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Author(s): Sylvie Gauthier, Yves Bergeron and Jean-Pierre Simon

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Effects of fire regime on the serotiny level of jack pine

SYLVIE GAUTHIER,*† YVES BERGERON* and
JEAN-PIERRE SIMON†

*Groupe de recherche en écologie forestière, Université du Québec à Montréal, C.P. 8888, Succ. Centre-Ville, Montréal, Canada H3C 3P8 and †Département de Sciences biologiques, Université de Montréal, C.P. 6128, Succ. A, Montréal, Canada H3C 3J7

Summary

1 Serotiny, the capacity to retain seed in the plant canopy, has evolved in many species under the selective pressure of fires. The effect of disturbance type (lethal or nonlethal fire), time-since-fire and different fire regimes on the serotiny of jack pine (*Pinus banksiana*), was evaluated in populations from two adjacent landscapes in the southern part of the Canadian boreal forest. The island landscape (Lake Duparquet) has a complex fire regime of small fires of variable intensity, whereas the adjacent mainland has a fire regime characterized by large intense fires.

2 Twenty-four jack pine populations (11 island and 13 mainland) on xeric sites were sampled for the degree of serotiny of trees. Fire history and age structure were reconstructed for each population using the fire scar method. For each tree, recruitment was categorized as after a lethal fire, after a nonlethal fire or in the absence of fire.

3 Likelihood chi-square tests were used to investigate the variation in serotiny at individual, population and landscape levels.

4 At the individual level, the results support our prediction that the occurrence of lethal fires favours trees with high serotiny while low serotiny trees are favoured by other types of disturbances.

5 At the population level, the frequency of low serotiny trees increases with time since stand initiation, as a result of higher establishment opportunities after disturbances other than lethal fires. The proportion of low serotiny trees also increases with the occurrence of nonlethal fires.

6 Significant differences were found between the two landscapes. On the mainland, serotinous trees were more abundant, whereas on the islands where nonlethal fires were recorded, low serotiny trees were more frequent. These results support the hypothesis that fire imposes differential selective pressures on serotiny in jack pine.

Keywords: cone polymorphism, disturbance regime, fire intensity, fire interval, *Pinus banksiana* Lamb.

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Introduction

Jack pine (*Pinus banksiana* Lamb.) has a wide distribution in North America and is a major species in fire-prone boreal forests (Fowells 1965). The spatial and temporal distribution of its populations is controlled by fire (Eyre & LeBarron 1944; Cayford & McRae 1983; Gagnon 1990; Gauthier *et al.* 1993b). It

is one of many plant species that has shown serotiny, an ability to retain seeds in the plant canopy (Lamont *et al.* 1991). The inflorescences or cones of many serotinous species remain closed until exposed to high temperatures such as those created by fires. In jack pine, the resin of serotinous cones melts only at or above 50 °C, so seed release mostly occurs after a fire (Cameron 1953; Beaufait 1960). Serotiny is considered to be the main adaptation of jack pine to the recurrence of fires, as it cannot resprout (Cayford & McRae 1983). Despite genetic studies, the mode of inheritance of serotiny in jack pine and the interaction

between character expression and the environment are not fully understood (Teich 1970; Sittman & Tyson 1971; Lamont *et al.* 1991). In jack pine, an individual may bear either mainly serotinous (closed) or mainly nonserotinous (open) cones or a mixture of the two (Rudolph *et al.* 1959; Schoenike 1976) and, unlike other serotinous species such as lodgepole pine (*Pinus contorta* Dougl.) and pitch pine (*Pinus rigida* Mill.), the frequency of 'mixed' trees bearing both types of cones is relatively high (Rudolph *et al.* 1959; Teich 1970; Sittman & Tyson 1971).

Several studies have suggested that parameters such as intensity, frequency, size and spatial distribution of fires are the main factors involved in the evolution of variable degrees of serotiny both among congeneric species and between populations of the same species, although other selection agents such as seed predation might also be important (Vogl 1973; Schoenike 1976; Keeley 1981; McMaster & Zedler 1981; Borchert 1985; Cowling & Lamont 1985; Zammit & Westoby 1987a,b; Lamont *et al.* 1991). Large and intense fires may favour highly serotinous trees because regeneration will result mainly from seed release from *in situ* serotinous progenitors (Tinker *et al.* 1994), so that the resulting population will also show a high level of serotiny. On the other hand, nonserotinous trees may have an advantage in the absence of fire because their seed release does not rely on fire. Trees with low and moderate serotiny levels could also be favoured when fires are of low intensity as the temperature may not rise high enough to open the serotinous cones (Johnson & Gutsell 1993).

Lake Duparquet (Québec) and its surrounding area offer an opportunity to study the variability of serotiny level in jack pine populations subjected to different fire regimes. The islands in the lake are affected by a complex fire regime involving frequent fires of variable intensity, whereas the adjacent mainland forests are subjected to infrequent but intense fires (Table 1; Bergeron 1991; Dansereau & Bergeron

1993). The variation in serotiny levels was investigated at three levels to test the following predictions:

1 Individual level. Lethal fire favours highly serotinous trees, whereas nonlethal fires or non-fire-related disturbances select for jack pine trees with low and mixed serotiny.

2 Population level. (a) The proportion of low serotiny trees within populations increases with time-since-fire because disturbances other than lethal fire result in an increasing number of recruitment opportunities through time; (b) this increase in the proportion of low serotiny trees is higher on islands where nonlethal fires are prevalent.

3 Landscape level. A higher frequency of serotinous trees is expected on the mainland as opposed to that seen on islands, due to the difference in fire regimes between the two landscapes.

STUDY AREA

Both island and mainland populations are located in the southern part of the boreal forest in western Québec, in the Missinaibi–Cabonga Section defined by Rowe (1972) (Fig. 1). Mature forests are characterized by balsam fir (*Abies balsamea* (L.) Mill.) and paper birch (*Betula papyrifera* Marsh.). The forest vegetation of this region has been described in detail in previous studies (Bergeron & Bouchard 1984; Bergeron & Dubuc 1988). The region is within the Northern Clay Belt of Québec and Ontario, a large physiographic unit of lacustrine deposits of proglacial Lake Ojibway and Lake Barlow (Vincent & Hardy 1977).

Lake Duparquet occupies ≈ 50 km² and has more than 150 islands of various sizes (Fig. 1). The islands are affected by a complex fire regime with a long return interval for lethal fires (≈ 130 –150 years) and a short return interval for fires of variable intensities (35–50 years; Table 1; Bergeron & Brisson 1990; Bergeron 1991). Fire years for individual islands are not

Table 1 Comparison of the fire regimes of two landscapes in the Lake Duparquet region for the last three centuries*

	Landscape	
	Mainland	Island
Spatial pattern of ignition	<i>In situ</i> and <i>ex situ</i> ignition ^c ; occurrence at different sites correlated ^c	<i>In situ</i> ignition ^b ; independently at various sites ^b
Occurrence (fires per 100 km ² per year)	0.009–0.130 ^{b,c}	0.300–0.870 ^{a,b}
Cycle (years)		
before 1870	59–67 ^b	69–79 ^b
after 1870	80–118 ^b	98–128 ^b
Area burnt per fire (ha)	> 100 ^c	< 100 ^a
Intensity	Lethal	Variable: from nonlethal to lethal ^{a,b}
Average time since stand-initiating fire (years)†	150–205 ^b	131–148 ^{a,b}
Average interval between fire (years)‡	–	35 ± 26 years ^b

*Synthesis of the work of ^aBergeron & Brisson (1990), ^bBergeron (1991) and ^cDansereau & Bergeron (1993).

†These differ from the estimated fire cycle because of changes in the fire cycle after 1870.

‡Computed only for islands where the occurrence of nonlethal fire was recorded.

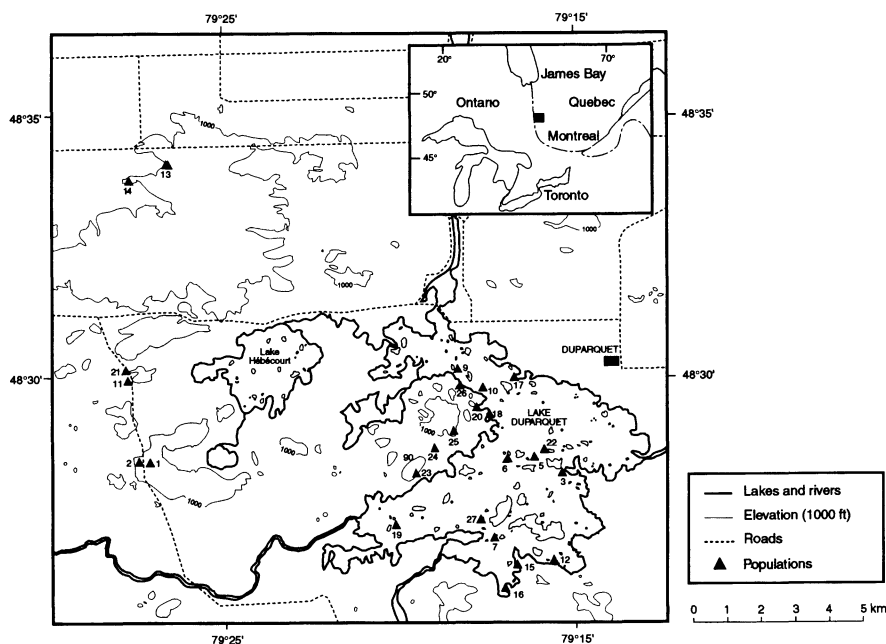


Fig. 1 Geographical position of the study area and location of the 24 jack pine stands.

temporally correlated either between islands or between islands and the surrounding forested shore, suggesting *in situ* ignition (Bergeron 1991). The mainland fire regime is typical of the boreal forest, with a long return interval for large lethal fires (≈ 150 – 200 years; Table 1; Van Wagner 1983; Bergeron 1991; Johnson 1992; Dansereau & Bergeron 1993). The occurrence of fire (number of fires per 100 km^2 per year) is higher in the island landscape than on the mainland (Bergeron 1991). It is believed that, as lightning tends to avoid water, islands have a higher probability of being struck by lightning (Hébert 1995). The area burned by each fire is smaller in the island landscape, resulting in a longer fire cycle than on the mainland (Table 1). Following lethal fires, jack pine populations regenerate both on xeric and mesic sites (Bergeron & Bouchard 1984) but are mainly restricted to xeric sites on islands.

Methods

FIELD METHODS

Twenty-four jack pine populations, consisting of 11 island and 13 mainland stands located on xeric sites, were sampled in 1987 and 1988 (Fig. 1). Vegetation composition and tree density were recorded at each of 20 points systematically positioned in each stand using the point-centred-quadrant method (Cottam & Curtis 1956). The two jack pine trees closest to each point (40 jack pine/stand) were measured for diameter at breast height (d.b.h.) and cored to determine age. The fire scar method of Arno & Sneek (1977) was used to reconstruct the fire history. These data were collected in this study and from previous studies in

the region (Bergeron & Gagnon 1987; Archambault 1990; Bergeron & Brisson 1990; Gagnon 1990; Bergeron 1991; Dansereau & Bergeron 1993; Gauthier *et al.* 1993b). Fire events that killed all the jack pine trees in the original stand and thus led to stand initiation were defined as lethal, while fires that allowed one or more jack pine to survive were classified as nonlethal (Table 2).

The age structure and fire history of the stand were used to assign the individual jack pine trees different establishment classes according to whether they germinated within 10 years of fire occurrence (i.e. a post-fire recruit) or established more than 10 years after a fire (i.e. considered to be a recruit in the absence of fire). To discriminate between the effects of lethal and nonlethal fires, four classes were defined (see Fig. 2): (1) after a lethal fire: ≤ 10 years after the occurrence of a lethal fire; (2) in the absence of fire (lethal): > 10 years after the occurrence of a lethal fire within the population; (3) after a nonlethal fire: ≤ 10 years following the occurrence of a nonlethal fire; and (4) in the absence of fire (nonlethal): > 10 years after the occurrence of a nonlethal fire within the population.

SEROTINY LEVEL CLASSIFICATION

In jack pine, the cones maturing in the current year (new cones) will only open in the fall if nonserotinous (Neumann *et al.* 1964). Therefore the serotiny level can be determined in the laboratory (see Gauthier 1991; Gauthier *et al.* 1993a for a complete description of the methodology). A subsample of one quarter of the trees within each establishment class (10 jack pine per stand) were randomly selected and felled for

Table 2 Jack pine population characteristics (fire history and number of trees > 10 cm of d.b.h. (*N*), and mean percentage of serotinous cones (*PSC*)) by establishment classes and stand initiation periods

Population number* (fire years)†	Lethal fire				Nonlethal fire			
	After a fire		Abs. of fire		After a fire		Abs. of fire	
	n	psc	n	psc	n	psc	n	psc
Mainland								
1760–1796								
11 (1760)	6	69	10	62				
21 (1760)	1	29	12	57				
1797–1887								
15 (1887)‡	24	84	6	86				
18 (1870)‡	6	73	3	95				
20 (1870)	10	79	20	88				
23 (1797)	8	83	19	82				
24 (1870 , 1909)	6	78	1	100	18	79	6	67
26 (1870)	13	87	14	84				
1888–1987								
1 (1923)	16	89	3	47				
2 (1923)	17	94	3	64				
14 (1944)	9	87	1	94				
16 (1944)‡	5	70	5	87				
25 (1919)	7	81	7	63				
Overall	128	83	104	77	18	79	6	67
Island without nonlethal fires								
1797–1887								
6 (1845, 1875)	13	82	6	81				
17 (1870)§	3	69	9	53				
1888–1987								
7 (1819, 1935)	5	89	9	89				
12 (1944)	10	93	2	26				
Overall	31	85	26	70				
Island with nonlethal fires								
1797–1887								
3 (1833 , 1928)	10	75	5	84	1	30	4	78
5 (1854 , 1880, 1891)	1	19	2	72	3	47	13	49
9 (1845, 1868 , 1892)	1	100	3	66	5	53		
22 (1766, 1840 , 1905, 1911)	3	71	17	80				
27 (1799 , 1849, 1881, 1901, 1914)	9	58	15	62				
1888–1987								
10 (1881, 1900 , 1943)	9	83	11	50	1	83	1	100
19 (1795, 1825, 1829, 1862, 1905 , 1930, 1949)	5	90	8	54	8	79	1	4
Overall	26	79	26	59	28	65	56	64

*The population numbers correspond to Fig. 1.

†Fire years in bold are stand-initiating fires (lethal); fire years following those were nonlethal fires, while fire years before may have been either lethal or nonlethal.

‡Shore population.

§Peninsula population.

extensive sampling of their serotiny level. For each of the felled trees, serotinous and nonserotinous cones were counted on the terminal 50 cm of each branch by cone age. New cones were collected and tested for serotiny in the laboratory (Gauthier *et al.* 1993a). The proportion of new cones (laboratory tested) that were serotinous did not differ significantly from the proportion observed for older cones when compared on a tree by tree basis (Gauthier 1991). Therefore, the numbers of serotinous and nonserotinous cones, excluding the new cones, were counted by branch on the terminal 50 cm of each branch of the 30 unfelled trees per stand using binoculars. Trees under 10 cm d.b.h. were excluded from subsequent analyses

because studies have shown that their level of serotiny is lower than that of typical mature trees (Gauthier *et al.* 1993a).

Each tree was assigned to one of five serotiny levels based on the percentage of serotinous cones (PSC): (1) nonserotinous (NS) trees, PSC = 0; (2) quasi-nonserotinous (QNS) trees, $0 < \text{PSC} \leq 30$; (3) mixed (M) trees, $30 < \text{PSC} \leq 70$; (4) quasi-serotinous (QS) trees, $70 < \text{PSC} < 100$; and (5) serotinous (S) trees, PSC = 100. This classification modifies that used in previous work on jack pine (Rudolph *et al.* 1959; Teich 1970; Sittman & Tyson 1971) by adding NS and S classes to include 'pure' nonserotinous and 'pure' serotinous trees at both extremes.

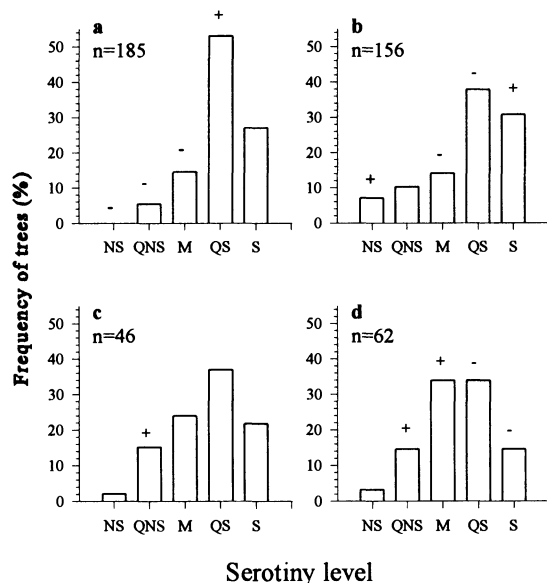


Fig. 2 Frequency distributions of tree serotiny levels between the four establishment classes ($\chi^2_{1,2} = 46.58$, $P < 0.001$): (a) after a lethal fire; (b) in the absence of a lethal fire; (c) after a nonlethal fire; (d) in the absence of a nonlethal fire; Significant deviation from the expected distribution of serotiny levels at $P < 0.01$ following Pearson chi-square component tests is indicated (+, excess; -, deficiency).

DATA ANALYSIS

Individual-level analysis

In order to determine whether high levels of serotiny are promoted by lethal fires as compared with nonlethal fires or other types of disturbances, comparisons of the frequency distribution of serotiny levels between trees in the four establishment classes were made using a likelihood chi-square test (χ^2). Pearson chi-square components were computed in order to compare the observed frequencies within the serotiny levels among the establishment classes (Legendre & Legendre 1984). It should be noted that trees are not independent representatives of landscape populations as they were not randomly selected. Chi-square analyses were also realized using stands as cases (see next section).

Population- and landscape-level analysis

The frequency distribution of trees within serotiny levels was computed for each stand. In order to test whether the proportion of low serotiny trees increases with time since stand initiation, each stand was classified into one of three stand initiation periods: (1) from 1888 to 1987; (2) from 1797 to 1887; or (3) from 1760 to 1796. The first two periods cover ≈ 100 years while the last period is shorter because no earlier stands were recorded (even on the mainland where stands over 200 years old do occur, albeit rarely). Finally,

the effect of nonlethal fires within island populations was assessed by further dividing the populations into two groups: (1) with and (2) without nonlethal fires since stand initiation.

The overall heterogeneity among stands was calculated using a likelihood chi-square test [χ^2 ; 24 rows (stands) by five columns (serotiny levels)]. The advantage of likelihood chi-square tests is that they are completely additive (Sokal & Rohlf 1981), allowing decomposition into several components in a nested fashion. This property allows us to evaluate the effects of (a) the landscape, (b) the time since stand initiation, and (c) the occurrence of nonlethal fire on the frequency of trees within serotiny levels among the 24 stands. For example, the difference between the sum of the chi-squared values determined for the heterogeneity of serotiny among stands in each of the two landscapes and the overall value is due to the heterogeneity between landscapes. The same decomposition procedure was used to determine the effect of time since stand initiation within each landscape, and finally, on the islands, the effect of nonlethal fire occurrence. Pearson chi-square components were used to assess the serotiny levels whose excess or deficiency led to the observed heterogeneity among the 24 stands.

The occurrence of fires is higher on islands than on the mainland and nonlethal fires are exceptional on the mainland (Tables 1 and 2). Thus, the populations in the two landscapes do not have the same number of trees within a given establishment class or stand initiation period. The use of log-linear models (Proc CATMOD; SAS Institute 1985) allowed us to obtain better estimates of the differences observed between the two landscapes by controlling differences in the number of trees within establishment classes and stand initiation periods. Briefly, the best log-linear model was selected using the method described by Bishop *et al.* (1975) and did not include any of the third-level or higher level interactions since these were not significant (Gauthier 1991). By fitting the log-linear model with and without the interaction term between serotiny levels and landscape groups, an estimate could be obtained of the differences between the landscapes in the proportion of trees within the serotiny levels while controlling for the differences in tree number in each establishment type and/or stand initiation period. Finally, the log-linear parameters and their standard errors were computed to evaluate significant differences among landscapes in the number of trees within the serotiny classes. For the purpose of the log-linear model, only two establishment classes were used: (1) after a fire (either lethal or nonlethal), and (2) in the absence of fire (> 10 years after any fire). As no island populations had a fire-free period exceeding 200 years, the two oldest populations (originating from a fire in 1760) on the mainland were excluded from the analysis.

Results

CHARACTERISTICS AND FIRE HISTORY OF
THE POPULATIONS

Only one of the mainland stands had been affected by a nonlethal fire (Table 2). However, 63.6% of the islands had experienced one or several nonlethal fires following the stand-initiating fire. Table 2 shows the number of trees and the average PSC within stands among the four establishment classes. Although 40 trees were sampled in each stand, the exclusion of trees with a d.b.h. ≤ 10 cm from the analysis (see methods) reduced the population size.

EFFECT OF ESTABLISHMENT CLASSES ON THE
SEROTINY LEVEL OF TREES

A highly significant difference was observed among the four establishment classes in the frequency distribution of the serotiny levels of trees (Fig. 2). Significant deficiencies of NS, QNS, and M trees together with an excess of QS trees were observed in individuals established after a lethal fire (Fig. 2a) compared with other establishment classes. After nonlethal fire, there was a significant excess of QNS trees (Fig. 2c). For individuals established in the absence of fire (Fig. 2b,d), there was an excess of low serotiny level trees (NS or QNS). When the previous fire had been lethal (Fig. 2b), there was also a significant excess of S trees, compared with a deficiency of QS and S trees and an excess of M trees if the previous fire was nonlethal (Fig. 2d).

VARIABILITY OF SEROTINY LEVEL AMONG
POPULATIONS

The global chi-square ($\chi^2 = 156.22$) indicated a highly significant heterogeneity among the 24 stands in the frequency of trees within serotiny levels (Table 3). To assess the effect of stand initiation period and nonlethal fire occurrence on stand frequency distribution, the global chi-square was decomposed for each landscape. This chi-square decomposition revealed a higher heterogeneity among island stands than among mainland stands ($\chi^2_{48} = 69.12$ and $\chi^2_{40} = 72.04$, respectively; Table 3).

For the mainland, the frequency distributions were homogeneous among stands within each of the three stand initiation periods. However, the frequency of trees within serotiny levels was significantly different between these periods ($\chi^2 = 33.18$; Table 3; Fig. 3). For the 1760–96 period, there was a highly significant excess of NS and QNS trees, while for the more recent periods, there were excesses of trees in the M or QS levels (Fig. 3). In other words, the frequency of low serotiny trees increases with time since stand initiation.

In the island landscape, there was significant het-

Table 3 Heterogeneity among stands in frequencies of tree serotiny levels (decomposed likelihood chi-squares, χ^2)

Effect	χ^2	d.f.	P
Stand initiation period			
Mainland			
1760	7.96	4	0.093
1797–1887	17.44	15*	0.293
1888–1987	13.47	16	0.638
between periods	33.18	8	0.000
mainland heterogeneity	72.04	48	0.014
Island			
1797–1887	47.98	24	0.003
1888–1987	16.98	12	0.150
between periods	4.16	4	0.385
island heterogeneity	69.12	40	0.003
Non-lethal island fire occurrence			
1797–1887	47.98	24	0.003
without nonlethal	6.33	4	0.176
with nonlethal	27.35	16	0.038
between fire regimes	14.31	4	0.006
1888–1987	16.98	12	0.150
without nonlethal	2.39	3†	0.176
with nonlethal	4.98	4	0.290
between fire regimes	9.62	4	0.047
Landscape			
mainland heterogeneity	72.04	48	0.014
island heterogeneity	69.12	40	0.003
between landscapes	15.06	4	0.005
Overall	156.22	92	0.000

*One of the stands had no NS trees. †None of these stands had NS trees.

erogeneity among stands ($\chi^2 = 69.12$; Table 3). Within stand initiation periods, significant heterogeneity was observed among stands within the 1797–1887 period ($\chi^2 = 47.98$; Table 3), but not within the 1888–1987 period ($\chi^2 = 16.98$; Table 3). The chi-square decomposition reveals that the occurrence of nonlethal fires after stand initiation may explain the observed heterogeneity between island stands (Table 3). For both stand initiation periods, the stands affected by nonlethal fires were significantly different from those without nonlethal fire, particularly for the older stands (1797–1887 $\chi^2 = 14.31$; 1888–1987 $\chi^2 = 9.62$; Table 3). The occurrence (or absence) of nonlethal fires has a greater effect on the frequency of trees within serotiny levels than does the time elapsed since stand initiation ($\chi^2_4 = 13.48$, $P = 0.009$, data not shown; $\chi^2 = 4.16$, Table 3). The frequency of QS or S trees is lower on islands with nonlethal fires than on islands without nonlethal fires (Fig. 4).

Finally, a significant difference in the frequency of trees within serotiny levels was observed between the two landscapes (Table 3). The Pearson chi-square components show that on the mainland there are significantly more S trees, and significantly fewer trees in the QNS level than expected (Fig. 5). An overall difference of 13% in the distribution of trees among serotiny levels was estimated between the two land-

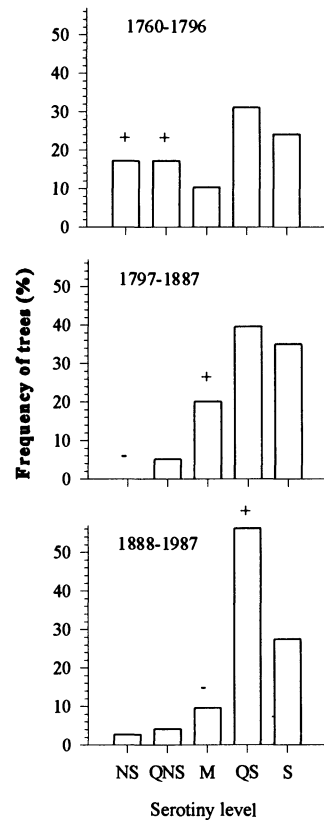


Fig. 3 Frequency distributions of tree serotiny levels for three stand initiation periods for the mainland. Significant deviation from the expected distribution of serotiny levels at $P < 0.01$ following Pearson chi-square component tests is indicated (+, excess; -, deficiency).

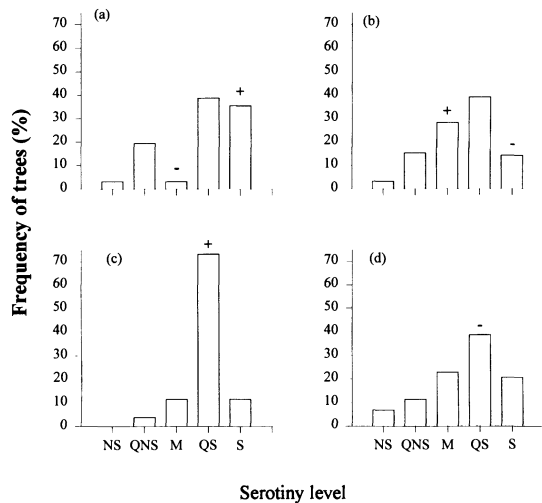


Fig. 4 Frequency distributions of tree serotiny levels for the islands with and without nonlethal fires between stand initiation periods. (a) 1797–1887 without nonlethal fire; (b) 1797–1887 with nonlethal fire; (c) 1888–1987 without nonlethal fire; (d) 1888–1987 with nonlethal fire. Significant deviation from the expected distribution of serotiny levels at $P < 0.01$ following Pearson chi-square component tests is indicated (+, excess; -, deficiency).

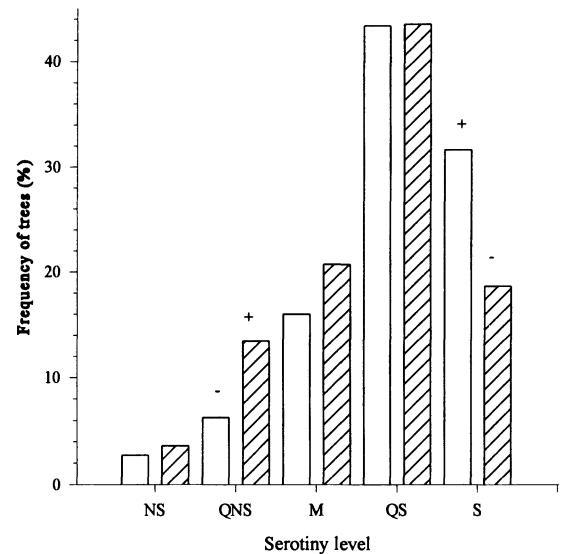


Fig. 5 Frequency distributions of tree serotiny levels for (□) mainland and (▨) island sites. Significant deviation from the expected distribution of serotiny levels at $P < 0.01$ following Pearson chi-square component tests is indicated (+, excess; -, deficiency).

differences between landscapes in the number of trees in establishment types or stand initiation periods, log-linear models were fitted with and without the interaction between the serotiny levels and landscape groups and showed the interaction to be highly significant (difference between the models $\chi^2_8 = 30.33$, $P < 0.001$; Gauthier 1991). A significant deficiency of QNS trees was observed on the mainland, compensated by a significant excess of S trees (Fig. 6). For islands with nonlethal fires, there were significant deficiencies of high serotiny trees (QS and S; Fig. 6). The frequency distribution of trees within serotiny levels from the islands without nonlethal fire is intermediate between the other two groups (Fig. 6). Mixed serotiny level trees (M) were under-represented in this group, and this deficiency was compensated for in all the other serotiny levels.

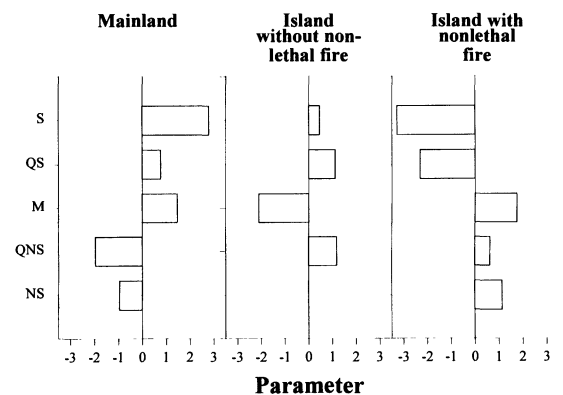


Fig. 6 Standardized parameters of the log-linear model for the interaction effect of landscape groups on the frequency distribution of trees within serotiny levels. Parameters with absolute values > 1.96 are significantly different from 0 at $P < 0.05$.

Discussion

Our results indicate that a higher frequency of highly serotinous trees are recruited after lethal fires whereas recruits with low and mixed levels of serotiny appear to be favoured after nonlethal fires. Some nonlethal fires do not reach temperatures high enough to open the serotinous cones, reducing the chance for a serotinous progenitor to disperse seeds and ensure regeneration (Johnson & Gutsell 1993; Tinker *et al.* 1994). The comparison of islands with and without nonlethal fires after stand initiation supports the prediction that nonlethal fires tend to increase the frequency of low serotiny trees in the population (Fig. 4). Low intensity fires also appear to favour nonserotinous individuals in *Pinus* and *Banksia* species (Givnish 1981; Borchert 1985; Muir & Lotan 1985; Cowling & Lamont 1985; Enright & Lamont 1989).

When establishment occurs in the absence of fire, the frequency of highly serotinous trees is lower than after a fire, and this trend is even stronger on sites previously affected by nonlethal fires. These results suggest that nonserotinous or mixed trees are favoured in the absence of fire. The fact that there is a higher proportion of nonserotinous or mixed trees in the absence of fire suggests that these trees may ensure regeneration after other types of disturbance by dispersing their seeds relatively continuously (Muir & Lotan 1985). At the population level, the frequency of low serotiny trees increases with time since stand initiation, supporting the hypothesis that a long fire-free interval would favour low serotiny-type trees because establishment opportunities after nonfire disturbances are also increasing (Perry & Lotan 1979; Givnish 1981; Muir & Lotan 1985). Any effect of time since stand initiation may be obscured on the islands because: (1) the populations had shorter fire-free intervals (all < 200 years), and (2) the frequent occurrence of nonlethal fires may lead to an increase in trees with low serotiny levels that are better able to disperse seeds after such fires, and so mask the effects of establishment class.

When comparing the two classes established in the absence of fire, we observed a higher proportion of low serotiny trees where nonlethal rather than lethal fire had occurred prior to tree establishment (Fig. 2b,d). This suggests that, within a population, the frequency of low serotiny trees increases as a result of the recurrence of nonlethal fires. Furthermore, our results suggest that recent fire history in a population does not explain all of the variation in the serotiny levels of trees observed between landscapes. In fact, we observed significant differences among landscapes after controlling for differences in establishment types and time since stand initiation. The islands without nonlethal fires after stand initiation, i.e. those under conditions similar to those encountered on the mainland, show an excess of low serotiny trees when compared with the mainland (Fig. 6), suggesting a long-

term effect of fire regime on serotiny levels. In fact, as fire occurrence is high in the island landscape (Bergeron & Brisson 1990), most islands have probably experienced nonlethal fires at some point in the past so that some low and mixed serotiny level trees would be expected to be present at the time of the stand-initiating fire. Further, in the island landscape, fire years are independent from one island to another (Bergeron 1991), resulting in a higher heterogeneity in the frequency of trees in the serotiny levels among islands than observed among mainland stands. At any given time, there are, overall, more nonserotinous and mixed trees in the island landscape than on the mainland, increasing the probability of cross-pollination between serotiny types. The low serotiny trees which predominate after a nonlethal fire may provide seeds for recruitment on adjacent islands.

A considerable amount of variation in serotiny levels ($\approx 50\%$) of trees remains unexplained by establishment class, time since stand initiation or occurrence of nonlethal fires. This may be a consequence of our sampling design which does not control for natural variation between stands and/or landscapes and tends to sample trees from within the same population which are more likely to be alike (Tinker *et al.* 1994). Several studies on lodgepole pine have indicated potential effects of site characteristics on the expression of serotiny (Tinker *et al.* 1994). As the genetic basis of jack pine serotiny and the genetic-environment interaction are not yet understood, it is possible that environmental effects are responsible for a portion of the variation in serotiny, despite our effort to minimize environmental variation among stands. Another possible cause is the different history of stands with, for instance, short intervals between lethal fires or very intense fire favouring nonserotinous trees (Muir & Lotan 1985; Lamont *et al.* 1991; Tinker *et al.* 1994; Enright *et al.* 1996). Selection pressures by squirrels on serotinous cones have been reported for lodgepole pine (Smith 1970), suggesting that factors other than fire could also affect the level of serotiny in jack pine. In the absence of comparative data on squirrel density, it is difficult to predict their relative effects on the two landscape populations. However, the differences between islands with and without nonlethal fires suggest that predation probably plays a minor role in the explanation of differences among islands and that fire intensity has a stronger effect than predation on the serotiny levels of trees.

The difference in serotiny levels between the two landscapes is relatively small, despite the difference in fire regimes. In our study area, the majority of jack pine trees were highly serotinous even in the landscape (island) affected by the more complex fire regime (QS and S: Mainland = 74%; Island = 62%). In the boreal forest, the fire-free interval is relatively long and the fires are large and intense (Heinselman 1981; Bergeron 1991; Payette 1992; Johnson 1992) while the islands studied here are affected by lethal as well as

nonlethal fires. The background cycle of lethal fires on islands may well prevent a large reduction in serotinous type trees. Perry & Lotan (1979) hypothesize that a fire regime that is variable in space but relatively constant in time would allow for the maintenance of polymorphism for lodgepole pine serotiny. Our results, which showed a slight but significant difference (13%) in serotiny between the two landscapes, are in agreement with their predictions. The complex fire regime on the islands of Lake Duparquet appears to favour low and mixed serotiny level trees, although highly serotinous trees appear to have an overall advantage in a region with a disturbance regime of large and intense fires.

The complex fire regime of Lake Duparquet is thought to have an impact on forest community and population dynamics. It is, for instance, invoked to explain the presence or abundance on islands of several species of trees that are absent or uncommon on the mainland, such as red pine (*P. resinosa* Ait.; Bergeron & Gagnon 1987), eastern cedar (*Thuja occidentalis* L.; Bergeron & Dubuc 1988) and common juniper (*Juniperus communis* L.; Diotte & Bergeron 1989). The fire regime also appears to have an effect on island population structure. For example, uneven-aged populations of jack pine are observed on islands as a result of the occurrence of nonlethal fires (Gauthier *et al.* 1993b). Moreover, the higher recruitment rate in the absence of fire on the islands than on the mainland is probably due to the greater abundance of trees with low levels of serotiny (NS, QNS or M). The observed differences in age structure of jack pine populations between the two landscapes are therefore probably due to differences in fire regimes and in serotiny levels of populations.

Previous studies suggesting that disruptive selective pressures are acting on serotiny levels of trees (Givnish 1981; Muir & Lotan 1985), with lethal fires selecting for highly serotinous trees and nonlethal fires or nonfire disturbances favouring low serotiny level trees, are confirmed by our results. Variation in serotiny levels allows jack pine to regenerate under a range of conditions and this flexibility may be an important feature for species maintenance in a context where climate change alters fire regimes (Bergeron & Flannigan 1995). Although our results suggest that fire exerts selective pressures on the evolution of serotiny in jack pine, further work on the genetic basis of jack pine serotiny and interaction with the environment is required.

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