

Spruce budworm outbreaks in eastern Quebec over the last 450 years

Yan Boulanger and Dominique Arseneault

Abstract: In this study we used dendrochronology to reconstruct the history of eastern spruce budworm (*Choristoneura fumiferana* (Clem.)) outbreaks over the last 450 years in the Bas-Saint-Laurent region of southeastern Quebec. In total, 260 tree cores were sampled from 204 beams in seven historic buildings and 12 trees in a virgin forest stand. Eight previously documented outbreaks (1975–1992, 1947–1958, 1914–1923, 1868–1882, 1832–1845, 1805–1812, 1752–1776, 1710–1724) and three presumed previous outbreaks (1678–1690, 1642–1648, 1577–1600) were identified based on periods of growth reduction. Of these 11 confirmed or presumed outbreaks, six were documented for the first time in eastern Quebec. Such data suggest that outbreak frequency has remained quite stable, with a mean interval of about 40 years between the midpoint of successive outbreaks since the mid-16th century. In addition, together with previous studies, our results indicate a strong spatial synchrony of spruce budworm outbreaks across central and eastern Quebec during the last 300 years. Consequently, our study does not support the hypothesis that spruce budworm outbreak frequency and synchrony increased during the 20th century.

Résumé : Dans cette étude, nous utilisons la dendrochronologie pour reconstituer les derniers 450 ans d'histoire des épidémies de tordeuse des bourgeons de l'épinette (*Choristoneura fumiferana* (Clem.)) dans la région du Bas-Saint-Laurent au sud-ouest du Québec. Au total, 260 carottes de tronc d'arbre ont été échantillonnées dans 204 poutres de sept bâtiments anciens et 12 arbres d'une forêt vierge. Huit épidémies précédemment documentées (1975–1992, 1947–1958, 1914–1923, 1868–1882, 1832–1845, 1805–1812, 1752–1776, 1710–1724) et trois épidémies présumées plus anciennes (1678–1690, 1642–1648, 1577–1600) ont été identifiées à partir de réductions de largeur des cernes annuels de croissance dans les échantillons. Parmi ces 11 épidémies confirmées ou présumées, six sont documentées pour la première fois dans l'Est du Québec. Ces données suggèrent que la fréquence des épidémies est demeurée stable depuis le milieu du 16^e siècle, avec un intervalle moyen de 40 ans entre l'année centrale des épidémies successives. De plus, en association avec des études précédentes, nos données mettent en lumière une synchronie spatiale des épidémies dans le centre et l'Est du Québec au cours des derniers 300 ans. En conséquence, cette étude ne supporte pas l'hypothèse voulant que les épidémies de tordeuse aient été plus fréquentes et mieux synchronisées dans l'espace au cours du 20^e siècle en comparaison des siècles précédents.

Introduction

Outbreaks of the eastern spruce budworm (*Choristoneura fumiferana* (Clem.)) represent one of the most important forest disturbances in the coniferous and mixedwood forests of eastern North America (Maclean 1984; Morin and Laprise 1990). Recurrent outbreaks mostly affect balsam fir (*Abies balsamea* (Payette and L.) Mill.) and white spruce (*Picea glauca* (Moench) Voss), which are the main host species, and strongly drive forest dynamics over large areas. During a typical outbreak, high defoliation occurs repeatedly over a period of 5–25 years, leading to substantial decline of vigor and increased mortality of affected trees and stands. The budworm-induced canopy gaps are rapidly filled by released seedlings and saplings of the hosts, along with those of addi-

tional species, thus leading to rapid forest renewal and ecosystem recovery (Morin 1994; Bergeron 2000). Describing the frequency, duration, and severity of past outbreaks is a major research objective in sustainable forest management. Such knowledge could eventually lead to the development of logging models based on a long-term, natural disturbance regime (Harvey et al. 2002).

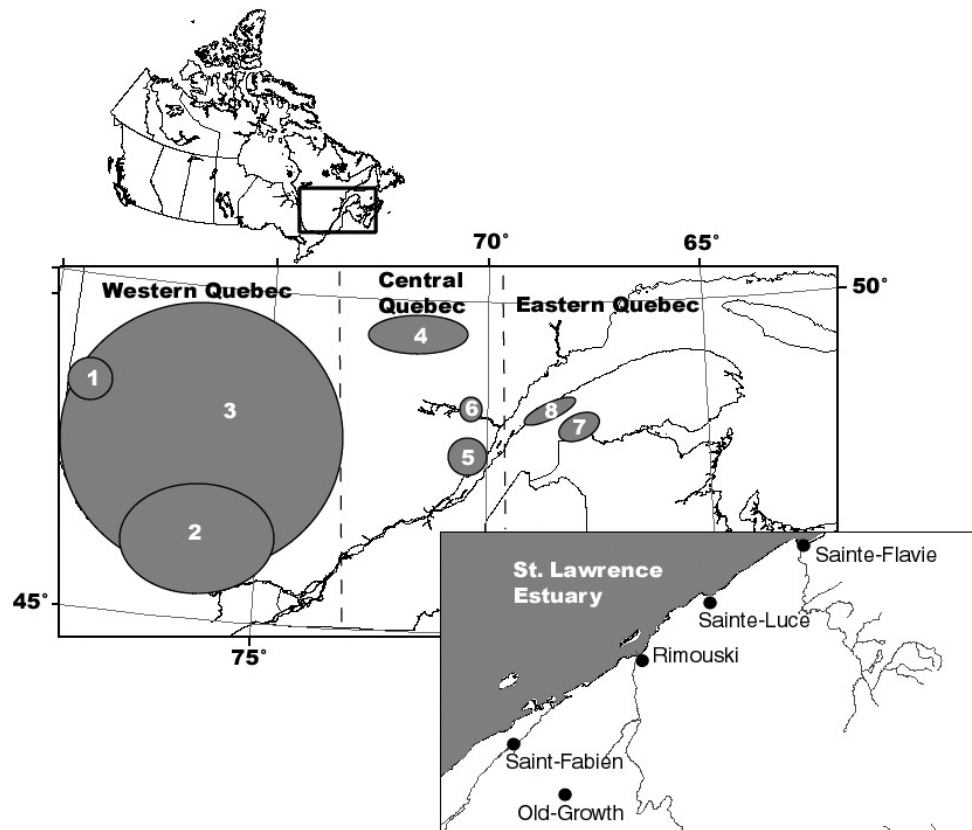
Dendrochronological methods have frequently been used to reconstruct the history of past forest-damaging insect outbreaks (Mott et al. 1957; Blais 1958, 1962, 1983; Schweingruber et al. 1986; Swetnam and Lynch 1989, 1993; Morin and Laprise 1990; Jardon et al. 1993; Girardin et al. 2001; Speer et al. 2001). Such methods are based on the fact that insect-induced reduction in foliage cover can be detected from tree-ring width patterns (Kulman 1971; Krause and Morin 1995). Accordingly, the history of spruce budworm outbreaks has been reconstructed over the last three centuries from several locations across eastern North America (Blais 1983; Morin and Laprise 1990; Morin et al. 1993; Krause 1997; Jardon 2001). Overall, three distinct outbreaks have been identified in the 20th century, three in the 19th century, and two in the 18th century (Figs. 1 and 2). Reconstructed outbreaks are generally less frequent, less severe, or less spatially synchronous during the 18th and 19th centuries

Received 27 May 2003. Accepted 13 November 2003.
Published on the NRC Research Press Web site at
<http://cjfr.nrc.ca> on 12 May 2004.

Y. Boulanger¹ and D. Arseneault. Département de biologie, Centre d'études nordiques et Chaire de recherche sur la forêt habitée, Université du Québec à Rimouski, 300, allée des Ursulines, Rimouski, QC G5L 3A1, Canada.

¹Corresponding author (e-mail: yan_boulanger@uqar.qc.ca).

Fig. 1. Location of the sampled sites within the Bas-Saint-Laurent region and regions covered by previous reconstructions of spruce budworm outbreaks in Quebec. We consulted only published studies that mentioned the covered period, as well as the onset and termination of each identified outbreak episode: 1, Morin et al. (1993); 2, Blais (1981); 3, Jardon (2001); 4, Morin and Laprise (1990); 5, Blais (1965); 6, Krause (1997); 7, Blais (1961); 8, present study.



than during the 20th century. Hypotheses to explain such differences fall into three categories: (1) forest logging and fire suppression during the 20th century increased the abundance of balsam fir across wide areas, thus increasing the frequency, severity, and spatial synchrony of outbreaks (Blais 1983); (2) reduced fire frequency during the 20th century (due to both climate change and fire suppression) increased the abundance of mature, budworm-sensitive stands, thus increasing outbreak severity, but the frequency and spatial synchrony of outbreaks were only slightly affected (Royama 1984; Jardon 2001); and (3) outbreak reconstructions are less reliable going backward in time, as sampled individuals were less prone to defoliation during the seedling and sapling life stages (Jardon 2001).

More numerous and longer reconstructions of past spruce budworm outbreaks are thus clearly needed to improve our understanding of this disturbance agent. Most dendrochronological reconstructions of past outbreaks have been performed based on tree-ring chronologies from living white spruce individuals, as this species has a longer life span than balsam fir (Blais 1965). However, spruce trees older than 200 years are rare, such that reconstructing past outbreaks over longer periods must also rely on well-preserved woody material, as found in old buildings (Krause 1997). Surprisingly, this approach has rarely been used, and to our knowledge no study has combined dead and live trees to build a long, continuous record of eastern spruce budworm outbreaks. In this study we reconstruct the history of spruce

budworm outbreaks over the last 450 years, using samples from an old-growth forest stand, as well as from historic buildings in the Bas-Saint-Laurent region of southeastern Quebec. Previous reconstructions from this area and surrounding regions have demonstrated the occurrence of the three known 20th-century outbreaks, as well as two 19th-century outbreaks (Blais 1961, 1964). Specifically, the objectives of this study were to (1) build a continuous, multicentury chronology of spruce budworm outbreaks; and (2) evaluate the hypothesis that compared with outbreaks in the 20th century, previous outbreaks may have been less frequent in eastern Quebec (Blais 1983).

Study area

Sampling sites were all located within 40 km of the town of Rimouski, along the south shore of the St. Lawrence estuary in eastern Quebec (Fig. 1). This area belongs to the Appalachian geological formation composed mainly of sedimentary rocks (Robitaille and Saucier 1998). Mean annual temperature is 2.5 °C. The growing season lasts for about 170 days, from early May to mid-October, and corresponds to 2200–2400 growing degree-days (>5.6 °C). Mean annual precipitation is 900 mm, with about 65% falling as rain (Environment Canada 1993). In the bioclimatic ecosystem classification, this area is in the Eastern subdomain of the Balsam Fir – Yellow Birch (*Betula alleghanensis* Britt.) domain (Robitaille and Saucier 1998). Balsam fir and yellow birch (*Betula alleghanensis* Britton) mostly occur together

Table 1. Sampling intensity and percentage spruce samples cross-dated at each study site.

Sites	Interval	<i>Thuja occidentalis</i>		<i>Picea</i> spp.		Spruces successfully dated (%)
		Cores	Beams	Cores	Beams	
Old growth	1816–2002	—	—	12	12	100.0
Sainte-Flavie house	1736–1845	—	—	7	6	100.0
Barn 1	1728–1898	—	—	26	24	54.7
Barn 2	1711–1902	15	12	30	20	50.0
Sainte-Luce church	1706–1838	—	—	24	24	87.5
Barn 3	1695–1919	15	11	41	32	75.0
Saint-Fabien church	1647–1898	—	—	34	34	100.0
Maison Lamontagne	1513–1745	29	19	23	19	36.8
All sites	1513–2002	59	32	197	171	86.8

on mesic sites, whereas sugar maple (*Acer saccharum* Marsh.) and yellow birch frequently occur together on well-drained and exposed sites. Black spruce (*Picea mariana* (Mill.) BSP) and eastern white-cedar (*Thuja occidentalis* L.) are frequent on organic soils. The forest vegetation has been extensively disturbed by human activities since the late 18th century. The conversion of forest to agricultural lands began around 1790 along the St. Lawrence River. Sustained logging activities began around 1820 and increased in amplitude until the early 20th century (Fortin and Lechasseur 1999). Extensive logging occurred subsequently, so virgin forest stands are extremely scarce.

For this study, seven historic buildings were selected on the basis of known or suspected date of construction, along with architectural criteria such as the presence of manually shaped beams. We identified three historic barns and a church in the town of Saint-Fabien, the Maison Lamontagne in Rimouski (the only building remaining from the French regime in the Rimouski area), the church in the village of Sainte-Luce, and a historic house in Sainte-Flavie (Fig. 1 and Table 1). Although historical data confirm that the trees used to erect the Saint-Fabien and Sainte-Luce churches were logged in the corresponding parishes, the origin of the timber used in the houses and barns is less clear. However, during the 18th and 19th centuries, local people usually constructed their buildings using trees logged on their own property (Lavoie 2000). This is also suggested by testimony from the present-day owners of the sampled buildings. Only one old-growth, virgin forest stand with sufficiently abundant white spruce trees could be found to allow us to identify outbreaks during the most recent period. This stand covers about 1 ha on a well-drained upper slope in the Nicolas-Riou Seigniory, which is managed by the Lower St. Lawrence Model Forest. Although the stand is dominated by sugar maple, it also has white spruce, balsam fir, and eastern white-cedar.

Materials and methods

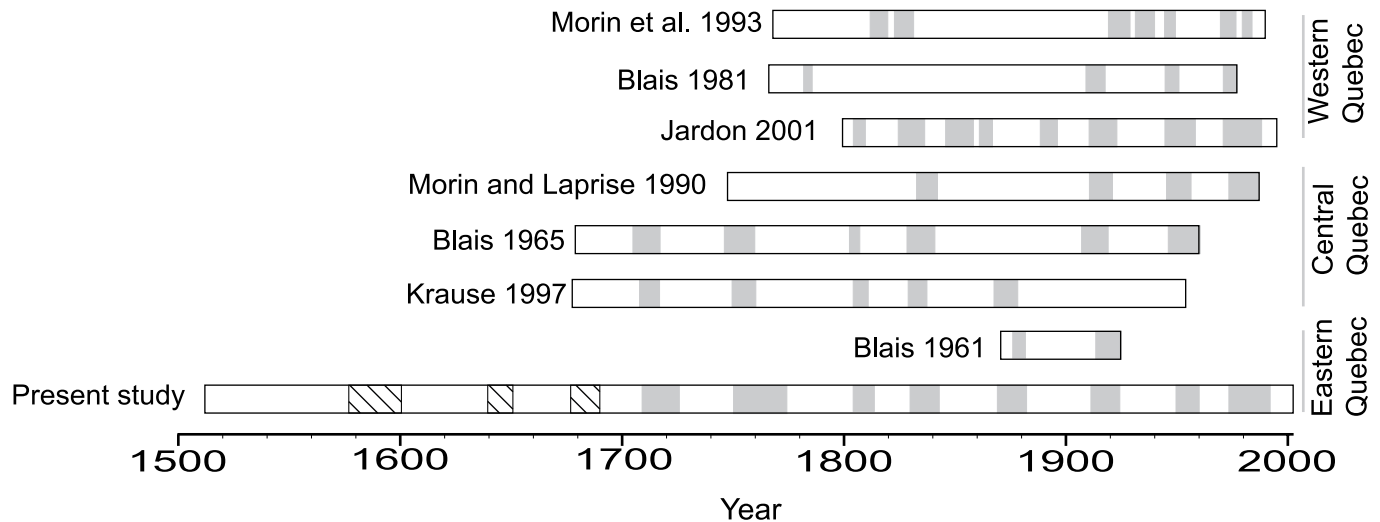
A maximum number of wood pieces were sampled (one or two cores per beam) at each building (Table 1). In all buildings, the majority of samples came from the structural components of the roof. Some additional samples were taken from the bell tower of the Saint-Fabien church and from large wall components in the three barns. Large white spruce

individuals in the old-growth stand were systematically searched and sampled (one core per tree; $n = 12$). Samples from the buildings were identified to species or genera on the basis of wood anatomy criteria (Hoadley 1990). Because there is no absolute criterion for differentiating white spruce from black spruce or red spruce (*Picea rubens* Sarg.), we are not certain that all the samples are from white spruce trees. However, most samples classified as spruce are probably white spruce, as this species is by far the most abundant spruce in the study area. Samples from other genera were excluded from the data set.

All spruce samples were glued to a frame and finely sanded, and the width of tree rings was measured with a Velmex micrometer. To avoid pseudoreplication (Hurlbert 1984), ring widths measured along two cores from the same piece of wood were averaged to produce a mean raw chronology. However, we do not know whether different beams were from the same tree. All raw chronologies (from timber with one or two cores) were then standardized with the ARSTAN program (Cook and Holmes 1999) to remove the long-term, age-related growth trend. Standardization was achieved by dividing each raw series by a cubic smoothing spline with a 50% frequency response of 60 years. To preserve the outbreak signal, the autocorrelation was not removed from the standardized chronologies. We cross-dated these standardized chronologies within sites and then between sites, using the PAST32 program (SCIEM 2002), along with the COFECHA program (Holmes 1983) as a validation tool. Mean standardized chronologies were thus built for each sampled site by averaging all cross-dated series according to the calendar years of tree-ring formation.

Past outbreaks were identified separately for each site with the use of the corresponding mean standardized chronology and the OUTBREAK program (Holmes and Swetnam 1996). On the basis of previous works (Swetnam and Lynch 1989, 1993; Jardon 2001; Speer et al. 2001), we considered as a possible outbreak any growth reduction longer than 5 years that included at least 1 year less than -1.28 standard deviation from the mean. The onset and termination of each outbreak were set at the first and last years of below-mean growth level, respectively. Identifying insect-induced growth reduction in tree rings is frequently achieved by comparing chronologies from host and nonhost species. The nonhost chronology may be used to extract the climatic signal (common to both species) from the host chronology, thus

Fig. 2. Intervals of spruce budworm outbreaks (gray bars) identified during previous reconstructions based on tree-ring chronologies of various lengths (white bars). Corresponding studied areas are depicted in Fig. 1. Hatched bars correspond to presumed outbreaks identified from a limited number of samples.



amplifying the outbreak signal (Swetnam et al. 1985). Although a regional, 500-year chronology for eastern white-cedar (a nonhost species) was available (C. Sorel and D. Arseneault, unpublished data), we did not use it to identify outbreaks in our spruce chronologies. This nonhost chronology contains a strong, 22-year quasi-periodic component that is asynchronous with abrupt growth reductions in spruce individuals. Subtracting the nonhost chronology from the host chronology would have amplified and lengthened outbreaks during peaks and weakened and shortened outbreaks during troughs of the cycle. Additionally, this would have generated a few erroneous outbreaks (not corresponding to a clear decrease of spruce growth) during the most abrupt increases of cedar growth. Instead, we validated possible outbreaks during the last 300 years by using previously published outbreak reconstructions, which were in most cases based on host–nonhost comparison. More ancient outbreaks could be identified almost exclusively from the Maison Lamontagne samples. Fortunately, this building contained several white-cedar beams that could be sampled and cross-dated with the regional cedar chronology. We constructed a mean cedar chronology from 16 beams as a tool with which to visually differentiate pre-18th-century outbreaks from climate-induced growth decreases. In contrast to the regional chronology, this cedar chronology contained no cyclic component.

Results and discussion

In total, 248 cores were obtained from 204 beams in seven buildings. Spruce (77.9% of the beams) was the dominant taxon, whereas eastern white-cedar (20.6%) and balsam fir (1.5%) were much less frequent. A large proportion of the spruce material could be cross-dated (50%–100%, depending on the building), except at the Maison Lamontagne, where because of poor preservation only 7 of the 19 sampled beams could be successfully cross-dated. These samples, along with the 11 living and 1 recently killed white spruce from the old-growth stand, allowed us to build a continuous, 490-year tree-ring chronology covering the years 1513–

2002. Overall, we identified 11 growth reductions likely to indicate outbreaks in the past: three in the 20th century, three in the 19th century, two in the 18th century, two in the 17th century, and one in 16th century (Figs. 2 and 3, Table 2).

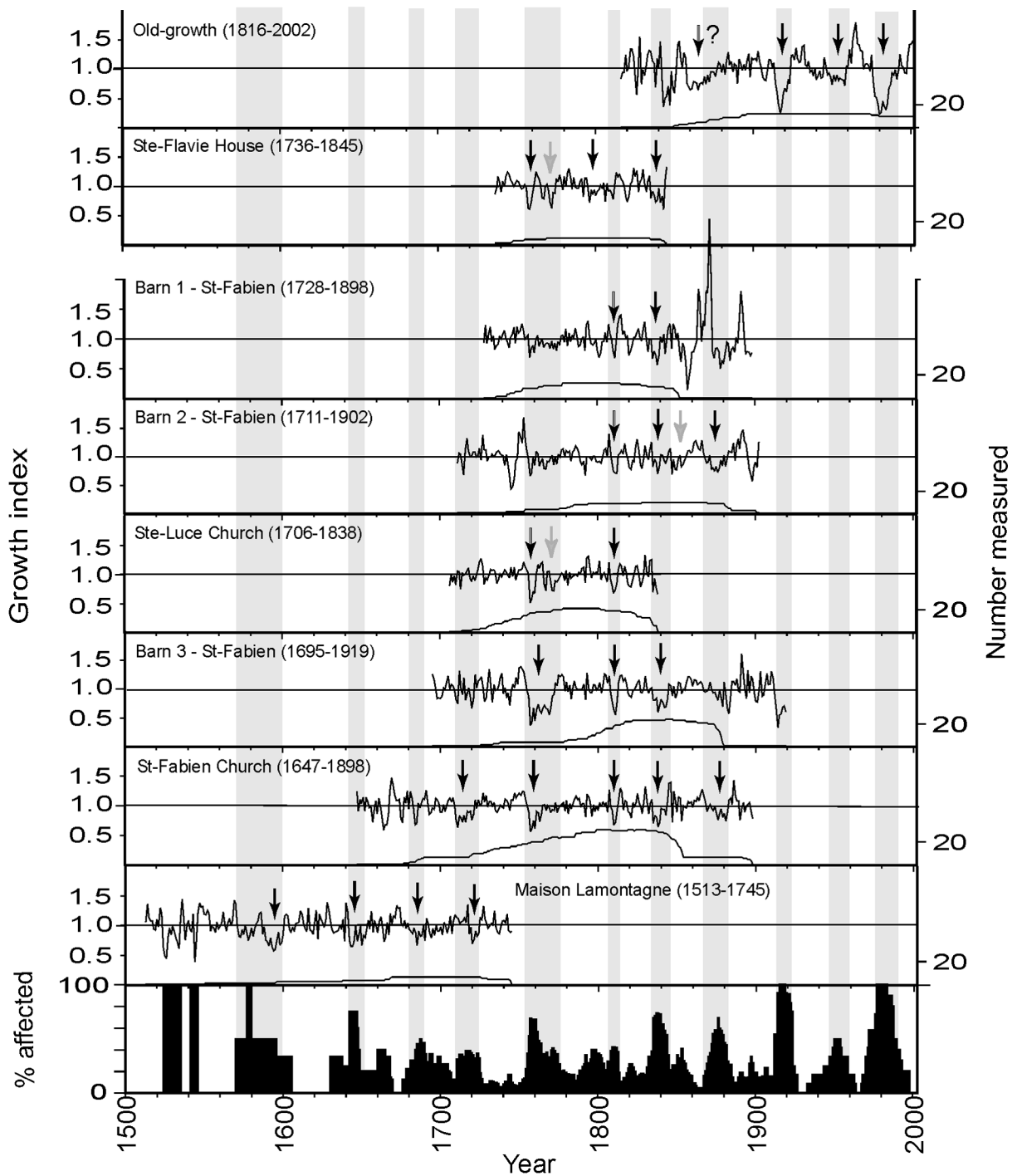
20th-century outbreaks (1975–1992, 1947–1958, 1914–1923)

During the 20th century, two severe growth reductions occurred at the old-growth site in 1975–1992 and 1914–1923, and a less intense reduction occurred in 1947–1958 (Fig. 3, Table 2). These growth reductions closely correspond to the well-documented sequence of spruce budworm outbreaks in eastern Canada during the 20th century (Fig. 2), confirming their association with the spruce budworm. The intensity of these growth reductions in our results is also similar to that of previous studies: researchers have repeatedly observed less intense reductions during mid-century outbreaks than during the early- and late-century ones (Jardon 2001). In our study, the growth of all measured individuals decreased below the threshold of -1.28 SD in 1975–1992 and 1914–1923, whereas this occurred with only 50% of individuals in 1947–1958 (Table 2).

19th-century outbreaks (1868–1882, 1832–1845, 1805–1812)

In addition to the old-growth site, six chronologies from historic buildings were available to enable us to reconstruct spruce budworm outbreaks of the 19th century (Fig. 3). Taken together, these chronologies display three regional periods of growth reduction (1868–1882, 1832–1845, 1805–1812), which are also in close synchrony with outbreaks identified elsewhere in eastern and central Quebec (Fig. 2). The 1868–1882 growth reduction affected 69% of all measured specimens and is best expressed at the barn 2 and Saint-Fabien church sites, where decreases in ring width occurred in 57%–78% of individuals (Table 2). This growth reduction is less apparent at the barn 1 and barn 3 sites, probably because only one sample covered the entire 1868–

Fig. 3. Standardized spruce tree-ring chronologies showing the identified spruce budworm outbreaks (black arrows) at the sampled sites. Dotted arrows point to abrupt growth reductions, probably corresponding to an outbreak episode, even if not meeting the 5-year duration criterion. Gray arrows indicate growth reductions likely to correspond to a second wave of the preceding outbreak. The lower-most panel shows the percentage of affected individuals (those with >5 years of growth reduction) over the entire study area.



1882 interval in both cases. Previous studies based on tree rings have suggested an outbreak in our study area around 1878 (Blais 1961, 1964; Swaine and Craighead 1924). This outbreak was also recorded in tree-ring chronologies from a large area of boreal forest, north of the St. Lawrence River in western and central Quebec (Fig. 2), as well as in New Brunswick and northeastern Ontario (Blais 1983; Royama 1984; Krause 1997; Jardon 2001). There are also tree-ring

series from eastern Canada that do not clearly record any effects of the 1868–1882 outbreak (Morin and Laprise 1990; Blais 1981, 1983).

The 1832–1845 growth reduction affected 74% of all measured individuals and 50%–83% of individuals at each site, except at the old-growth site (100%), where only one sample covered the corresponding interval (Fig. 3 and Table 2). Although previous studies did not indicate an out-

Table 2. Site and number of individuals affected during each identified spruce budworm outbreak.

Outbreak	Sites affected	Local interval	Individuals affected	
			%	<i>n</i>
1975–1992	Old growth	1975–1992	100.0	11
1947–1958	Old growth	1947–1958	50.0	6
1914–1923	Old growth	1914–1923	100.0	12
1868–1882	Barn 2	1868–1882	77.8	7
	Saint-Fabien church	1869–1882	57.1	4
1832–1845	Barn 1	1832–1841	80.0	8
	Barn 2	1835–1839	50.0	5
	Barn 3	1835–1844	73.9	13
	Saint-Fabien church	1835–1843	82.8	24
1805–1812	Sainte-Flavie house	1835–1843	100.0	5
	Barn 3	1808–1812	50.0	8
	Saint-Fabien church	1806–1812	8.3	14
1752–1776	Sainte-Luce church	1805–1812	42.1	8
	Barn 3	1756–1772	75.0	3
	Saint-Fabien church	1756–1764	78.9	15
1752–1776	Sainte-Luce church	1757–1760 ^a ; 1770–1776	76.5	13
	Sainte-Flavie house	1752–1760; 1766–1774	83.8	5
1710–1724	Saint-Fabien church	1710–1723	71.4	5
	Maison Lamontagne	1710–1724	71.4	5
1678–1690	Maison Lamontagne	1678–1690	71.4	5
1642–1648	Maison Lamontagne	1642–1648	75.0	3
1577–1600	Maison Lamontagne	1577–1582 ^a ; 1587–1600	100.0	2

Note: The local interval corresponds to the identified outbreak interval at each affected site.

^aAbrupt growth reduction probably corresponding to an outbreak episode, even if not meeting the 5-year duration criterion or the intensity criterion of -1.28 SD.

break to the southwest (Swaine and Craighead 1924; Blais 1983) or southeast of our study area (Royama 1984) during this period, other studies identified an outbreak at numerous locations from northern Ontario to central Quebec (Turner 1952; Blais 1965, 1983; Krause 1997; Morin and Laprise 1990; Jardon 2001; see Fig. 2).

A short-lasting but well-defined growth reduction occurred during the period 1805–1812 at the barn 3, Saint-Fabien church, and Sainte-Luce church sites (Fig. 3). Similar growth reductions, although spanning less than the 5-year duration criterion, also occurred at the barn 1 and barn 2 sites. Surprisingly, the Sainte-Flavie house site displayed a growth reduction in 1794–1804. This growth reduction is probably a local artifact, as it did not occur at the other sites. In total, only 42% of the measured samples displayed a significant growth reduction during the period 1805–1812 (varying between 42% and 50% between affected sites; Table 2). Although of short duration, this growth reduction most likely corresponds to a spruce budworm outbreak as observed elsewhere in tree-ring series from eastern Canada and Maine (Swaine and Craighead 1924; Blais 1965, 1983; Fig. 2), occasionally on the basis of host–nonhost comparison (Krause 1997; Jardon 2001). Moreover, this growth re-

duction did not occur simultaneously among sites within our study area (table 2) or among trees within sites, as would be likely during a regional climatic stress.

18th-century outbreaks (1752–1776, 1710–1724)

Few studies have identified spruce budworm outbreaks during the 18th century. Tree-ring series from either old living white spruces (Blais 1965) or dead spruces from old buildings (Krause 1997) have suggested two outbreaks around 1748–1760 and 1710–1720 (Fig. 2) in central Quebec, north of the St. Lawrence River. Our results confirm these defoliation periods and extend the affected area to eastern Quebec, south of the St. Lawrence River, as we observed evidence of growth reduction in 1752–1776 and 1710–1724. A third 18th-century outbreak may have occurred in western Quebec in 1783–1787 (Blais 1981; Fig. 2), although this event has not been confirmed elsewhere.

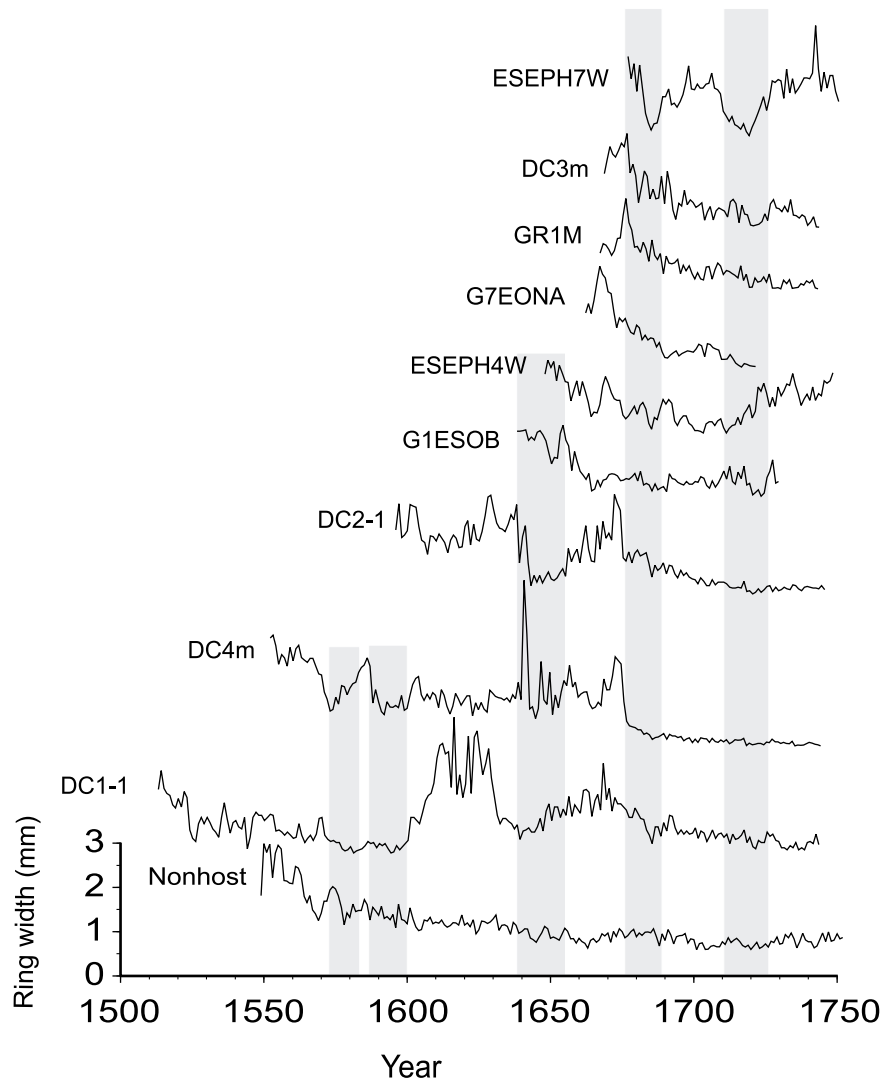
Although it varied in duration among sites, the 1752–1776 growth reduction is clearly expressed in all available chronologies (Fig. 3). Overall, 68% of all measured individuals and 75% to 84% of individuals at each affected site exhibited a growth reduction (Table 2). This growth reduction was continuous at the three barns and the church in Saint-Fabien, but it separated into two distinct periods of slow growth (1752–1760 and 1766–1776) eastward at the Sainte-Luce church and the Sainte-Flavie house (Fig. 3).

The 1710–1724 growth reduction is also well expressed in the two chronologies covering the corresponding period (Saint-Fabien church and Maison Lamontagne), although the growth decrease was delayed until 1718 in samples from the Maison Lamontagne (Fig. 3). In contrast to previous studies that indicated a two-wave outbreak north of the St. Lawrence River during this period (Blais 1965; Krause 1997), our data suggest a continuous growth reduction in the Bas-Saint-Laurent region. In total, five of the seven measured samples (71%) within each chronology displayed a growth reduction (Table 2).

16th- and 17th-century outbreaks

The spruce and white-cedar chronologies from the Maison Lamontagne, along with the most ancient samples from the Saint-Fabien church, allowed us to identify three growth reductions, possibly corresponding to spruce budworm outbreaks, in 1678–1690, 1642–1648, and 1577–1600 (Fig. 3). Because of the low number of samples available for this interval, we also examined the growth pattern of individual spruce samples to get additional information on the growth history of the corresponding trees (Fig. 4). The 1678–1690 growth reduction affected 71% ($n = 5$) of trees at the Maison Lamontagne, as well as the more ancient samples from the Saint-Fabien church. Two old spruce (samples DC2–1 and DC4M; Fig 4) did not recover to the previous growth level, a pattern also observed elsewhere in several black spruce and balsam fir individuals after the most recent outbreak (Simard and Payette 2001). The link between spruce budworm and the 1577–1600 and 1642–1648 growth reductions is less clear, as only 2–3 samples were measured. However, almost all measured samples exhibited obvious growth decreases, sometimes followed by sustained growth releases (DC1–1 and DC2–1; Fig. 4), a frequent response to canopy-opening

Fig. 4. Raw tree-ring series showing the pattern of tree growth in response to presumed spruce budworm outbreaks in samples from the Maison Lamontagne and Saint-Fabien church (samples ESEPH7W and ESEPH4W are from Saint-Fabien) and the nonhost eastern white-cedar chronology.



outbreaks (Morin et al. 1993, Jardon 2001). In addition, none of the growth reductions in spruce samples corresponded to similar growth decreases in the nonhost eastern white-cedar chronology. Although these three presumed outbreaks await further confirmation, they possibly represent the most ancient spruce budworm outbreaks dated by tree-ring chronology in eastern North America.

Outbreak frequency over the last 450 years

Tree-ring data from this study have confirmed the eight previously documented spruce budworm outbreaks in eastern North America, along with three presumed previous outbreaks. Of these 11 confirmed and presumed outbreaks, 6 were documented for the first time in eastern Quebec (Figs. 1 and 2). Such data suggest that outbreak frequency has remained quite stable, with a mean interval of 39.5 ± 8.6 (mean \pm SD) years between the midpoint of successive outbreaks since the mid-16th century. Previous studies have suggested slightly shorter return intervals of 30–36 years over the last 200 years (Royama 1984; Candau et al. 1998;

Jardon 2001). However, our estimation of the return interval may be conservative, as only one chronology from a limited number of samples was available to cover the 16th century.

In addition, together with previous studies, our study indicates a strong spatial synchrony of spruce budworm outbreaks during the last 300 years, at least across central and eastern Quebec (Fig. 2). All clear outbreaks previously detected in central Quebec (Blais 1965; Morin and Laprise 1990; Krause 1997) were observed at our study sites. Outbreaks in our study area preceded those in central Quebec (Krause 1997) by only 1.2 ± 2.8 years (mean \pm SD of differences in outbreak onset between areas) during the 18th and 19th centuries. In contrast, tree rings and survey records of spruce budworm defoliation showed that 20th-century outbreaks tended to appear in the west, to propagate eastward in Quebec (Hardy et al. 1986; Gray et al. 2000; Jardon 2001), and to appear later in western Ontario than in eastern Ontario (Candau et al. 1998). Although such differences between regions and periods probably relate to the complex dynamics of outbreak initiation and propagation as influ-

enced by internal and external factors at the local and regional scales (Candau et al. 1998; Jardon et al. 2003), they do not support the idea that outbreak frequency and synchrony increased during the 20th century (Blais 1965, 1983). Similar conclusions have been reached regarding outbreaks of the western spruce budworm (*Choristoneura occidentalis* Freeman) in western North America (Swetnam and Lynch 1989; Ryerson et al. 2003). It is likely that previous studies that reconstructed past outbreaks from living material cored at breast height underestimated the budworm signal prior to the mid-19th century. The fact that such samples would overlap the sapling life stage of trees, along with the possibility that seedlings and saplings are less affected than dominant trees by the spruce budworm (Bauce 1994), most likely precluded the identification of ancient outbreaks (Jardon 2001). The scarcity of long outbreak reconstructions probably amplified this perception. In contrast, our results, based on material from progressively older buildings, are in close synchrony with results from a similar study (Krause 1997).

Acknowledgements

We thank P. Rioux, who helped us find old buildings, and É. Boucher for laboratory assistance. R. Malenfant permitted the sampling of the Maison Lamontagne. We also thank B. Hins and G. Lagacé, who allowed sampling in the Saint-Fabien and Sainte-Luce churches. R. Côté, M. A. Gaudreau, and R. Gagnon permitted sampling in old barns, and J. Drapeau let us sample his historic house in Sainte-Flavie. This research has been financially supported by the Fondation de l'Université du Québec à Rimouski. Two anonymous referees provided useful comments on a previous version of this paper.

References

- Bauce, E., Crépin, M., and Carisey, N. 1994. Spruce budworm growth, development and food utilization on young and old balsam fir trees. *Oecologia*, **97**: 499–507.
- Blais, J.R. 1958. Effects of defoliation by spruce budworm (*Choristoneura fumiferana* Clem.) on radial growth at breast height of balsam fir (*Abies balsamea* (L.) Mill.) and white spruce (*Picea glauca* (Moench) Voss.). *For. Chron.* **34**: 39–47.
- Blais, J.R. 1961. Spruce budworm outbreaks in the Lower St. Lawrence and the Gaspé regions. *For. Chron.* **37**: 192–202.
- Blais, J.R. 1962. Collection and analysis of radial-growth data from trees for evidence of past spruce budworm outbreaks. *For. Chron.* **38**: 474–484.
- Blais, J.R. 1964. History of spruce budworm outbreaks in the past two centuries in southeastern Quebec and northern Maine. *Can. For. Entomol. Pathol. Branch Bi-mon. Prog. Rep.* 20.
- Blais, J.R. 1965. Spruce budworm outbreaks in the past three centuries in the Laurentide Park, Quebec. *For. Sci.* **11**: 130–138.
- Blais, J.R. 1981. Recurrence of spruce budworm outbreaks for two hundred years in western Quebec. *For. Chron.* **58**: 273–275.
- 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.
- Candau, J.-N., Fleming, R.A., and Hopkin A. 1998. Spatiotemporal patterns of large-scale defoliation caused by the spruce budworm in Ontario since 1941. *Can. J. For. Res.* **28**: 1733–1741.
- Cook, E.R., and Holmes, R.L. 1999. User manual for program ARSTAN. Laboratory of Tree-Ring Research, University of Arizona, Tucson, Ariz.
- Environment Canada. 1993. Canadian climate normals / Normales climatiques au Canada 1961–1990. Atmospheric Environment Service, Environment Canada, Ottawa, Ont.
- Fortin, J.-C., and Lechasseur, A. 1993. Histoire du Bas-Saint-Laurent. Institut québécois de recherche sur la culture, Québec, Que.
- Girardin, M.-P., Tardif, J., and Bergeron, Y. 2001. Radial growth analysis of *Larix laricina* from the Lake Duparquet area, Quebec, in relation to climate and larch sawfly outbreaks. *ÉcoScience*, **8**: 127–138.
- Gray, D.R., Régnière, J., and Boulet, B. 2000. Analysis and use of historical patterns of spruce budworm defoliation to forecast outbreak patterns in Quebec. *For. Ecol. Manage.* **127**: 217–231.
- Hardy, Y., Mainville, M., and Schmitt, D.M. 1986. An atlas of spruce budworm defoliation in eastern North America 1938–1980. USDA For. Serv. Misc. Pub. 1449.
- Harvey, B.D., Leduc, A., Gauthier, S., and Bergeron, Y. 2002. Stand-landscape integration in natural disturbance-based management of the southern boreal forest. *For. Ecol. Manage.* **155**: 369–385.
- Hoadley, R.B. 1990. Identifying wood: accurate results with simple tools. Tauton Press, Newton, Conn.
- Holmes, R. 1983. Computer-assisted quality control in tree-ring dating and measurement. *Tree-Ring Bull.* **43**: 69–78.
- Holmes, R.L., and Swetnam, T. 1996. Detecting outbreaks of spruce budworm and tussock moth in annual tree-ring growth, and distinguishing between the insect species. Laboratory of Tree-Ring Research, University of Arizona, Tucson, Ariz.
- Hurlbert, S.H. 1984. Pseudoreplication and the design of ecological field experiments. *Ecol. Monogr.* **54**: 187–211.
- Jardon, Y. 2001. Long term analysis of spruce budworm outbreak in a large scale area, a dendrochronological approach. Ph.D. thesis. Université du Québec à Montréal, Montréal, Que.
- Jardon, Y., Morin, H., and Dutilleul, P. 2003. Périodicité et synchronisme des épidémies de la tordeuse des bourgeons de l'épinette au Québec. *Can. J. For. Res.* **33**: 1947–1961.
- Krause, C. 1997. The use of dendrochronological material from buildings to get information about past spruce budworm outbreaks. *Can. J. For. Res.* **27**: 69–75.
- Krause, C., and Morin, H. 1995. Changes in radial increment in stems and roots of balsam fir [*Abies balsamea* (L.) Mill.] after defoliation by spruce budworm. *For. Chron.* **71**: 747–754.
- Kulman, H.M. 1971. Effects of defoliation on growth and mortality of trees. *Annu. Rev. Entomol.* **16**: 289–324.
- Lavoie, R. 2000. La maison Lamontagne : une architecture, un héritage. Site historique de la Maison Lamontagne, Rimouski-Est, Que.
- MacLean, D. A. 1984. Effects of spruce budworm outbreaks on the productivity and stability of balsam fir forest. *For. Chron.* **60**: 273–279.
- Morin, H. 1994. Dynamics of balsam fir forests in relation to spruce budworm outbreaks in the boreal zone of Quebec. *Can. J. For. Res.* **24**: 730–741.
- Morin, H., and Laprise, D. 1990. Histoire récente des épidémies de la tordeuse des bourgeons de l'épinette au nord du lac Saint-Jean (Québec) : une analyse dendrochronologique. *Can. J. For. Res.* **20**: 1–8.
- Morin, H., Laprise, D., and Bergeron, Y. 1993. Chronology of spruce budworm outbreaks near Lake Duparquet, Abitibi region, Quebec. *Can. J. For. Res.* **23**: 1497–1506.

- Mott, D.G., Nairn, L.D., and Cook, J.A. 1957. Radial growth in forest trees and effects of insect defoliation. *For. Sci.* **3**: 286–304.
- Robitaille, A., and Saucier, J.-P. 1998. Paysages régionaux du Québec méridional. Publications du Québec. Québec, Que.
- Royama, T. 1984. Population dynamics of the spruce budworm *Choristoneura fumiferana*. *Ecol. Monogr.* **54**: 429–462.
- Ryerson, D.E., Swetnam, T.W., and Lynch, A.M. 2003. A tree-ring reconstruction of western spruce budworm outbreaks in the San Juan Mountains, Colorado, U.S.A. *Can. J. For. Res.* **33**: 1010–1028.
- SCIEM. 2002. PAST32 build 700 user manual. Available from <http://www.sciem.com>.
- Simard, M., and Payette, S. 2001. Black spruce decline triggered by spruce budworm at the southern limit of lichen woodland in eastern Canada. *Can. J. For. Res.* **31**: 2160–2172.
- Speer, J.H., Swetnam, T.W., Wickman, B.E., and Youngblood, A. 2001. Changes in pandora moth outbreak dynamics during the past 622 years. *Ecology*, **82**: 679–697.
- Swaine, J.M., and Craighead, F.C. 1924. Studies on the spruce budworm (*Cacoecia fumiferana* Clem.). Part 1: A general account of the outbreaks, injury and associated insects. *Agric. Can. Bull. Tech.* **37**. pp. 3–27.
- Swetnam, T.W., and Lynch, A.M. 1989. A tree-ring reconstruction of western spruce budworm history in the southern Rocky Mountains. *For. Sci.* **35**: 962–986.
- Swetnam, T.W., and Lynch, A.M. 1993. Multicentury, regional-scale patterns of western spruce budworm outbreaks. *Ecol. Monogr.* **63**: 399–424.
- Swetnam, T.W., Thompson, M.A., and Sutherland, E.K. 1985. Spruce budworm handbook. Using dendrochronology to measure radial growth of defoliated trees. *USDA For. Serv. Handb.* 639.
- Turner, K.B. 1952. The relation of mortality of balsam fir caused by the spruce budworm to forest composition in the Algoma forest of Ontario. *Can. Dep. Agric. Publ.* 875.