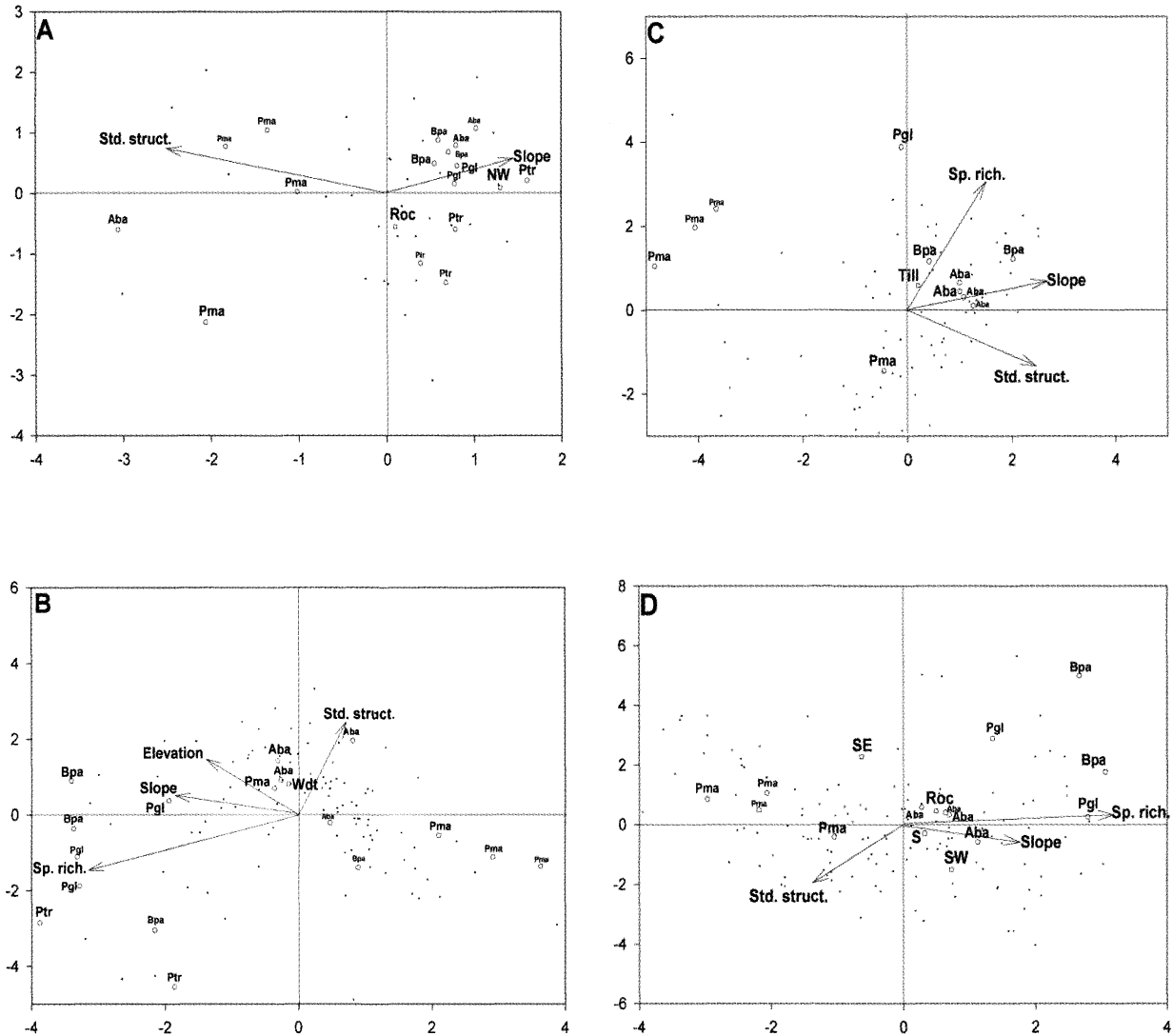
along the chronosequence. With increasing time elapsed since last fire, the DBH distribution of these species became more uneven. Although pure *A. balsamea* and *P. mariana* dominated stands were found on the extremes of axis 3, there was a large proportion of stands with both species present (Fig. 4, App. 1).

*Stand dynamics along the chronosequence in relation to environment*

Separate partial CCAs (constrained by geographical location) were computed by age class, to assess the effect of environmental factors and stand characteristics on compositional differences between stands. One of the major distinctions in stand composition throughout the chronosequence was characterized by stands dominated by *Picea mariana* and the transition from a

**Table 2.** Summary statistics of the four constrained canonical correspondence analyses.

Time-since-fire classes	Total inertia of CCA	Inertia after fitting covariables	Variance explained by environmental variables
50 yr	2.68	2.34	34.6%
100 yr	2.41	2.17	19.0%
175 yr	1.5	1.3	20.5%
225 yr	1.2	1.13	18.5%



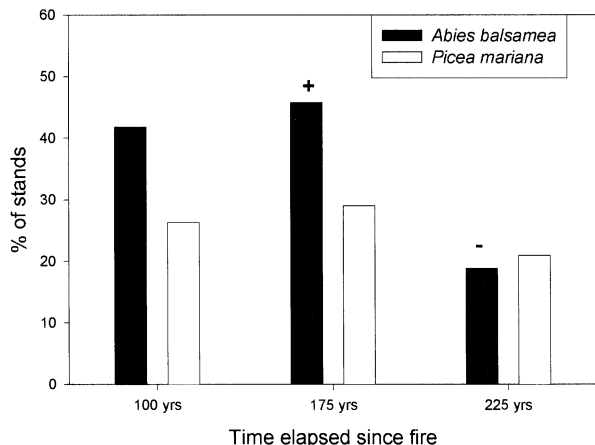
**Fig. 5.** Ordination diagram based on constrained canonical correspondence analyses of (A) 50, (B) 100, (C) 175 and (D) 225 yr-old forest stands data. The position of the pseudo-species is also shown on the ordination diagram and the size of the letters refers to the diameter classes. Only the explanatory variables selected by the forward selection option of CCA are shown on the diagram.

deciduous or mixed canopy to one dominated by *Abies balsamea* (Fig. 5). As time since fire increased, the total inertia of the partial CCAs decreased as stand composition became more similar (Table 2). The total variance explained by the variables included in each CCA was highest in the younger community (50 yr after fire) and stabilized afterwards (Table 2). The percentage of slope was the only environmental factor significantly associated with the compositional differences throughout the chronosequence.

In the youngest age class, stands dominated by *Picea mariana* were located on a rather flat topography and appeared more irregular in their size distribution (Fig. 5a). On the right end of axis 1, the presence of all other

species was significantly associated with rock outcrops, northwest slope aspect and steeper slopes.

In forest stands that belong to the 100 yr-old time-since-fire class, partial windthrow was a significant variable contributing to the differences observed in species composition (Fig. 5b). This disturbance was mainly associated with stands dominated by coniferous species. The structure of these stands was also more irregular. Species richness was highest where deciduous species and *Picea glauca* were present (Fig. 5b) and these species were found on steeper slopes and at higher elevations. In the 175 yr-old age class, stands dominated by *A. balsamea* presented an irregular distribution in their size structure (Fig. 5c). In comparison, pseudo-



**Fig. 6.** Frequency of occurrence of windthrow in relation to the dominant species association in the stand and the time elapsed since last fire. A “+” sign represents a significant excess of stands affected by windthrow and a “-” represents a significant deficiency of stands.

species characterizing *Picea mariana* were farther apart on axis 1. It was in the oldest stands (Fig. 5d) that an irregular size distribution was observed for *Picea mariana*, as emphasized by the significant relationship of stand structure with axis 1.

The frequency of windthrow was analysed along the chronosequence for deciduous, *Abies balsamea* and *Picea mariana* dominated stands. Windthrow did not affect the youngest successional community (50 yr-old stands). For stands dominated by balsam fir, the contingency analysis revealed a significant deviation from the expected distribution ( $df = 2$ ;  $\chi^2 = 10.5$ ;  $p = 0.005$ ) (Fig. 6). There was a significant excess of plots affected by windthrow in the 175 yr-old age class, while a significant deficiency of plots affected by the same disturbance characterized the oldest age class. For *Picea mariana*-dominated stands, there was no significant deviation from the expected distribution (Fig. 6). Finally, deciduous dominated stands were only present in the 100 yr-old age class where more than 35% of the stands were affected by windthrow.

## Discussion

### *Changes in size structure*

Although the environmental factors were responsible for explaining part of the variability in species composition, their effect decreased with increasing time elapsed since fire, as canopy composition became more similar between stands. Despite this apparent convergence, the occurrence of small-scale disturbances contributed to

create suitable conditions for the establishment of new species. The presence of small and large diameter stems of *Betula papyrifera* in these old communities reflected the dynamic nature of these stands (App. 1).

The composition of the youngest successional communities was influenced by environmental conditions, as revealed by the separate CCA and the variance explained by the abiotic factors. However, with increasing time elapsed since the last fire, other disturbances affected forest dynamics. Windthrow was a significant factor contributing to the development of irregular size distribution of coniferous stands. Ruel (2000) has shown that pure *A. balsamea* stands and old individuals were especially vulnerable to windthrow. Since this disturbance does not affect all the individuals in a stand, it may contribute to the development of a multi-layered canopy. Canopy gaps resulting from natural tree mortality or spruce budworm outbreaks were identified as major factors controlling the dynamics of some boreal regions (Kneeshaw & Bergeron 1998). Even with a fire cycle of 100 yr (Bergeron 1991), gap dynamics was an important element contributing to long-term forest dynamics in this region. Groot & Horton (1994) also suggested that partial canopy disturbances could control the dynamics of *Picea mariana* stands older than 160 yr, leading to the development of uneven aged structures. It is thus highly probable that in the Quebec North Shore region similar processes will affect forest development, considering that the fire cycle could be much longer. A fire rotation of 500 yr has been estimated for southeastern Labrador (Heinselman 1973; Foster 1985), a region close to our study area.

### *Changes in forest composition along the chronosequence*

The results revealed two major post-fire successional trends. They were characterized by the early dominance following fire of *Picea mariana* or by a deciduous or mixed canopy. For the successional trend of *P. mariana*, there were no major changes in species composition in the first 100 yr following fire. However, in forests of more than 175 yr old, close to 40% of the stands were sharing their dominance between *P. mariana* and *Abies balsamea*. Throughout the range occupied by *P. mariana*, it was suggested that a short fire recurrence was responsible for the absence of any successional changes (Dix & Swan 1971; Black & Bliss 1978; Cogbill 1985; Morneau & Payette 1989). Although recruitment was possible and uneven-aged stands were observed (Foster 1985; Foster & King 1986; Bergeron & Charron 1994), the understory cohort had a very low probability of reaching the canopy because recruitment was too low, mortality very high and fires too frequent (Johnson 1992). Although there



were no major changes in canopy composition of *P. mariana* stands, the results suggested that the size structure evolved towards a multi-layered forest. In the absence of fire, *P. mariana*-dominated stands slowly developed an uneven size distribution. The presence of *A. balsamea* in old *P. mariana* stands also suggested that changes in stand composition could still occur. This observation was supported by previous studies in which it was hypothesized that *A. balsamea* could succeed *P. mariana* in stands on fertile swamps (Groot & Horton 1994; Carleton & Maycock 1978).

Although not very frequent, *Pinus banksiana* occurred on sandy deposits with *Picea mariana*. *Pinus banksiana* and *Picea mariana* established shortly after fire and the changes in canopy dominance with time elapsed since last fire only reflected the relative growth rate of each species (St-Pierre et al. 1992). In the absence of fire, these stands will evolve towards a forest dominated by *P. mariana*.

Deciduous and mixed-species-dominated stands evolved towards an increased dominance of *A. balsamea* with time elapsed since last fire. As these communities grew older, intolerant species like *Populus tremuloides* and *Betula papyrifera* were slowly replaced in the canopy by *A. balsamea* (Foster & King 1986; Bergeron & Dubuc 1989; Bergeron & Charron 1994). Our results suggested that the occurrence of windthrow in 100 yr-old deciduous dominated stands might be involved in this change in canopy composition. Bergeron (2000) showed that as the aspen cohort starts to die back, openings are created contributing to release the growth of suppressed individuals in the understory. From a monospecific canopy layer, the composition of the canopy changed to a mosaic of *Abies balsamea*, *Betula papyrifera*, *Populus tremuloides* and *Picea glauca* (Bergeron 2000).

With time elapsed since last fire, forest dynamics was increasingly influenced by other types of disturbances. In stands over 175 yr-old, gaps resulting from a spruce budworm outbreak or windthrow affected close to 50% of the stands dominated by *A. balsamea*. Windthrow was also a significant variable to enter the forward selection in the CCA. The first 100 yr of community development in these deciduous dominated stands could be interpreted and predicted from the life history of the species present in the stand (Noble & Slatyer 1980; Huston & Smith 1987). Following this stage, it became hard to predict further community development from the actual species composition as disturbances influenced and changed this directional pathway. The results suggested that *A. balsamea* should become a major component of these communities and that windthrow could contribute in creating suitable

conditions for a rapid accession to the canopy by *A. balsamea*. Studies have shown that gap formation did not significantly increase seedling recruitment of *A. balsamea* (MacLean 1988) but it did affect the growth in height of the advanced regeneration (Kneeshaw et al. 1998). Since *A. balsamea* was frequently encountered in the advanced regeneration of deciduous and mixed-species-dominated stands (App. 1), it could eventually dominate the canopy.

## Conclusion

Gap formation resulting from windthrow or spruce budworm outbreaks are variable in size and in shape, thus creating highly diversified conditions for species establishment or the release of the advanced regeneration (Drobyshev 1999; Kneeshaw & Bergeron 1998). In the absence of fire, establishment, growth and mortality of both *Picea mariana*- and *Abies balsamea*-dominated stands will be controlled by gap dynamics. This process will have to be studied in more detail in order to be able to understand and predict the effect of these disturbances on the outcome of succession.

**Acknowledgements.** This project was supported by the Ministère des Ressources naturelles du Québec, région de la Côte-Nord, Unité de Gestion 94. The authors are grateful to Claude Allain and Jacques Duval for sharing their interest and great knowledge of the Quebec North Shore forests. The authors also acknowledge the Ministère des Ressources naturelles du Québec for allowing us to use the forest inventory data. We thank Rosa Orlandini for her help in the field and in tree dating. We also thank Pamela Cheers for editing the English and Diane Paquet for correcting the manuscript. We also are grateful to Josette and the late Rolland D'Astout and to Michèle Paradis for housing and feeding us at the Pourvoirie du Lac Dionne (Baie-Comeau) and for providing us with a very warm and friendly welcome.

## References

- Anon. 1996. *Canadian climate normals 1947-1996*. Canadian climate program. Environment Canada, Atmospheric Environment Service. Downsview, Ontario. CD-ROM.
- Bergeron, Y. 1991. The influence of island and mainland lakeshore landscapes on boreal forest fire regimes. *Ecology* 72: 1980-1992.
- Bergeron, Y. 2000. Species and stand dynamics in the mixed woods of Quebec's southern boreal forest. *Ecology* 81: 1500-1516.
- Bergeron, Y. & Charron, D. 1994. Postfire stand dynamics in a southern boreal forest (Québec): A dendroecological approach. *Écoscience* 1: 173-184.
- Bergeron, Y. & Dubuc, M. 1989. Succession in the southern

- part of the Canadian boreal forest. *Vegetatio* 79: 51-63.
- Bergeron, Y., Engelmark, O., Harvey, B., Morin, H. & Sirois, L. 1998. Key issues in disturbance dynamics in boreal forests: Introduction. *J. Veg. Sci.* 9: 464-468.
- Black, R.A. & Bliss, L.C. 1978. Recovery sequence of *Picea mariana*-*Vaccinium uliginosum* forests after burning near Inuvik, Northwest Territories, Canada. *Can. J. Bot.* 56: 2020-2030.
- Blais, J.R. 1983. Trends in the frequency, extent, and severity of spruce budworm outbreaks in eastern Canada. *Can. J. For. Res.* 13: 539-547.
- Carleton, T.J. & Maycock, P.F. 1978. Dynamics of the boreal forest south of James Bay. *Can. J. Bot.* 56: 1157-1173.
- Cogbill, C.V. 1985. Dynamics of the boreal forests of the Laurentian Highlands, Canada. *Can. J. For. Res.* 15: 252-261.
- Dix, R.L. & Swan, J.M.A. 1971. The roles of disturbance and succession in upland forest at Candle Lake, Saskatchewan. *Can. J. Bot.* 49: 657-676.
- Drobyshev, I.V. 1999. Regeneration of Norway spruce in canopy gaps in *Sphagnum*-*Myrtillus* old-growth forests. *For. Ecol. Manage.* 115: 71-83.
- Foster, D.R. 1985. Vegetation development following fire in *Picea mariana* (black spruce)-*Pleurozium* forests of south-eastern Labrador, Canada. *J. Ecol.* 73: 517-534.
- Foster, D.R. & King, G.A. 1986. Vegetation pattern and diversity in S.E. Labrador, Canada: *Betula papyrifera* (birch) forest development in relation to fire history and physiography. *J. Ecol.* 74: 465-483.
- Gauthier, S., Leduc, A. & Bergeron, Y. 1996. Forest dynamics modelling under natural fire cycles: a tool to define natural mosaic diversity for forest management. *Environ. Monit. Assess.* 39: 417-434.
- Groot, A. & Horton, B.J. 1994. Age and size structure of natural and second-growth peatland *Picea mariana* stands. *Can. J. For. Res.* 24: 225-233.
- Heinselman, M.L. 1973. Fire in the virgin forests of the Boundary Waters Canoe Area, Minnesota. *Quat. Res.* 3: 329-382.
- Heinselman, M.L. 1981. *Fire intensity and frequency as factors in the distribution and structure of northern ecosystems*. Proceedings of the conference 'Fire Regimes and Ecosystems Properties'. U.S.D.A. For. Serv., Gen. Tech. Rep. WO-26, pp. 7-57.
- Huston, M. & Smith, T. 1987. Plant succession: Life history and competition. *Am. Nat.* 130: 168-198.
- Johnson, E.A. 1979. Fire recurrence in the subarctic and its implications for vegetation composition. *Can. J. Bot.* 57: 1374-1379.
- Johnson, E.A. 1992. *Fire and vegetation dynamics: studies from the North American boreal forests*. Cambridge Studies in Ecology, Cambridge University Press, Cambridge.
- Johnson, E.A., Miyanishi, K. & Weir, J.M.H. 1998. Wildfires in the western Canadian boreal forest: Landscape patterns and ecosystem management. *J. Veg. Sci.* 9: 603-610.
- Kneeshaw, D.D. & Bergeron, Y. 1998. Canopy gap characteristics and tree replacement in the southeastern boreal forest. *Ecology* 79: 783-794.
- Kneeshaw, D.D., Bergeron, Y. & De Grandpré, L. 1998. Early response of *Abies balsamea* seedlings to artificially created openings. *J. Veg. Sci.* 9: 543-550.
- Lässig, R. & Mocalov, S.A. 2000. Frequency and characteristics of severe storms in the Urals and their influence on the development, structure and management of the boreal forests. *For. Ecol. Manage.* 135: 179-194.
- MacLean, D.A. 1988. Effects of spruce budworm outbreaks on vegetation, structure and succession of balsam fir forests on Cape Breton Island, Canada. In: Werger, M.J.A., van der Aart, P.J.M. & Verhoeven, J.T.A. (eds.) *Plant form and vegetation structure*, pp. 253-261. Academic Publishing, The Hague.
- Morneau, C. & Payette, S. 1989. Postfire lichen - spruce woodland recovery at the limit of the boreal forest in northern Québec. *Can. J. Bot.* 67: 2770-2782.
- Noble, I.R. & Slatyer, R.O. 1980. The use of vital attributes to predict successional changes in plant community subject to recurrent disturbances. *Vegetatio* 43: 5-21.
- Oliver, C.D. & Larson, B.C. 1996. *Forest stand dynamics*. Updated ed. John Wiley & Sons, New York, NY.
- Pickett, S.T.A. & White, P.S. 1985. *The ecology of natural disturbance and patch dynamics*. Academic Press, New York, NY.
- Robitaille, A. & Saucier, J.P. 1998. *Paysages régionaux du Québec méridional*. Les publications du Québec, Québec.
- Romme, W.H. 1982. Fire and landscape diversity in subalpine forests of Yellowstone National Park. *Ecol. Monogr.* 52: 199-221.
- Romme, W.H. & Knight, D.H. 1982. Landscape diversity: The concept applied to Yellowstone Park. *BioScience* 32: 664-670.
- Rowe, J.S. 1972. *Forest regions of Canada*. Environment Canada, Ottawa.
- Rowe, J.S. 1983. Concepts of fire effects on plant individuals and species. In: Wein, R.W. & MacLean, D.A. (eds.) *The role of fire in northern circumpolar ecosystems*. Scope 18: 135-154. Wiley, New York, NY.
- Ruel, J.C. 2000. Factors influencing windthrow in balsam fir forests: from landscape studies to individual tree studies. *For. Ecol. Manage.* 135: 169-178.
- Shugart, H.H., Leemans, R. & Bonan, G.B. 1992. *A system analysis of the boreal forest*. Cambridge University Press, Cambridge.
- St-Pierre, H., Gagnon, R. & Bellefleur, P. 1992. Régénération après feu de l'épinette noire (*Picea mariana*) et du pin gris (*Pinus banksiana*) dans la forêt boréale, Québec. *Can. J. For. Res.* 22: 474-481.
- Thibault, M. & Hotte, D. 1985. *Les régions écologiques du Québec méridional (2ième approximation)*. Ministère de l'Énergie et des Ressources du Québec, Serv. de la recherche, Québec (colour map at the scale of 1: 1 250 000).
- White, P.S. 1979. Pattern, process, and natural disturbance in vegetation. *Bot. Rev.* 45: 229-299.

Received 23 December 1998;

Revision received 22 June 1999;

Final version received 10 December 2000;

Accepted 10 December 2000.

Coordinating Editor: O. Engelmark.

**App. 1** Stand dominance and composition along the chronosequence. Dominance was determined based on the basal area calculated in each stand. For complete species names, see Table 1.

Dominant association	Deciduous > 75 % of basal area						Mixed composition						<i>Picea mariana-Pinus banksiana</i> > 75 % of basal area						<i>Picea mariana</i> > 75 % of basal area						<i>Abies balsamea</i> > 75 % of basal area						<i>Picea mariana-Abies balsamea</i> > 75 % of basal area											
	Ptr	Bpa	Pha	Pgl	Pma	Aba	Ptr	Bpa	Pha	Pgl	Pma	Aba	Ptr	Bpa	Pha	Pgl	Pma	Aba	Ptr	Bpa	Pha	Pgl	Pma	Aba	Ptr	Bpa	Pha	Pgl	Pma	Aba	Ptr	Bpa	Pha	Pgl	Pma	Aba						
<b>&lt; 50 yr after fire; No. of sites = 42</b>																																										
Nb stands with stems > 10 cm	16	12	2	7	8	4	13	12	3	4	12	3	1	2	5	0	5	0	1	1	0	0	4	3	-	-	-	-	-	-	-	-	-	-	-	-	0	0	0	1	1	1
Basal area (m <sup>2</sup> /ha)	6.9	1.9	0.3	0.5	0.5	0.3	2.1	0.8	7.2	1.4	3.4	0.4	1.3	0.5	12.3	0.0	1.7	0.0	1.8	1.4	0	0	5.5	2.3	-	-	-	-	-	-	-	-	-	-	-	-	0	0	0	1.1	5.6	12.9
Nb stands with stems < 10 cm	13	11	1	2	6	5	11	12	0	7	12	11	0	4	1	0	4	0	0	1	0	0	4	1	-	-	-	-	-	-	-	-	-	-	-	-	0	1	0	0	0	1
<b>50-100 yr after fire; No. of sites = 121</b>																																										
Nb stands with stems > 10 cm	4	5	0	2	5	3	23	25	5	10	27	22	1	1	9	4	9	1	10	21	0	1	52	34	1	4	0	2	2	6	5	16	3	3	19	20						
Basal area (m <sup>2</sup> /ha)	8.5	13.0	0	1.1	2.5	3.1	8.8	8.4	4.0	3.2	9.8	6.0	3.7	0.2	11.8	1.7	6.6	1.1	1.8	1.2	0	1.1	28.7	1.6	1.0	2.2	0	2.0	1.7	17.3	1.3	3.8	3.3	1.1	14.6	8.3						
Nb stands with stems < 10 cm	0	2	0	1	3	4	4	9	0	5	9	23	0	0	1	1	7	1	0	9	0	0	49	22	0	2	0	2	2	6	1	4	0	1	11	16						
<b>&gt; 175 yr after fire; No. of sites = 79</b>																																										
Nb stands with stems > 10 cm	-	-	-	-	-	-	0	12	1	9	6	13	-	-	-	-	-	-	0	2	0	0	18	13	0	9	0	3	7	14	0	25	0	3	34	34						
Basal area (m <sup>2</sup> /ha)	-	-	-	-	-	-	0	4.9	2.8	4.6	3.4	12.4	-	-	-	-	-	-	0	0.2	0	0	21.3	1.5	0	1.8	0	1.6	2.8	15.9	0	2.0	0	1.5	10.1	9.5						
Nb stands with stems < 10 cm	-	-	-	-	-	-	0	4	0	0	3	9	-	-	-	-	-	-	0	0	0	0	13	8	0	2	0	2	1	12	0	7	0	3	12	29						
<b>&gt; 225 yr after fire; No. of sites = 138</b>																																										
Nb stands with stems > 10 cm	-	-	-	-	-	-	1	8	0	7	4	8	0	2	6	0	6	2	0	3	0	0	31	24	0	14	0	11	17	24	1	40	0	19	69	69						
Basal area (m <sup>2</sup> /ha)	-	-	-	-	-	-	2.9	8.2	0	5.8	2.6	19.6	0	2.0	10.1	0	8.6	0.9	0	0.3	0	0	16.3	2.6	0	1.5	0	3.3	2.9	21.0	0.2	1.5	0	1.7	11.6	10.8						
Nb stands with stems < 10 cm	-	-	-	-	-	-	0	2	0	0	4	6	0	1	0	0	5	1	0	2	0	0	30	19	0	3	0	2	4	19	0	13	0	5	55	65						