

Biotic disturbance in expanding subarctic forests along the eastern coast of Hudson Bay

Marco Caccianiga^{1,3}, Serge Payette¹ and Louise Filion²

¹NSERC Northern Research Chair, Centre d'études nordiques, Université Laval, Québec, Canada G1K 7P4; ²Département de géographie and Centre d'études nordiques, Université Laval, Québec, Canada G1K 7P4; ³Present address: Dipartimento di Biologia, Sezione di Botanica Sistemática, Università di Milano, 20133 Milano, Italy

Summary

Author for correspondence:

Marco Caccianiga

Tel: +39 0250314848

Fax: +39 0250314840.

Email: marco.caccianiga@unimi.it

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- The past and present occurrence of insect disturbance on white spruce (*Picea glauca*) trees was evaluated at their northern range limit on the eastern coast of Hudson Bay, and its effects on tree growth and population dynamics studied.
- Three sites were sampled along an altitudinal gradient. Ring-width chronologies and stem analysis were used to evaluate tree growth. The occurrence of holes in the bark, of resin pockets and blue-stain fungi, and ring-width evidence for growth releases were used to assess the impact of bark beetle.
- The white spruce population was established at these sites in the 17th century. Since their establishment, the spruce trees have developed a tree growth form, except at the uppermost site, where severe growth suppression occurred in the 19th century. Bark beetle and blue-stain fungi occurred with different timing and intensity. Their highest occurrence, associated with high mortality rates, was at the lowest site in the late 20th century. In the uppermost sites, biotic disturbance has occurred since the 18th century, associated with evidence for mechanical disturbance.
- The simultaneous arrival of white spruce in the area resulted in a synchronous onset of spruce beetle activity driven by tree ageing. Unfavourable climatic conditions affected tree growth severely in the most exposed sites.

Key words: bark beetle, blue-stain fungi, climate change, dendrochronology, *Picea glauca*, subarctic Québec, treeline.

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Introduction

Knowledge of tree growth responses to environmental parameters is crucial for interpreting the effects of past and present climate forcing on ecosystems. Although tree-ring analysis has been used widely as a proxy of climatic conditions, many studies have demonstrated the complexity of the relationship between tree growth and all environmental parameters. In boreal ecosystems, biotic disturbances (insect outbreaks, herbivory and fungal attacks) play a major role in nutrient turnover and in the overall dynamics of forest ecosystems, often in association with fire (McCulloch *et al.*, 1998; Malmström & Raffa, 2000; Cairns & Moen, 2004).

Biotic disturbances can result in anomalous growth patterns and major variations in tree population structure, particularly when associated with other disturbances or unfavourable climatic conditions (Veblen *et al.*, 1991; Zhang *et al.*, 1999; Lemieux & Filion, 2004; Rolland & Lempérière, 2004; Jasinski & Payette, 2005). Moreover, underestimation of the effects of pests and herbivores can severely affect the accuracy of tree ring-based climatic reconstructions (Trotter *et al.*, 2002).

In subarctic forests (forest–tundra ecotone) fire frequency decreases with the increasing fragmentation of forest patches, and old-growth stands can be found near the treeline (Payette *et al.*, 2001). The role of ageing trees in the occurrence of

biotic disturbance could be important as mature trees are preferential hosts for spruce beetle (Werner *et al.*, 2006), and their availability could be a limiting factor, as observed for recent beetle outbreaks in Alaska (Berg *et al.*, 2006; Soja *et al.*, 2007). Synchronous senescence of evenly aged stands could be a favourable situation for the occurrence of outbreaks.

In northern Québec–Labrador, contrasting dynamics of forest–tundra ecosystems have been outlined according to (i) specific traits of the tree species involved (white spruce, *Picea glauca* (Moench) Voss and black spruce, *Picea mariana* (Mill.) B.S.P., Payette & Filion, 1985; Caccianiga & Payette, 2006), and (ii) contrasting patterns of postglacial migration (Ritchie, 1987; Payette, 1993, 2007; Caccianiga & Payette, 2006). Unlike western North America (Berg *et al.*, 2006; Werner *et al.*, 2006 and references therein), biotic disturbance seems to play a minor role. The main pest affecting white spruce close to the treeline in North America, spruce bark beetle (*Dendroctonus rufipennis* Kirby; Coleoptera: Scolytidae), has been recorded here only sporadically. Twentieth century white spruce dieback in northern Labrador has recently been attributed to this insect (Payette, 2007), which may have played a significant role in the past. In general, the role of insects in the dynamics of the northernmost forest ecosystems of eastern North America remains largely unexplored.

The aim of this study is to evaluate the occurrence of biotic (insect herbivory) disturbance on white spruce trees at their northern range limit on the eastern coast of Hudson Bay over the past 400 yr and its possible effects on tree growth. The time span investigated corresponds to the major climatic excursion of the Little Ice Age and the present, and to consequent changes in the structure of subarctic ecosystems. We have used a dendroecological approach that allows a high temporal resolution in reconstructing the events that affected the growth of the populations investigated. Disturbance events were analysed using radial (tree-ring) and vertical (tree-stem) growth data of trees from three expanding white spruce populations along an altitudinal gradient.

Materials and Methods

Study sites

The study was carried out along the east shore of Hudson Bay, in northern Quebec, Canada (Fig. 1). The study area lies in the forest–tundra ecotone, consisting of forest stands in the lowlands and treeless tundra on the hills. It belongs to the oceanic domain of the forest–tundra under the climatic influence of Hudson Bay, characterized by the occurrence of white spruce trees and forests (Payette, 1983, 1993). White spruce is the dominant species in the study area; the other tree species occurring are black spruce and tamarack (*Larix laricina* (Du Roi) K. Koch). Both white spruce and black

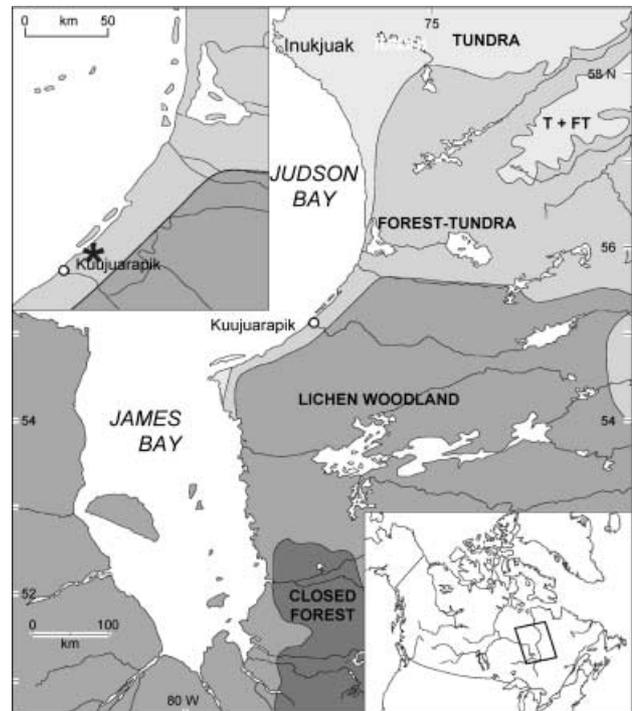


Fig. 1 Study site and main vegetation types.

spruce occur as krummholz (stunted individuals) in the coastal tundra along the Hudson Bay coast, north of the forest–tundra ecotone (Payette & Filion, 1985; Caccianiga & Payette, 2006).

The study area (Cri Lake; 55°18'N, 77°41'W) is located close to the village of Whapmagoostui–Kuujuarapik and consists of a narrow, east–west-oriented valley, open towards the Hudson Bay. Within the valley, three sampling sites were investigated along an altitudinal gradient. Site 1 is located close to the shore of a small lake (Cri Lake) at 100 m asl, and is occupied by a dense forest dominated by white spruce with black spruce and tamarack as companion species. Site 2 lies at 135 m asl and consists of a mixed white spruce and black spruce forest with large openings caused by patches of marine-reworked boulder deposits. Site 3 lies at 175 m asl, at the top of the valley, and is occupied by an open white spruce stand.

The three stands form young forests composed of old white spruce trees established during the 17th and 18th centuries, and subject to infrequent disturbances such as occasional logging by Cree people from Whapmagoostui–Kuujuarapik. Insect outbreaks have not been recorded so far in the area. Long-lasting snow cover is currently recorded in the forest stands until July, particularly at site 3 (Filion & Payette, 1982). Previous dendroclimatic studies were performed on white spruce in the Cri Lake area (Parker *et al.*, 1981; Jacoby *et al.*, 1988). In these studies, ring-width and wood-density data were used to reconstruct the temperature of the growing season over the past centuries.

Dendroecological analysis

A total of 106 white spruce trees were sampled at Cri Lake (34 from site 1; 44 from site 2; 28 from site 3). In order to detect species-specific growth patterns, 11 black spruce trees were also sampled (four from site 1 and seven from site 2; black spruce does not occur at site 3). Two cores were taken from each living tree, with a Pressler increment borer, from opposite sides of the tree at the base of the trunk. Cross-sections were taken from dead trees at the lowest possible level along the trunk. Trees that showed reaction wood and rotten wood were discarded. Samples were air-dried and finely sanded. Annual ring width was measured with a Velmex micrometer at $\times 40$ with a precision of 0.01 mm. Cross-dating of the samples was performed using light rings (rings with exceptionally few latewood cells; Fillion *et al.*, 1986). High-frequency (> 75% of all dated tree-ring samples) light-ring years occurred 23 times since 1686. All the wood samples were searched for diagnostic markers (e.g. scars, diagnostic rings) of the events that could have affected tree growth.

Tree-ring chronologies A tree-ring chronology of white spruce was constructed for each site. To build a chronology, only highly intercorrelated individual curves ($r > 0.6$) were retained. Individual curves were standardized by regression lines or by polynomial functions of degree 2–4. Standardized curves were then averaged to obtain index chronologies. For each chronology, first-year autocorrelation and sensitivity (mean percentage change from each yearly ring value to the next) were calculated. Correlation values for the individual curves and statistics for the chronologies were calculated using the program COFECHA (Holmes, 1983). For each chronology, the subsample signal strength (SSS; Wigley *et al.*, 1984) was calculated. This test defines the minimum number of samples representative of the whole series, and consequently the significant length of the chronology. Only the part of the series with an SSS value > 0.85 was retained in the final chronologies. It was not possible to build a black spruce chronology.

Occurrence of insect damage Insect damage occurrence was assessed by direct observation of extant spruce trees. Of particular importance, insect galleries at the bark–wood interface and bore holes in the bark, probably attributable to bark beetle (*C. Cloutier*, pers. comm.), were recorded systematically on white spruce trees of all sites studied. Inferred past bark beetle attacks were identified and dated by recording resin pockets and blue-stain fungi. Resin pockets are crescent-shaped resin accumulations that can be found either between two annual rings or within a ring, which usually appears deformed. These structures are usually associated with bark beetle attacks that the tree survived (Franceschi *et al.*, 2000; Rolland & Lempérière, 2004), and can easily be dated when cross-sections are cut close enough to the level

of beetle attack. Although such structures are reported to be ‘clear evidence for insect attack’ (Rolland & Lempérière, 2004), a different traumatic origin could not be excluded.

Blue-stain fungi are a group of phytopathogens (e.g. genera *Ceratocystis*, *Ophiostoma*, *Leptographium*) vectored by bark beetles (Paine *et al.*, 1997; Franceschi *et al.*, 2005), which leave characteristic blue stains in the sapwood (Paine *et al.*, 1997; Haberkern *et al.*, 2002; Franceschi *et al.*, 2005). Although some blue-stain fungi are able to colonize wounds of living spruce in the absence of bark beetles (e.g. *Ceratocystis coerulea* complex, Paine *et al.*, 1997), they mostly colonize wounds caused by beetles or are associated with them (Paine *et al.*, 1997; Harrington & Wingfield, 1998). Thus most blue-stain fungal attacks on conifers are associated with these insects (Franceschi *et al.*, 2005). In the Great Lakes region, no blue-stain fungi were observed on white spruce trees that were not attacked by spruce beetles (Haberkern *et al.*, 2002). Given these considerations, we used the year of inception of each blue stain as an indicator of the probable year of bark beetle attack. As the exact year of inception of blue-stain fungi was often difficult to identify, data on blue-stain fungi were arranged in 5-yr classes.

Both individual ring-width curves and chronologies were searched for anomalous ring-width patterns that could be linked to past insect attacks. Unlike those of defoliator insects, bark beetle outbreaks cannot usually be detected by growth suppression (Veblen *et al.*, 1991), although ring-width reduction has been recorded following bark beetle attacks (Rolland & Lempérière, 2004). The most widely used signal of past bark beetle outbreaks is given by growth releases of understory spruce following the death of the dominant trees (Veblen *et al.*, 1991; Berg *et al.*, 2006). Following Berg *et al.* (2006), we detected growth releases for individual trees by calculating for each year a ratio of the forward 10-yr mean of ring widths to the backward 10-yr mean of ring widths. A growth release is marked by a ratio exceeding 2.0. When a growth release was detected, we discarded any release in the subsequent 10 yr. The percentage of trees showing growth release was calculated for each site; data were arranged in 5-yr classes.

Other diagnostic rings

Rings with a higher-than-normal concentration of resin ducts were recorded as an indicator of stress. Such stress could be mechanical (Thomson & Sifton, 1926), climatic (e.g. warmer than normal summer, Wimmer & Grabner, 1997) or biotic (e.g. bark beetle attack, Tomlin *et al.*, 1998; Franceschi *et al.*, 2000) in origin. Mechanical damage of any origin (biotic or abiotic) was assessed by the occurrence of traumatic scars. All these disturbance markers were compared with ring-width curves to look for associated growth anomalies. Both individual curves and ring-width chronologies were used for the comparison.

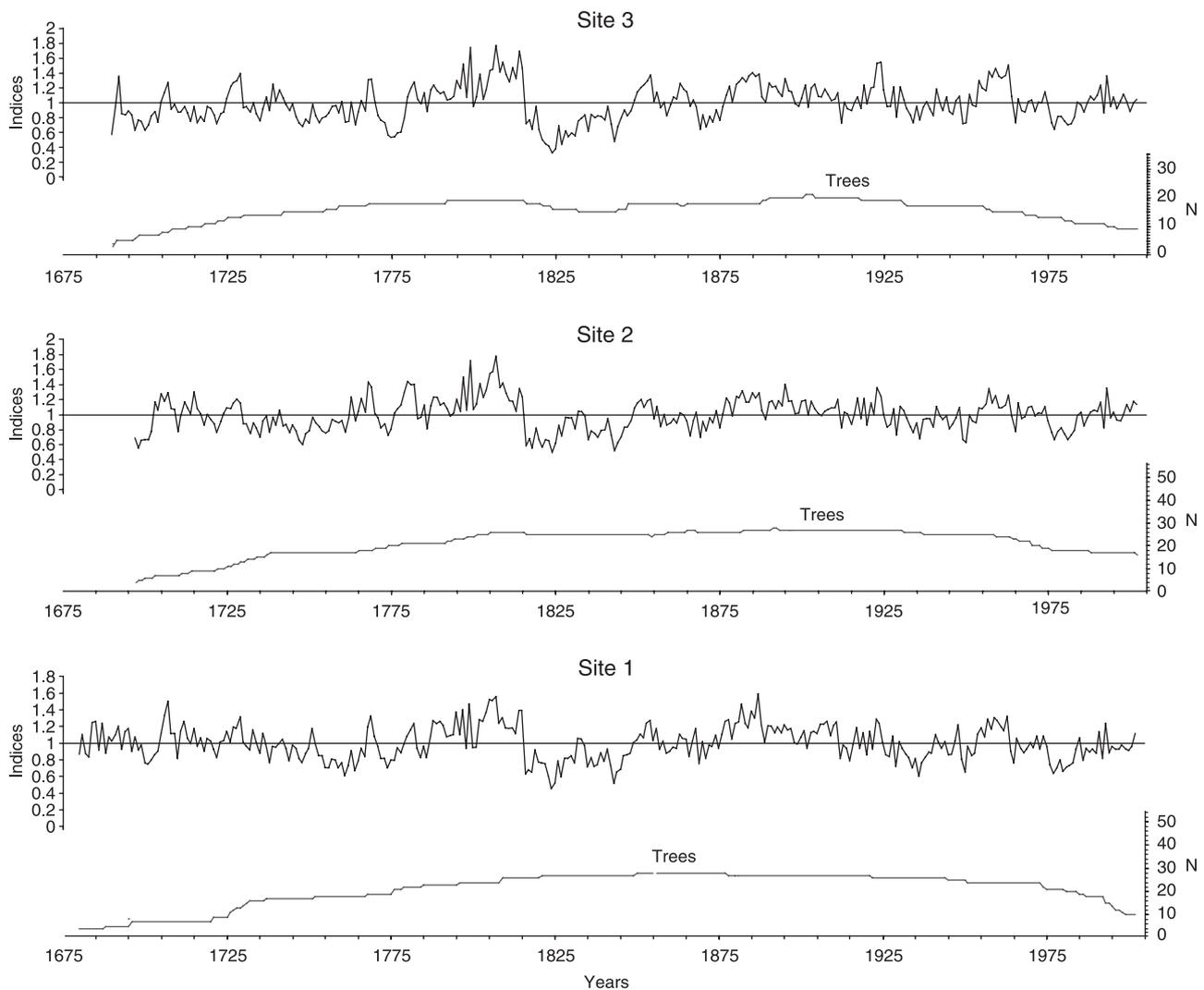


Fig. 2 Indexed chronologies of white spruce (*Picea glauca*) from Cri Lake. The number of individual trees is also indicated.

Stem analysis Sixteen white spruces were selected for stem analysis, three from site 1, eight from site 2 and five from site 3. These trees were mainly dead old spruces representative of the different growth forms from undisturbed, single-stemmed trees to multistemmed trees with obvious signs of axis mortality. Two moribund and one living white spruce were sampled at site 2. Tree height ranged from 3 m to approx. 15 m. Stem growth was reconstructed by taking a cross-section at every 50 or 100 cm along the stem; extra sections were taken at every 25 cm at the top of some trees and at significant levels at the base of reiterated axes (stem developed after loss of main apex). Each cross-section was air-dried and sanded. Tree rings were counted and tree-growth anomalies (scars, resin canals, resin pockets, blue-stain fungi) were recorded. Stem analysis was also performed on five black spruce trees from site 2 for further comparison with the growth patterns of white spruce trees.

Results

Tree-ring chronologies

The oldest white spruce trees were established in AD 1649, 1618 and 1652 for sites 1–3, respectively, and the chronologies extended from 1680–2002, 1687–2002 and 1690–2002 (Fig. 2). Mean ring width was similar among the chronologies (0.64, 0.58 and 0.62 mm, respectively). Mean index sensitivity and autocorrelation were both slightly higher for the site 3 chronology (Table 1). The chronologies showed an overall similarity in the low-frequency domain, and the correlation values among the series were very high for both ring width and ring indices (Table 2). Growth was generally good before 1816, except for the period 1755–65 at site 1, and 1748–58 at sites 2 and 3. A period of reduced growth around the 1770s became more important from site 1 to site 3, where the

Parameter	Site		
	1	2	3
Trees	28	31	26
Radii	51	57	45
Mean ring width (mm) ± SD	0.64 ± 0.155	0.58 ± 0.154	0.62 ± 0.191
Mean <i>r</i>	0.85	0.86	0.85
Sensitivity	0.14	0.15	0.16
First-year autocorrelation	0.71	0.75	0.78
Significant time series (SSS > 0.85)	1680–2002	1697–2002	1690–2002
Original time series	1675–2002	1685–2002	1659–2002
Min no. samples (SSS)	3 (0.89)	3 (0.88)	3 (0.86)
Mean index ± SD	0.99 ± 0.202	0.99 ± 0.210	1.00 ± 0.247
Mean index <i>r</i>	0.83	0.85	0.85
Index sensitivity	0.14	0.14	0.16
Index autocorrelation	0.61	0.63	0.69

Table 1 Characteristics and statistics of the Cri Lake tree-ring series

SSS = subsample signal strength.

Table 2 Correlation matrix between the Cri Lake ring-width (upper matrix triangle) and index (lower matrix triangle) series

Site	1	2	3
1		0.68	0.39
2	0.85		0.42
3	0.83	0.82	

whole decade showed a marked growth decrease. A trend of increased growth occurred at the beginning of the 19th century. This trend ended abruptly in 1816, when a severe drop in ring width started a period of reduced growth that lasted until *c.* 1850. The decrease in mean ring width in 1816 was from 0.89–0.40 mm (54%) for site 1, and 0.70–0.33 mm (53%) for sites 2 and 3. The recovery after 1816 was very slow, particularly at sites 2 and 3. Ring-width recovery, particularly effective at site 1, peaked in the 1880s; afterwards, growth slightly lowered until the beginning of the 1930s. Two abrupt growth suppressions occurred in 1949–50 and in 1965, and a longer period of reduced growth could be observed from 1976–82.

Black spruce trees showed very irregular growth patterns. Only young individuals (established after 1871) were recorded at site 1. The oldest spruce from site 2 established in 1699, but could be measured only since 1728. The correlation between samples was always very low and a tree-ring chronology could not be built. Individual curves (Fig. 3) showed slow growth during the 18th and most of the 19th centuries. The average ring width was always lower than 0.2 mm before 1850 (Table 3), suggesting stunted growth of black spruce in contrast to that of white spruce. The growth rate of the youngest individuals increased markedly in the 20th century, reaching that of white spruce (Table 3).

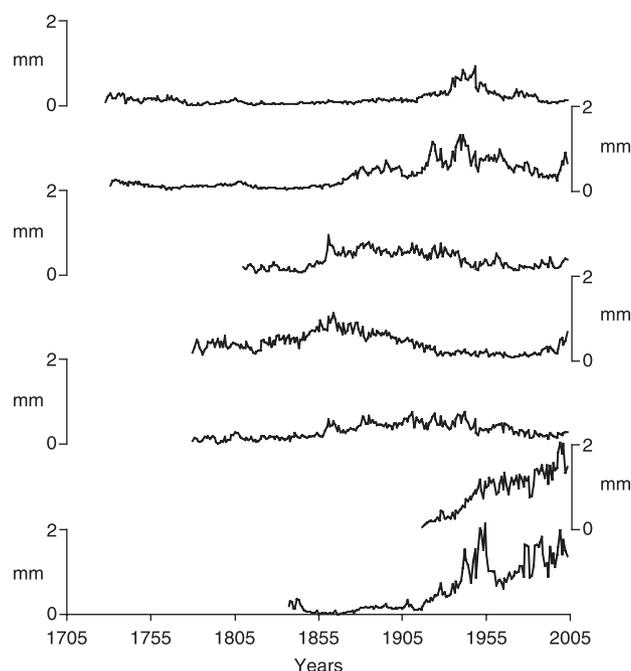


Fig. 3 Individual ring-width curves of black spruce (*Picea mariana*) from site 2.

Dendroecological analysis

Resin pockets and blue-stain fungi Resin pockets and blue-stain fungi were observed at every site. Resin pockets occurred from 1710 onwards, with high frequencies in 1861, 1909 and 1951 (Fig. 4). At site 1, they could be observed since 1807, with high-frequency years in 1909 and 1951. Trees at site 2 showed resin pockets from 1710–2002, with clustered distribution mostly in the second half of the 19th century, and years of highest occurrence in 1951, 1972 and 1986. At site 3, they occurred in the second half of the 18th century,

Table 3 Mean ring width of white spruce (*Picea glauca*) and black spruce (*Picea mariana*) for 50-yr time periods in all sites

Site/species	Mean ring width (mm)						
	1651–1700	1701–1750	1751–1800	1801–1850	1851–1900	1901–1950	1951–2003
White spruce							
1	0.729	0.695	0.633	0.592	0.737	0.613	0.494
2	0.761	0.692	0.707	0.524	0.555	0.47	0.528
3	0.63	0.647	0.55	0.426	0.582	0.708	0.812
Black spruce							
1					0.412	0.535	0.957
2			0.181	0.189	0.376	0.477	0.585

particularly from 1774–1807; they were also observed from 1815–21 and 1839–1951. High-frequency years were 1861, 1909, 1914 and 1951. No resin pockets were found after 1951 at this site. On black spruce samples, resin pockets occurred only on a single tree at site 1 in 1924, 1975 and 1999, and at site 2 in 1922 and 1951.

Blue-stain fungi were observed with the highest frequency at site 1. A general correspondence could be observed with the occurrence of resin pockets (Fig. 4). Most of the blue stains were found in the outermost part of the wood, usually associated with holes and galleries in the bark of recently dead trees (Fig. 5), but also within the wood, indicating that the tree survived former insect attacks. In one case, the cross-section allowed us to observe the association between a resin pocket and the inception of a blue stain (Fig. 5). At site 1, blue-stain fungi were observed throughout the 18th century, before the appearance of resin pockets. Their frequency increased in the 20th century, reaching a peak in the 1990s, when they occurred on more than 60% of the samples, mostly in the outermost part of the wood of recently dead trees. A similar pattern was apparent at site 2, but at a lower frequency and with a peak in the 1970s. At site 3, blue-stain fungi occurred infrequently in the 1670s, the 1730s, and more frequently in the 1770s, 1780s and 1810s, always associated with resin pockets. The subsequent occurrence of blue stain coincided with peaks of resin pockets (1860s, 1890s, 1910s, 1950s), with the exception of the 1970s and 1990s when no resin pockets were observed (Fig. 4), probably because the inception of blue-stain fungi corresponded mostly to tree death. No sample of black spruce trees showed blue-stain fungi at any site.

Growth release Growth release episodes were recorded with low frequency at sites 1 and 2 (< 10% of trees always showed growth releases in those sites; Fig. 6). At site 3, the highest frequency of growth release was recorded in the periods 1778–82 (16.6% of trees showing a release), 1828–32 (33.3%) and 1873–77 (25%) (Fig. 6). It must be stressed that our method did not allow the detection of growth releases of the first and last 10 yr of each chronology.

Resin ducts and scars High frequency (> 2/3) of rings with high resin canal concentration was recorded in 1819, 1916, 1955 and 1967 at all sites. A slight increase of years with high resin canal concentration was apparent during the 20th century (Fig. 7).

With the exception of a small scar on a tree at site 3 in year 1679, no scar was found before 1749 (Fig. 7). The pattern of scar distribution was different among sites. At site 1, scars occurred only twice (1830 and 1854) in the 19th century and then in the second half of the 20th century. At site 2, scattered traumatic events were recorded in 1796 and in the 19th century, with the highest scar occurrence in the mid-20th century. Trees at site 3 showed many scars in the 1760s–80s, in the first half of the 19th and in the 20th century. As a general pattern, scars occurred earlier and more frequently moving upward along the altitudinal gradient (Fig. 7).

Stem analysis

The trees sampled at site 1 showed relatively fast height growth throughout their life span (Fig. 8). At the beginning of the 19th century, some trees were approx. 10 m tall. Vertical growth lowered in the first half of the 19th century but recovered to the previous level in the 20th century. At site 2, trees established after 1800 showed a pattern similar to those of site 1. Older trees grew much more slowly and, in some cases, experienced severe growth suppression since the 18th century. At the beginning of the 19th century, the tallest trees were approx. 6 m tall. At site 3, growth was slower, and at the beginning of the 19th century approx. 150-yr-old trees were only 2–4 m tall. The growth of all trees sampled almost stopped from the mid-18th century to the 1850s; afterwards, only some trees were able to recover with a growth rate similar to that observed at the lower sites. Vertical growth of black spruce from site 2 (Fig. 8) followed the same pattern as nearby white spruce: fast growth was apparent after 1850, particularly for the youngest trees, established *c.* 1800. Before 1900, black spruce trees were shorter than 6 m.

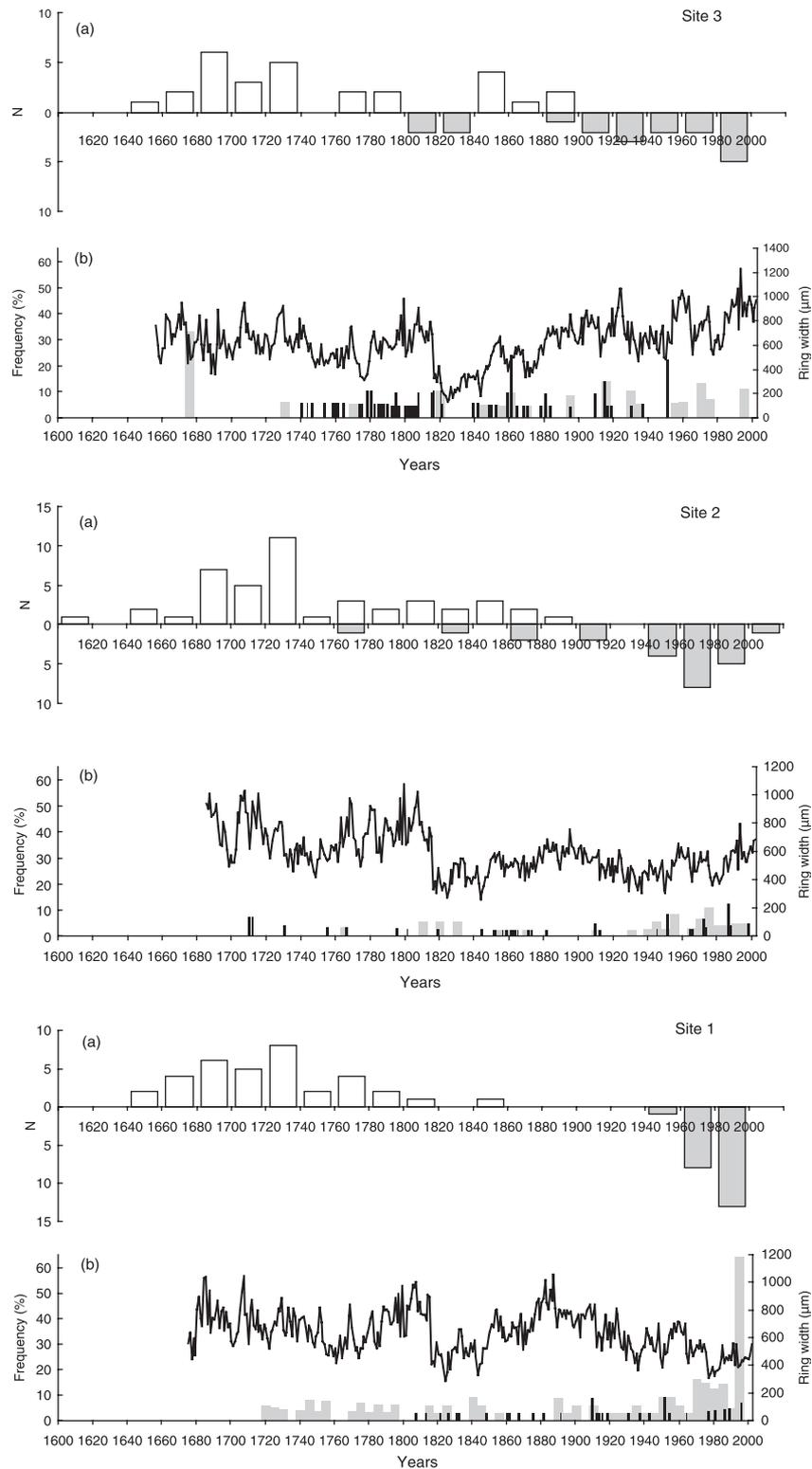


Fig. 4 Frequency of resin pockets and blue-stain fungi. Upper panels: date of establishment (a) and mortality (b) of white spruce (*Picea glauca*). Lower panels: frequency of resin pockets (black bars) and blue-stain fungi (grey bars) compared with ring-width chronologies. Blue-stain fungi data are arranged in 5-yr classes.

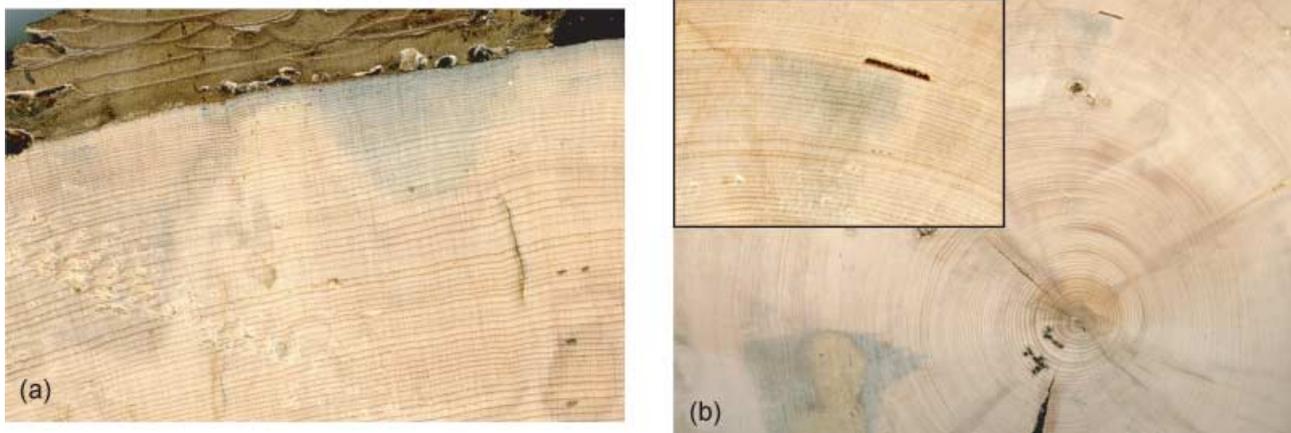


Fig. 5 Blue-stain fungi on white spruce (*Picea glauca*) stumps. (a) Blue stain occurring in the outermost part of the wood associated with bore holes in the bark: the tree died after the insect attack (site 1). (b) Blue stain inception in 1819: the tree survived after the insect attack. Inset, association between a resin pocket and inception of a blue stain (site 2).

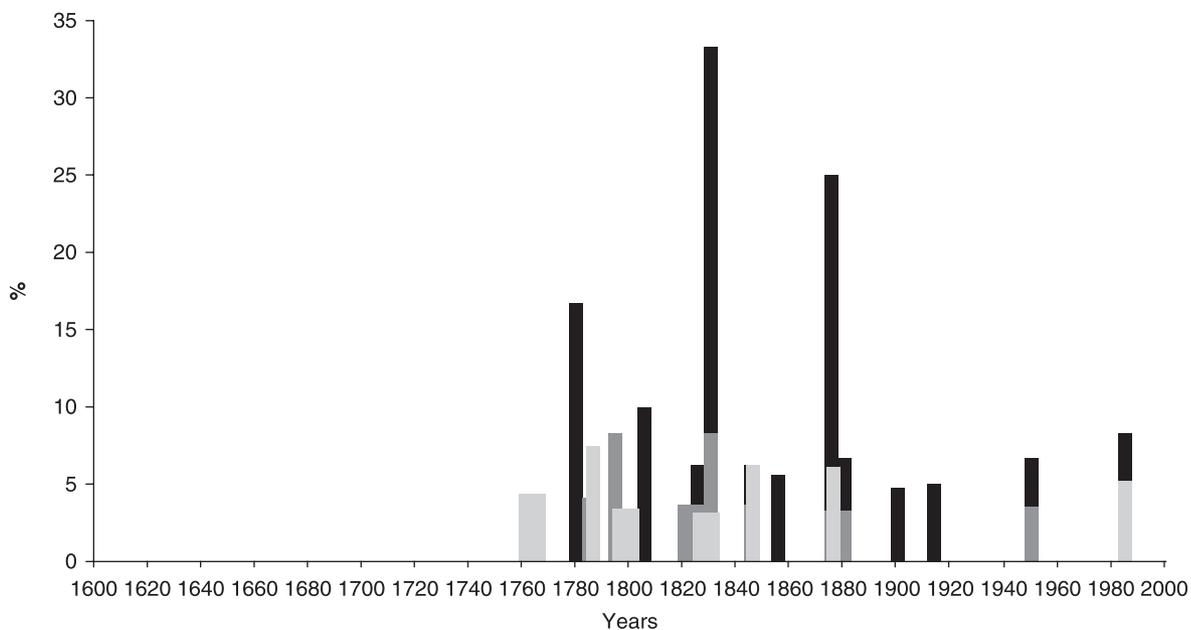


Fig. 6 Percentage of trees showing growth release at each site. Data are arranged in 5-yr classes. Site 1, light grey bars; site 2, dark grey bars; site 3, black bars.

Discussion

The ecological context in the last 400 yr

The overall stand structure of all sites studied was that of young, expanding forests composed of large living and dead trees in living position, and large dead trees lying on the ground after recent blowdowns. Except for the occasional presence of relatively small dead black spruce stems in site 2, no partly or completely decomposed medium- and large-sized tree stems were recorded on the ground at all sites. Both the lack of an all-size stand structure of dead trees and the dominance of large trees accompanied by scarce tree

regeneration indicate that the three stands are young forests, < 400 yr old, dominated by relatively old trees. The present white spruce population of Cri Lake established almost at the same time as the northernmost white spruce population in the coastal tundra of Hudson Bay (Caccianiga & Payette, 2006). During the period of establishment, site conditions were favourable for the arboreal growth form at site 1 and in protected depressions at site 2, while at site 3 the tree growth form could be achieved only after the mid-19th century. During the 18th century, an altitudinal treeline was probably located at the level of site 2. Black spruce reached growth levels close to those of white spruce only in the late 19th century (Figs 3, 8; Table 3). Before that period, white spruce

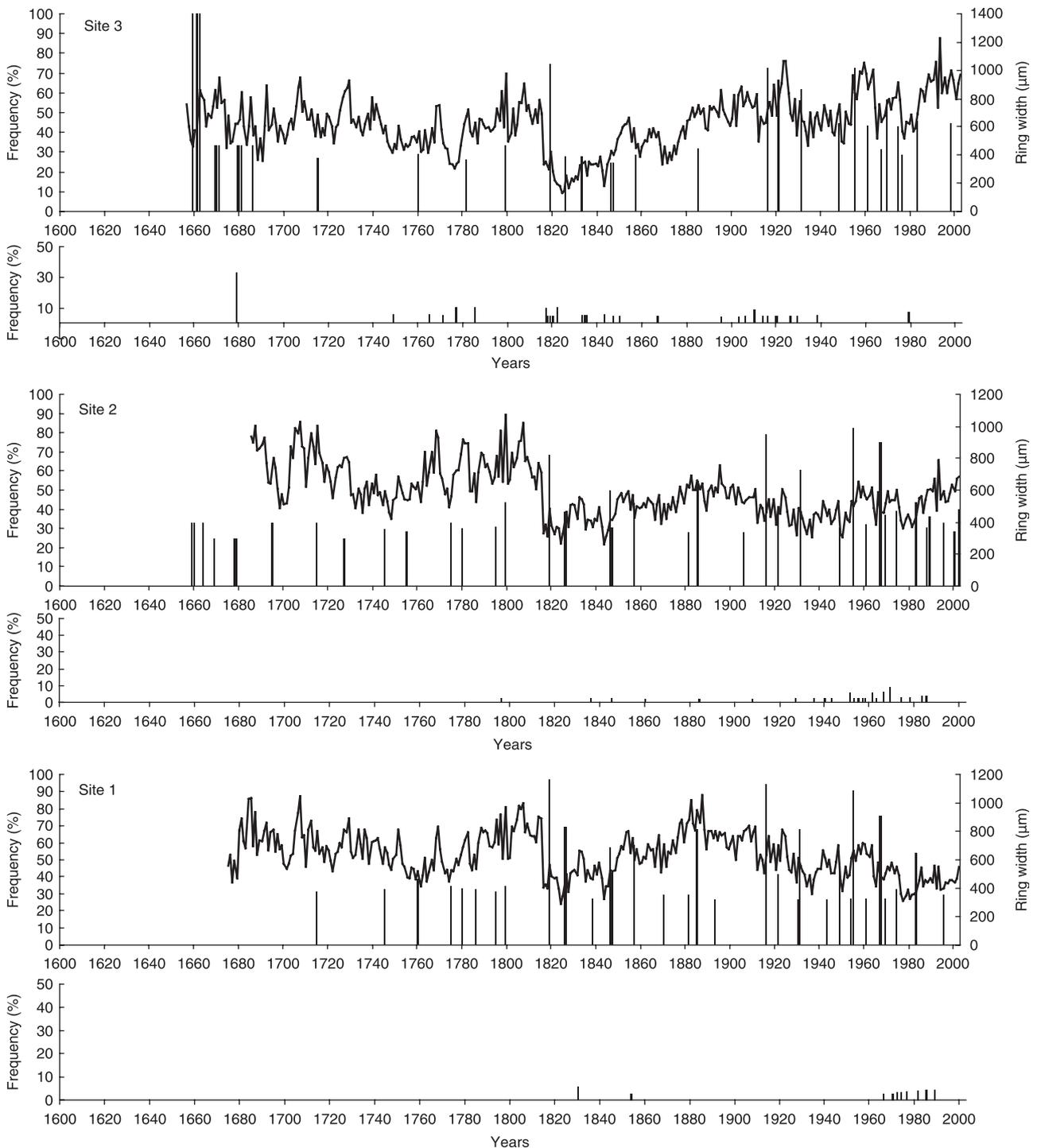


Fig. 7 Frequency of tree rings with above-normal resin-duct density (upper panels) and scars (lower panels) in comparison with ring-width chronologies.

trees were probably associated with black spruce krummholz, a pattern close to that observed presently at the northern range limit of white spruce in the tundra along the Hudson Bay coast (Payette & Filion, 1985; Caccianiga & Payette, 2006).

The most outstanding phenomenon was the period of suppressed growth that started abruptly in 1816 and lasted

until the 1850s at all sites. The negative peaks of 1816–17 (characterized by the formation of light rings in white spruce, Filion *et al.*, 1986), 1824–25 and 1843–44 are probably climate-controlled events, as they could also be observed in tamarack and black spruce chronologies from northern Québec (Arquillière *et al.*, 1990). However, the intensity and

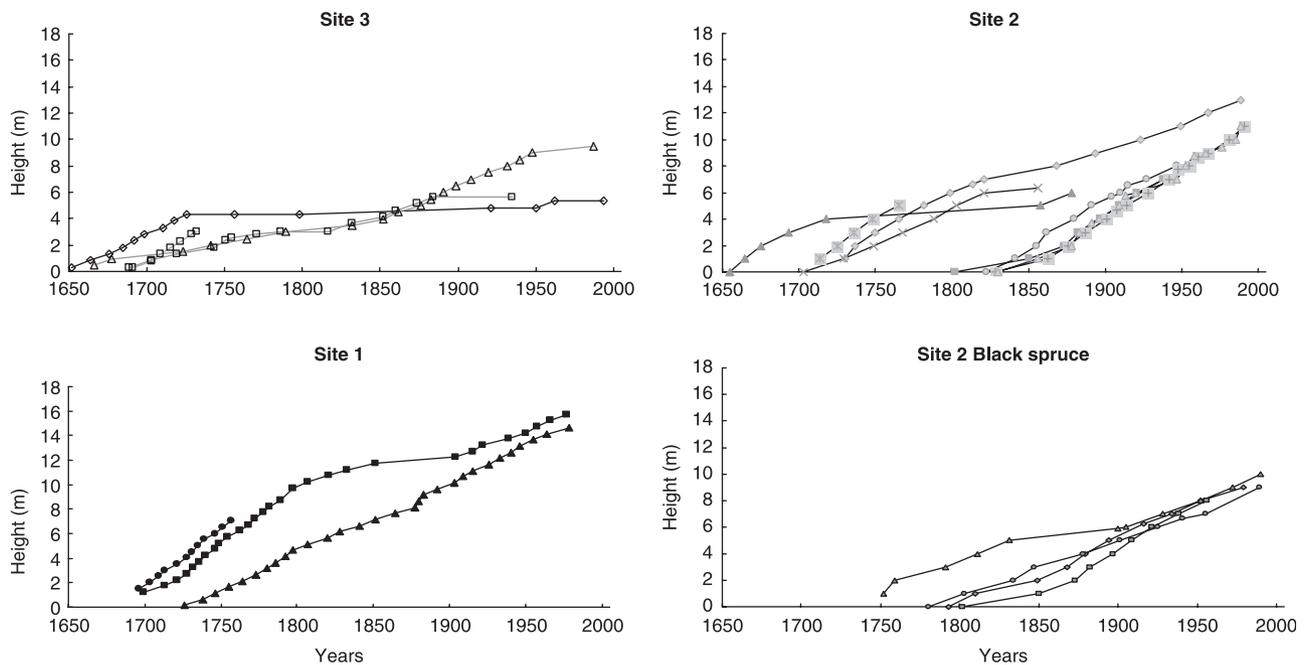


Fig. 8 Cumulative height growth of white spruce (*Picea glauca*) and black spruce (*Picea mariana*) trees from site 2.

duration of this growth suppression were particularly important for white spruce at Cri Lake (Parker *et al.*, 1981; Jacoby *et al.*, 1988; Arquillière *et al.*, 1990) and were interpreted by Jacoby *et al.* (1988) as a major temperature shift that lasted for almost three decades after 1816. The magnitude of growth reduction in 1816, the intensity of growth suppression and the lack of recovery in the most exposed sites 2 and 3 suggest a role for extreme climatic events that probably caused the reduction of photosynthetic efficiency by the loss of foliage in the upper crown and/or the destruction of terminal buds; these effects may have been enhanced by the already cold period.

The role of biotic disturbance

Evidence of bark beetle occurrence was widespread at all sites, but the timing and magnitude of beetle attacks differed markedly among sites. Thus outbreaks occurring at the regional scale could not be detected: the activity of bark beetle consisted mostly of occasional attacks, many of which were concentrated on single tree individuals (e.g. tree 27 at site 3, attacked 31 times from 1745–1951). This is probably caused by positive selection of previously attacked trees, as observed for many spruce beetles (Gilbert *et al.*, 2001; Werner *et al.*, 2006). The evidence for beetle occurrence was found mainly on mature trees. However, relatively young spruce were also attacked: the age of spruce trees at the first evidence for beetle attack (both blue-stain fungi and resin pockets) ranged from 21–235 yr, with the highest frequency between 45 and 150 yr (Fig. 9). These observations generally agree with the estimation

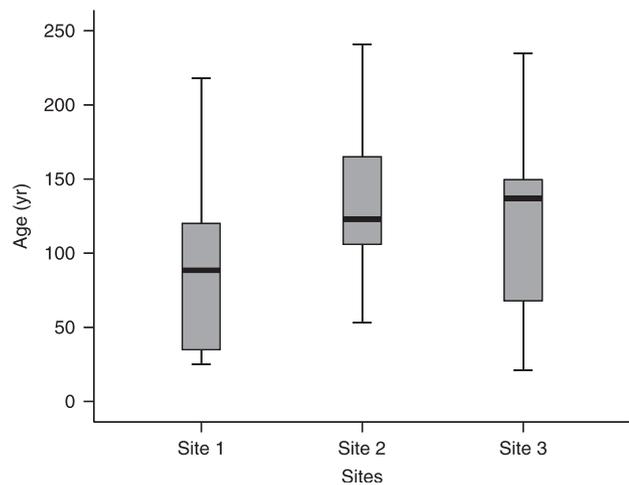


Fig. 9 Age of tree individuals at the first evidence of bark beetle attack. Boxes represent the interquartile range; the horizontal line is the median.

of approx. 40–50 yr given by Rolland & Lempérière (2004) for the minimum age of spruce attacked by bark beetle. However, Doak (2004) reports that spruce susceptibility is not influenced by age only, but other parameters, such as growth rate, must be taken into account.

Only at site 1, in the late 20th century, the activity of bark beetle and related blue-stain fungi became widespread and could be linked to extensive waves of mortality that affected the oldest trees in the 1970s, 1980s and especially in the 1990s. Spruce mortality caused by insect attacks was probably the result of synchronous senescence and increasing stand

density (Werner *et al.*, 2006). The main effect of bark beetle attacks was on tree mortality rather than on ring-width patterns: the lower ring-width values observed at site 1 since the late 19th century were probably caused by the increasing competition.

At the most exposed sites (site 3 and part of site 2), the 18th century was a period characterized by traumatic events, in contrast with site 1, which was much less disturbed until the late 19th–20th century. Traumatic scars and high concentration of resin ducts occurred on very young trees (18–20 yr old) at site 3, suggesting a role of snow and wind in this open and exposed site. Here the combination of insect attacks and traumatic events driven by unfavourable climatic conditions could have played a determining role in tree mortality: in such conditions trees are known to be particularly susceptible to beetle attack (Werner *et al.*, 2006).

The lack of large-scale outbreaks resulted in the rarity of growth release episodes. The only widespread occurrence of bark beetle, at site 1, took place in the past decade and thus could not be observed by our method of growth-release detection. Furthermore, most trees sampled were already old at the time of the most recent attacks, not belonging to the understorey layer, and thus were not supposed to experience a growth release following an outbreak. Growth release recorded at site 3 in the 18th and 19th centuries coincides with episodes of disturbance marked by scars and resin pockets. However, these episodes do not appear to be linked to a clearing effect, but could be caused by recovery following periods of exceptionally reduced growth, such as the 1828–32 episode after the slow growth of the 1820s. A clearing effect is unlikely in an open spruce stand such as that of site 3, where coverage of the dominant tree layer is presently very low and was even lower in past centuries. The observed growth releases are more likely to be a climate-induced phenomenon.

Conclusion

The role of insect outbreaks was important only at a local scale, when associated with synchronous senescence (as at site 1) or with traumatic events caused by unfavourable climatic events (as at site 3): in both cases trees are particularly sensitive to beetle attacks (Werner *et al.*, 2006). Extreme climatic events probably played a major role, particularly at the most exposed sites. However, the role of biotic disturbance should not be underestimated: it could explain the high mortality of the oldest white spruce cohorts in the study area, which also affected the northernmost white spruce population along the Hudson Bay coast in the 1980s–90s (Caccianiga & Payette, 2006), which was established at the same time of those at Cri Lake. Thus the synchronous and recent arrival of white spruce along the Hudson Bay coast resulted in a synchronous onset of spruce beetle activity driven by tree ageing. This phenomenon was previously absent in the area: black spruce, occurring there long before the arrival of white spruce

(Payette, 1993), are rarely attacked by bark beetles (Werner *et al.*, 2006). Even if the influence of climate warming on the increased beetle activity (Berg *et al.*, 2006; Soja *et al.*, 2007) cannot be excluded, the delayed arrival of white spruce does provide an explanation for the observed disturbance pattern.

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