

Dendrochronological reconstruction of spruce budworm (*Choristoneura fumiferana*) outbreaks in southern Quebec for the last 400 years¹

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Abstract: It is argued that spruce budworm (*Choristoneura fumiferana* (Clemens)) (SBW) outbreaks have tended to be more frequent, severe, and spatially synchronized since the beginning of the 20th century. However, few studies have assessed the long-term (>200 years) variations in SBW outbreak dynamics. We reconstructed the SBW outbreak history at the northern limit of the temperate forest in southern Quebec using dendrochronological material from old buildings and five old-growth stands. Our regional tree-ring chronology (1551–1995) represents one of the longest and most replicated insect outbreak reconstructions in North America. Nine potential outbreaks were identified (1976–1991, 1946–1959, 1915–1929, 1872–1903, 1807–1817, 1754–1765, 1706–1717, 1664–1670, and 1630–1638) with three additional uncertain outbreaks (1647–1661, 1606–1619, and 1564–1578). Results suggested that southern Quebec has experienced frequent and synchronized outbreaks throughout the last 400 years. Although outbreak frequency was higher during the 20th century (approximately 30 years) as compared with the 1660–1850 period (approximately 50 years), similar or even higher outbreak frequency might have occurred prior to 1660 (approximately 28 years). We did not find any evidence that the recent outbreak dynamics in southern Quebec is outside its historical range of the last 400 years. Previous studies based on living trees may have underestimated outbreak frequency and synchrony prior to 1900.

Résumé : Les épidémies de tordeuse des bourgeons de l'épinette (*Choristoneura fumiferana* (Clemens)) (TBE) tendent à être plus fréquentes, sévères et synchrones depuis le début du 20^e siècle. Cependant, peu d'études ont analysé les variations à long terme (>200 ans) de la dynamique épidémique de la TBE. Nous avons reconstitué l'historique des épidémies de TBE dans le nord de la forêt tempérée au sud du Québec en utilisant du matériel dendrochronologique provenant de bâtiments patrimoniaux et de vieux peuplements forestiers. Notre chronologie régionale (1551–1995) constitue l'un des plus longs historiques d'épidémies d'insectes jamais reconstitués en Amérique du Nord et l'un de ceux qui sont basés sur le plus grand nombre de répétitions. Neuf épidémies potentielles ont été identifiées à l'échelle régionale (1976–1991, 1946–1959, 1915–1929, 1872–1903, 1807–1817, 1754–1765, 1706–1717, 1664–1670 et 1630–1638), en plus de trois autres épidémies incertaines (1647–1661, 1606–1619 et 1564–1578). Ces résultats indiquent que le sud du Québec était propice au développement d'épidémies fréquentes et synchrones au cours des derniers 400 ans. Bien que la fréquence des épidémies ait été plus élevée au 20^e siècle (environ 30 ans) que pendant la période 1660–1850 (environ 50 ans), une fréquence similaire ou plus élevée aurait caractérisée la période antérieure à 1660 (environ 28 ans). Aucun indice ne suggère que la récente dynamique des épidémies de TBE dans la forêt tempérée excède sa variabilité naturelle des derniers 400 ans. Les études antérieures basées sur des arbres vivants ont pu sous-estimer la fréquence et le synchronisme des épidémies antérieures au 20^e siècle.

Introduction

Spruce budworm (*Choristoneura fumiferana* (Clemens)) (SBW) outbreaks are the most important natural disturbance in the southern part of the boreal forest in northeastern North

America (MacLean 1984; Morin and Laprise 1990). Balsam fir (*Abies balsamea* (L.) Mill.) is the main host of this defoliator although white spruce (*Picea glauca* (Moench) Voss) and to a lesser extent black spruce (*Picea mariana* (Mill.) B.

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S.P.) and red spruce (*Picea rubens* Sarg.) are also affected, especially at epidemic levels. During epidemic events, consecutive years of severe defoliation in host trees result in strong growth suppression and eventually mortality. Mass mortality of host species in the overstory, during severe outbreaks, especially for balsam fir, may affect the local and regional forest composition and is a strong determinant of the long-term forest dynamic in the southern boreal forest (Bouchard et al. 2006).

As for many other epidemic insects (Speer et al. 2001; Esper et al. 2007), SBW is characterized by regular and synchronous oscillations of its population level. The recurrence cycle of outbreaks has averaged about 32–40 years over the last three centuries (Royama 1984; Krause 1997; Morin 1998; Boulanger and Arseneault 2004). These population fluctuations are known to be synchronized over very large areas (Williams and Liebhold 2000; Peltonen et al. 2002; Boulanger and Arseneault 2004) through stochastic and spatially correlated phenomena of density-independent regulation (Moran effect, e.g., climate), change in forest landscape vulnerability (Blais 1983), or population levels of the natural enemy complex (Royama 1984; Régnière and Lysyk 1995; Peltonen et al. 2002).

Specific patterns of SBW outbreaks may be recognized at the regional and supraregional levels (Gray et al. 2000). SBW outbreaks tend to be more severe and long-lasting in bioclimatic domains where its preferred host, balsam fir, is abundant (Gray et al. 2000). On the contrary, outbreaks appear to be less severe, less frequent, and rather asynchronous at the northern (Jardon et al. 2003; Tremblay et al. 2011) and southern parts (Fraver et al. 2007) of the SBW range as well as in wetter coastal areas (Bouchard and Pothier 2010). Although a substantial part of this discrepancy is caused by unsuitable climatic conditions for the development of epidemic-level populations (Gray et al. 2000; Gray 2008; Bouchard and Pothier 2010), low regional host abundance and continuity is thought to be also important (Nealis and Régnière 2004; Campbell et al. 2008; Gray 2008).

Long reconstructions spanning several outbreak cycles are needed to accurately assess the SBW outbreak dynamics (Bouchard and Pothier 2010). A long history of SBW dynamics may be obtained through classical dendrochronological analyses. As for many forest-damaging insects, severe defoliation by SBW causes marked reductions in radial growth of host trees. Based on such growth reductions, several authors reported a recent shift in SBW outbreak dynamics in the boreal forest. Since the beginning of the 20th century, outbreaks have tended to be more frequent, more severe (Blais 1983), or synchronized over larger territories (Jardon et al. 2003) than previously. However, all dendrochronological reconstruction studies arguing of a recent change in SBW outbreak dynamics were performed using living trees. This material rarely led to chronologies longer than 200 years, especially in highly anthropized landscape where forests are young (Boucher et al. 2009). The lack of well-replicated multicentury chronologies may constrain our ability to accurately assess the natural variability as well as potential shifts in SBW outbreak dynamics. Such information is of crucial importance to implement meaningful ecosystem-based forest management guidelines

(Harvey et al. 2002) as well as to forecast future spatiotemporal patterns of SBW outbreaks (Gray et al. 2000).

Longer reconstructions may be obtained through the analysis of wood artifacts, subfossils, or archeological material (Boulanger and Arseneault 2004; Esper et al. 2007; Simard et al. 2011). Old buildings, especially early settlement churches (Krause 1997; Boulanger and Arseneault 2004), frequently include well-preserved, large beams from old-aged spruces that provide excellent dendrochronological material to build long and well-replicated SBW host chronologies. Surprisingly, dendroarcheological material was very rarely used in North America (Krause 1997; Boulanger and Arseneault 2004) to reconstruct insect outbreaks, including SBW.

In this study, we reconstructed the multicentury history of SBW outbreaks in southern Quebec based on dendrochronological material from old buildings and old-growth stands. As this area was settled early by Europeans (Laberge 1990), it comprises many old and well-preserved patrimonial buildings that offer great opportunities to build long and well-replicated SBW host chronologies. Our main objective was to verify if the outbreak dynamic has changed since the beginning of the 20th century compared with the previous 300 years. No previous SBW outbreaks reconstruction has been performed in this area, presumably because present-day forests are not host dominated and do not seem to be as conducive to extensive and severe outbreaks as are balsam fir dominated forests to the north.

Study area

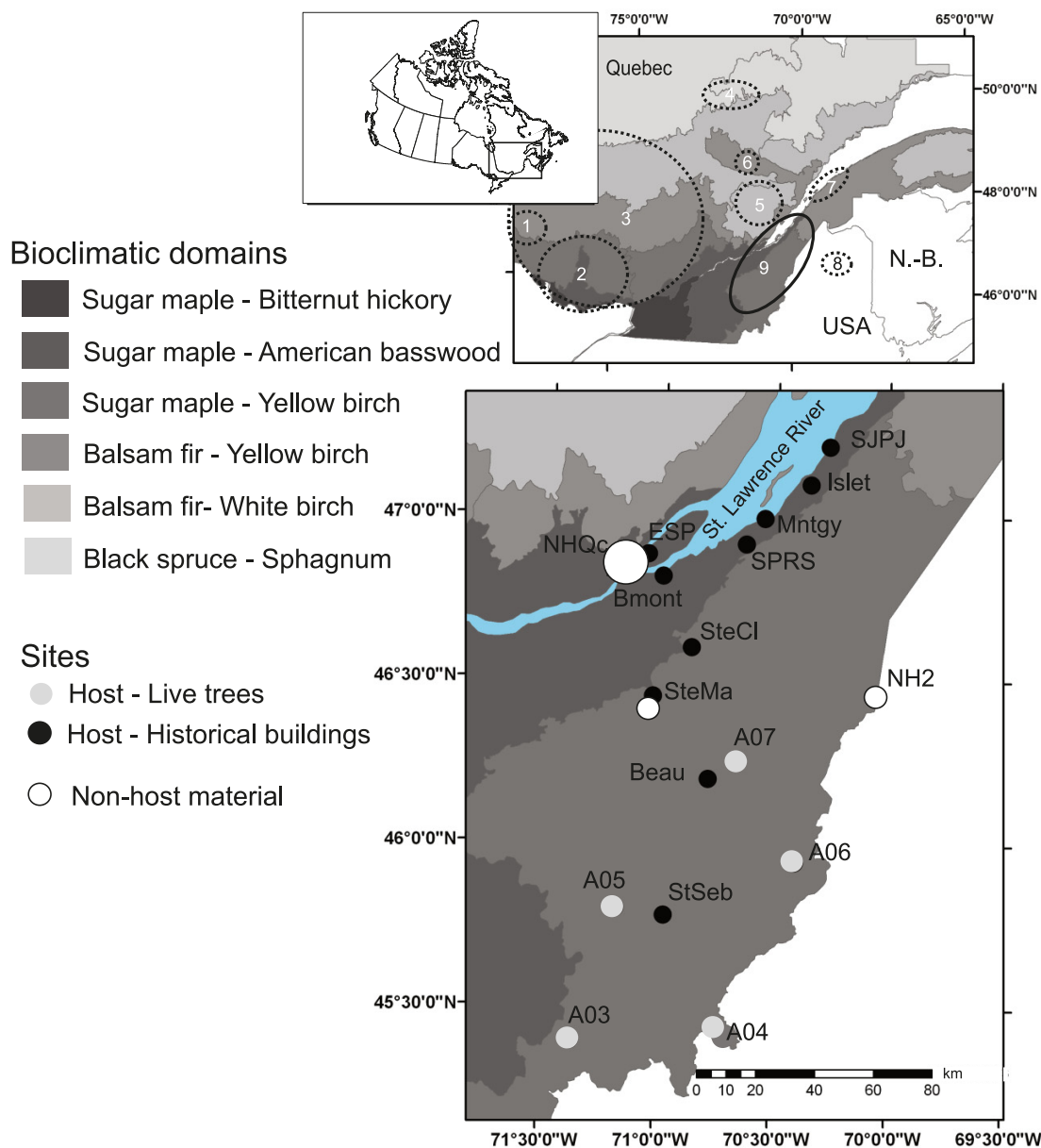
The study area is located in the northernmost northern hardwoods in the southeast of the province of Quebec, Canada (Fig. 1). Climate is subhumid subpolar continental with mean annual temperature ranging between 2.5 and 5 °C. Annual precipitation averages 900–1100 mm of which 25%–30% falls as snow. The area is characterized by a clear north-to-south gradient in topography, land use, and vegetation. The northern area belongs to the low-altitude plain of the St. Lawrence and Great Lakes Lowlands ecoregion (Rowe 1972) and roughly corresponds to the eastern sugar maple (*Acer saccharum* Marsh.) – American basswood (*Tilia americana* L.) bioclimatic subdomain (Robitaille and Saucier 1998). The southern part lies within the Appalachian Mountains and belongs to the eastern sugar maple – yellow birch (*Betula alleghaniensis* Britt.) subdomain. Lands were gradually cleared for agriculture between 1730 and 1850 along the St. Lawrence River, although population expansion was delayed to the early 1800s farther south. Large forest concessions along with industrial logging in forested lands began as early as 1806 but most concessions were granted between 1850 and 1875 (Laberge 1990). After that period, the majority of the landscape was logged at least once and old-growth forests are now extremely rare.

Material and methods

Sampling strategy

The dendrochronological material used in the present study comes from 12 heritage buildings (three houses and nine churches) located in 10 different sites as well as from five old-growth forest stands (Fig. 1; Table 1). Sites were selected to maximize the temporal and spatial extent of time series.

Fig. 1. Location of the study area and study sites. Top map: the study area (solid outline) relative to regions (broken outlines) covered by previous reconstructions of spruce budworm (*Choristoneura fumiferana*) outbreaks in Quebec and Maine. We consulted only published studies covering at least 200 years and that mentioned the covered period and (or) the onset 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, Boulanger and Arseneault 2004; 8, Fraver et al. (2007); 9, this study. Bioclimatic domains according to Robitaille and Saucier (1998) are also shown. Bottom map: location of the study sites. Solid circles, buildings (host); shaded circles, old-growth stands (host); open circles, non-host sites.



Historical buildings were erected between 1717 and 1919 (Saint-Pierre church) and between 1887 and 1890 (Saint-Sébastien church) as determined from previous work (Dagneau and Duchaine 2007) and from this study along with various historical documents. Although we do not know the exact origin of the wood used in these buildings, we assumed that it was harvested in the direct vicinity of the parishes or from the owner's property. Considering the history of settlement and forest logging in this area, we assumed that trees used in buildings were probably cut in pristine forests. Old-growth (>100 years old), host-dominated stands were located using

maps provided by the Ministry of Natural Resources of Quebec. Whenever possible, we selected stands in mesic drainage conditions. While none of the stands seemed to have been clearcut, visual inspection confirmed that the A03 stand showed signs of past selective logging. None of the samples from the old-growth forests showed marked radial growth releases that could be related to significant canopy openings outside presumed outbreak periods.

A maximum number of samples were collected in forest stands and buildings. The great majority of samples from buildings were collected from beams supporting the roof.

Table 1. Number, provenance, and crossdating success for samples included in the local host chronologies.

Chronology	Site sampled	Provenance	No. of spruce trees/beams	No. of spruce samples	No. of spruce dated (%)
Historical buildings					
ESP	Saint-Pierre Church	Roof, bell tower, joists second floor, roof	44	45	24 (54.5)
	Maison Drouin, Saint-Pierre		5	5	3 (60.0)
BMont	Beaumont church	Roof	17	17	12 (70.6)
Mntgy	Old house No. 1, Montmagny	Roof, joists second and third floors	24	26	21 (87.5)
	Old house No. 2, Montmagny	Roof	8	9	8 (100.0)
Islet	Islet church	Roof, bell tower	32	33	27 (84.4)
SJPJ	Saint-Jean-Port-Joli church	Roof, bell tower	37	38	34 (91.9)
SPRS	Saint-Pierre-de-la-Rivière-du-Sud church	Roof, bell tower	32	32	31 (96.9)
SteCl	Sainte-Claire church	Roof, bell tower	37	37	31 (83.8)
SteMa	Sainte-Marie church	Roof, joists first floor	23	23	21 (91.3)
Beau	Beauceville church	Roof, bell tower	27	28	24 (88.8)
StSeb	Saint-Sébastien church	Roof, bell tower	24	24	19 (79.2)
Old-growth stands					
A03		White (18) and red spruce (2) trees	20	32	20 (100.0)
A04		White (1), red (18), and black spruce (2) trees	21	40	21 (100.0)
A05		White (4), red (13), and black spruce (2) trees	19	37	19 (100.0)
A06		Red spruce trees	19	41	19 (100.0)
A07		Red spruce trees	20	39	20 (100.0)
		Total	427	499	354 (82.9)

Additional samples were collected from joists supporting the upper floors of the Drouin House and from the old house No. 1 in Montmagny. In most churches, supplementary samples were taken from structural components of the bell towers (Table 1). Although most sampled beams were several metres long, we cannot confirm that samples from different beams came from different trees. In old-growth stands, increment cores were taken at breast height (1.3 m) from nine to 21 dominant spruce individuals. Spruces were favored over fir, as they have a longer lifespan. Most individuals were red spruces but we also collected samples from white and black spruce trees when available.

One to three samples were collected per wooden beam or tree. Samples from historical buildings were identified to species or genera on the basis of wood anatomy criteria (Hoadley 1990). Because there is no absolute criterion for differentiating spruce species, we cannot ascertain from which species the beams were cut. However, most samples classified as spruce were probably white or red spruce, as these species are by far the most abundant spruce species in the study area. Samples from other genera were discarded from the data set.

Dendrochronological analyses

Cores were glued to a wooden frame, sanded using a fine-grit paper, and then scanned to a 2400–4800 dpi resolution using a flatbed scanner. Growth rings were measured on-screen using either OSM 3.35 (SCIEM 2005) or WinDendro (Regent Instruments Inc. 2005). Raw growth patterns from the same beam or tree were averaged. To remove long-term age-related and cyclical climatic growth trends without masking the outbreak signal, raw measurements were detrended by fitting a cubic spline function preserving at least 50% of the variance associated with ≤ 60 years cyclical components using ARSTAN (Cook and Holmes 1986). Autocorrelation in standardized time series was not removed for the sake of uniformity with similar studies (e.g., Krause 1997; Boulanger and Arseneault 2004). Detrended time series were visually and statistically cross-dated with PAST 4.5 (SCIEM 2004) and inspected for missing rings using COFECHA (Holmes 1983). Local chronologies were built using a biweight robust mean of individual detrended time series coming from the same study site. Individual time series coming from historical buildings located in the same parishes were pooled (Table 1). Local chronologies were then dated using a reference chronology for spruce (1513–2002) from an adjacent area (Boulanger and Arseneault 2004). For each local chronology, we estimated the expressed population signal (EPS) and the period for which subsample signal strength (SSS) was above 0.85 (Wigley et al. 1984).

Outbreak detection and analyses

Past outbreaks were identified by means of a host–non-host correcting method using the program OUTBREAK (Holmes and Swetnam 1996). This procedure was meant to extract the climatic signals in host series. A regional non-host chronology was built from eastern white cedar (*Thuja occidentalis* L.) dendrochronological series. Eastern white cedar has frequently been used as non-host in similar studies

(e.g., Morin and Laprise 1990; Jardon et al. 2003; Fraver et al. 2007). Moreover, eastern white cedar and black and white spruces all positively respond to warm spring and cool, moist July conditions (Tardif et al. 2001). Although red spruce was not evaluated, we endorsed Fraver et al.'s (2007) statement that it is reasonable to assume that this species probably responds to similar climatic conditions as the two other sympatric spruces. Eastern white cedar material was collected from old buildings at three locations in the vicinity of Quebec City (NHQc) (Dagneau and Duchaine 2007), within the Sainte-Marie church's basement (SteMa), from an old-growth stand near the Quebec–US border (NH2), and from various stands near Quebec City (NHQc) (Dagneau and Duchaine 2007) (Fig. 1). Individual eastern white cedar series were detrended and averaged as for the spruce series. Considering time periods with SSS values above 0.85, a large majority (12 out of 15) of spruce chronologies are significantly correlated with cedar chronologies after correcting for autocorrelation (Cook and Jacoby 1979) (see supplementary material S1).² Correlations are even higher and significant for all but one site (A06) when analyzing time periods outside significant growth reductions (that may be associated with SBW outbreaks) in standardized spruce chronologies. Non-host and host values were scaled to the same variance, while non-host indices above 1.0 were raised to the power of 0.3 to reduce the identification of spurious outbreaks during years of important radial growth in non-hosts (Holmes and Swetnam 1996; Fraver et al. 2007). Corrected indices were then computed by subtracting non-host from host growth indices. On the basis of previous work (Swetnam and Lynch 1993; Speer et al. 2001; Boulanger and Arseneault 2004), a presumed outbreak was defined for each tree as any growth reduction longer than 5 years that included at least one year with a corrected index of less than -1.28 standard deviation from the mean. The A06 spruce chronology was not corrected with non-host data, as it was poorly correlated with the eastern white cedar chronology even when considering suspected endemic periods only.

Mean corrected chronologies were produced by averaging individual corrected series from the same sites, except for A06 where an uncorrected chronology was produced. As old buildings are likely to include individuals of several species of spruce, we pooled data from red, white, and black spruce individuals coming from the same old-growth stand. Significant growth reduction events at the site level were identified on local standardized (A06) or corrected (remaining sites) chronologies using the same criteria as detailed above for individual trees. These were referred to as potential outbreaks. Time periods with at least 40% of individuals affected by significant growth reductions during a minimum of 5 consecutive years were also considered as uncertain site-level outbreak events. In this case, the onset and termination of the event were set as the first and last year when this criterion was met. Only portions of local chronologies with SSS above 0.85 were considered for analyses. Onset and termination of potential outbreak periods were assessed as the first and last year when at least one site recorded significant outbreak conditions, respectively.

²Supplementary data are available with this article through the journal Web site at <http://nrcresearchpress.com/doi/suppl/10.1139/x2012-069>.

Results and discussion

A total of 427 spruce individuals were sampled in the present study, including 99 living trees and 328 beams of which 82.9% ($n = 354$) were successfully cross-dated (Table 1). Among historical buildings, cross-dating success varied between 54.5% (Saint-Pierre church) and 100% (old house No. 2 in Montmagny). Length of host chronologies built from old buildings and old-growth stands averaged 215 ± 37 and 175 ± 19 years (mean ± 1 SD), respectively (Table 2). Sample depth was high with at least 20 individuals covering the 1601–1995 period. Maximum replication was achieved at the mid-18th century (maximum $n = 182$). Except for the Bmont chronology, all local chronologies were sufficiently replicated with EPS values above 0.85 (Table 2).

Detection and description of potential outbreaks

Our regional spruce chronology (1551–1995) (Fig. 2; also see supplementary material S2) is one of the longest ever built for this genus and one of the most replicated and longest insect outbreak reconstructions in North America (Speer et al. 2001; Boulanger and Arseneault 2004). Furthermore, considering relatively high sample depth ($n > 20$ after 1601 and $n > 50$ after 1629) (Fig. 3) and spatial replication, the present study probably provides the most complete dendrochronological assessment of potential SBW outbreaks that occurred before the 18th century in northeastern North America. At the site level, a total of 42 significant growth reduction events were recorded. These events averaged 10.2 ± 3.8 years (mean \pm SD) (Fig. 4) and were lumped in nine, possibly 12, distinct periods of potential outbreaks. Assuming that all significant growth reductions identified on corrected host chronologies are associated with SBW outbreaks, recurrence cycle during the 1593–1995 period (global SSS > 0.85) (Table 2) would average 44.8 years in the study area. However, when including the early part (1551–1592, global SSS < 0.85) of the regional chronology as well as uncertain outbreaks, the mean recurrence cycle decreases to 37.1 years.

Two potential outbreaks were recorded between 1976 and 1986 (O1) and between 1943 and 1959 (O2). Synchronous and important growth reductions occurred in the A03, A06, and A07 old-growth stands during O1, whereas growth reductions associated with O2 were faint, affecting few individuals and sites (Figs. 2 and 3). Only one site (A03) reached both outbreak criteria during O2 (Fig. 4). Outbreaks O1 and O2 correspond to known SBW outbreaks identified previously using either dendrochronological analyses (Fig. 4) or extensive aerial and field surveys in eastern Canada (e.g., Blais 1983; Hardy et al. 1986; Morin 1998; Boulanger and Arseneault 2004). Growth reduction intensities (Fig. 2) reported here for these episodes were similar to observations in other dendrochronological studies. Indeed, sharp growth reductions in host trees are frequently reported during O1, which is frequently seen as the most widespread and severe SBW outbreak of the last two centuries (Blais 1983; MacLean 1984). Throughout its range, this outbreak resulted in extensive mortality and growth reductions in host trees (Bouchard et al. 2006). Less intense and less extensive growth reductions were repeatedly observed in several areas during O2 (e.g., Blais 1983; Krause 1997; Boulanger and Arseneault

2004), while Fraver et al. (2007) failed to detect any outbreak between 1920 and 1970 in Maine (Fig. 4).

Two significant but asynchronous potential outbreaks occurred in 1915–1929 (O3) and 1872–1903 (O4) (Fig. 4). The proportion of individuals affected peaked in 1887 (O4) and 1920–1921 (O3) (Fig. 3). These potential outbreaks were already noticed in neighboring areas using dendrochronological data, although Fraver et al. (2007) did not record O4 (Fig. 4). Although O3 is generally described as severe in most of these regions, intensity of growth reductions along with the proportion of affected individual was rather low in the present study.

Earlier potential outbreaks were identified using dendrochronological material from old buildings only. Three additional and distinct growth reductions occurred between the beginning of the 18th and the early 19th centuries in 1807–1817 (O5), 1754–1765 (O6), and 1706–1717 (O7) (Fig. 2). These events were synchronous at the regional level, as the onset of each outbreak lagged only by 0–2 years among sites. Two of these (O5 and O7) were recorded at all available sites (Fig. 4), while O6 was recorded at all but one site (StSeb). Growth reductions of O5 and O7 were very sharp in all local chronologies (Fig. 2). All of these potential outbreaks have already been associated with SBW outbreaks in other dendrochronological reconstructions based on very old spruce trees (Blais 1965; Fraver et al. 2007) or old buildings (Krause 1997; Boulanger and Arseneault 2004) (Fig. 4).

At least three, potentially four, outbreaks were recorded during the 17th century. The regional proportion of individuals affected peaked at rather short intervals in 1613 (18/27 = 66.7%), 1634 (24/51 = 47.1%), 1650 (24/63 = 38.1%), and 1664 (59/87 = 67.8%) (Fig. 3), making it difficult to conclude if these periods corresponded to distinct outbreaks. Except for O8 (1664–1670), which reached outbreak criteria rather synchronously at all sites, spatial occurrence of previous events was patchy (Fig. 4). Indeed, SJPI was the only site to reach outbreak criteria (1630–1638, O9) prior to O8. Nevertheless, at least 40% of samples recorded significant growth reductions during 5 consecutive years in two different sites during the 1606–1619 and 1647–1661 periods (Fig. 3), which were thus considered as uncertain outbreaks even though the -1.28 SD growth reduction criterion was not met at the site level. Only one other study (Boulanger and Arseneault 2004) built sufficiently long chronologies to trace significant growth reductions associated with SBW outbreaks prior to 1700 (Fig. 4). These authors have identified three potential outbreak events spanning the 1577–1600, 1642–1648, and 1677–1690 time intervals. Although sampling depth in the present study is not sufficient to cover the 16th century, both Bmont and ESP chronologies showed marked double-wave growth reductions between ca. 1564 and 1590, while at least 40% of available individuals recorded potential outbreak conditions during the 1569–1577 and 1584–1586 intervals (Fig. 3). None of our chronologies showed significant growth reductions during the 1642–1648 and 1677–1690 periods.

The southern Quebec outbreak dynamics compared with neighboring areas

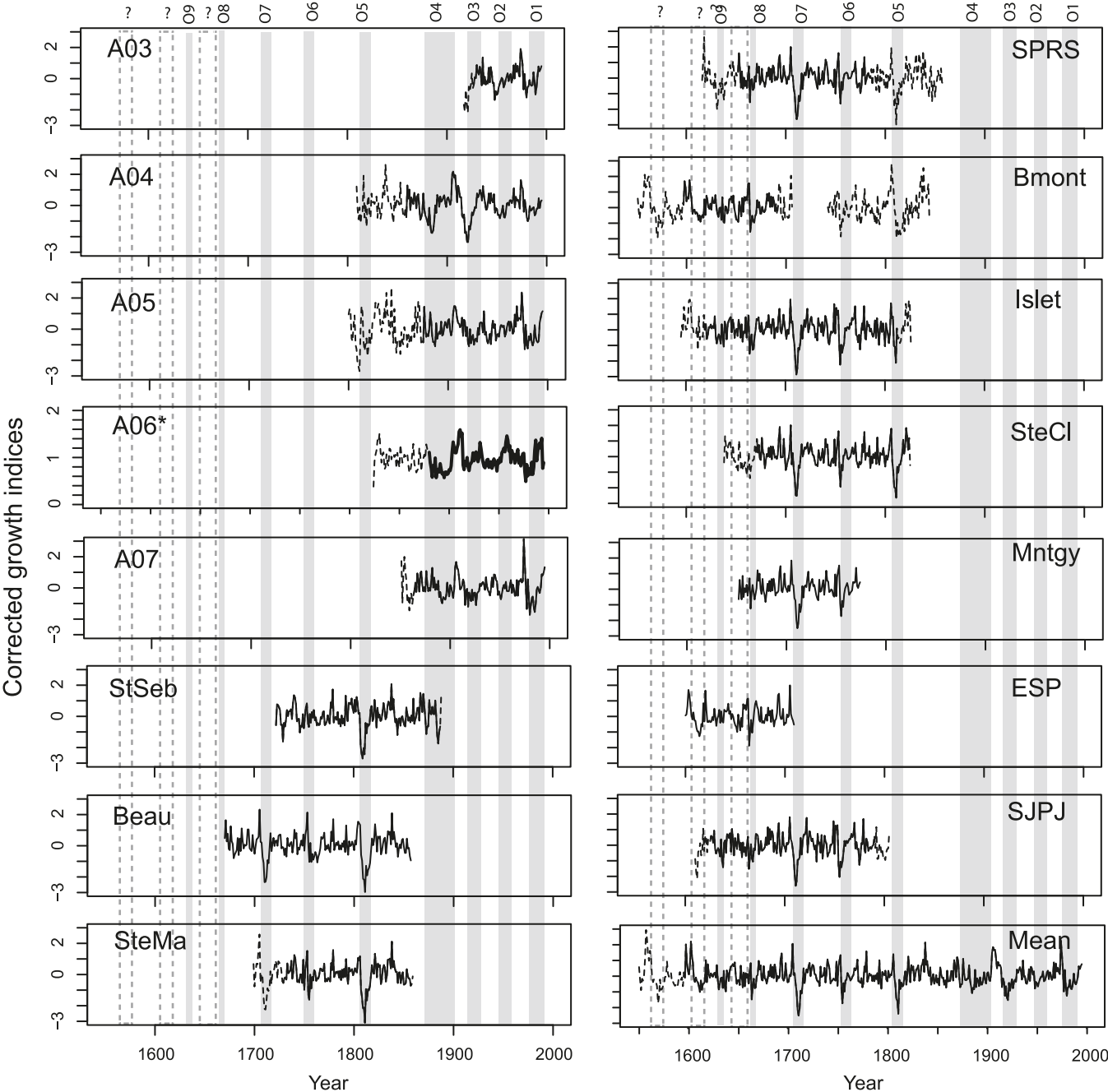
Our results suggest that conditions were conducive to frequent SBW outbreaks throughout the 1600–2000 time period.

Table 2. Characteristics of the site-level standardized host chronologies.

Site	Chronology length	Mean length of series (years)	Mean sensitivity	First-order autocorrelation	r.bar	EPS	Time interval where SSS > 0.85 (minimum <i>n</i>)
Old-growth stands							
A03	1917–1995	72.7	0.146	0.562	0.325	0.906	1927–1995 (7)
A04	1809–1995	113.3	0.185	0.673	0.504	0.955	1859–1995 (5)
A05	1800–1995	116.1	0.162	0.609	0.339	0.907	1875–1995 (7)
A06	1824–1995	109.8	0.158	0.608	0.425	0.934	1880–1995 (6)
A07	1851–1995	126.2	0.130	0.484	0.315	0.902	1863–1995
Historical buildings							
StSeb	1722–1888	135.8	0.141	0.608	0.457	0.931	1739–1887 (5)
Beauc	1645–1872	138.0	0.152	0.428	0.483	0.957	1670–1857 (5)
SteMa	1699–1859	128.7	0.142	0.597	0.456	0.941	1728–1857 (5)
SPRS	1616–1858	101.1	0.150	0.613	0.426	0.957	1652–1784 (6)
Bmont	1551–1706, 1742–1844	107.9	0.133	0.756	0.254	0.816	1597–1690 (7)
Islet	1595–1827	103.4	0.140	0.492	0.482	0.963	1619–1812 (5)
SteCl	1638–1825	109.2	0.133	0.592	0.400	0.955	1671–1824 (7)
Mntgy	1597–1828	102.4	0.151	0.457	0.349	0.942	1652–1774 (8)
ESP	1553–1826	101.1	0.124	0.509	0.256	0.903	1600–1709 (10)
SJPI	1610–1805	105.8	0.128	0.559	0.529	0.974	1625–1789 (5)
Regional chronology	1551–1995	110.7	0.106	0.608	0.295	0.993	1593–1995 (13)

Note: EPS, expressed population signal; SSS, subsample signal strength.

Fig. 2. Local host chronologies corrected for the climatic signal using the Quebec’s eastern white cedar (*Thuja occidentalis*) chronology, except for A06 for which the uncorrected chronology is shown. Periods with subsample signal strength below 0.85 on uncorrected chronologies are shown by a broken line. Identification number (O) and the interval covered by each potential outbreak (light gray) are also shown. Time intervals of uncertain outbreaks are shown by broken rectangles.

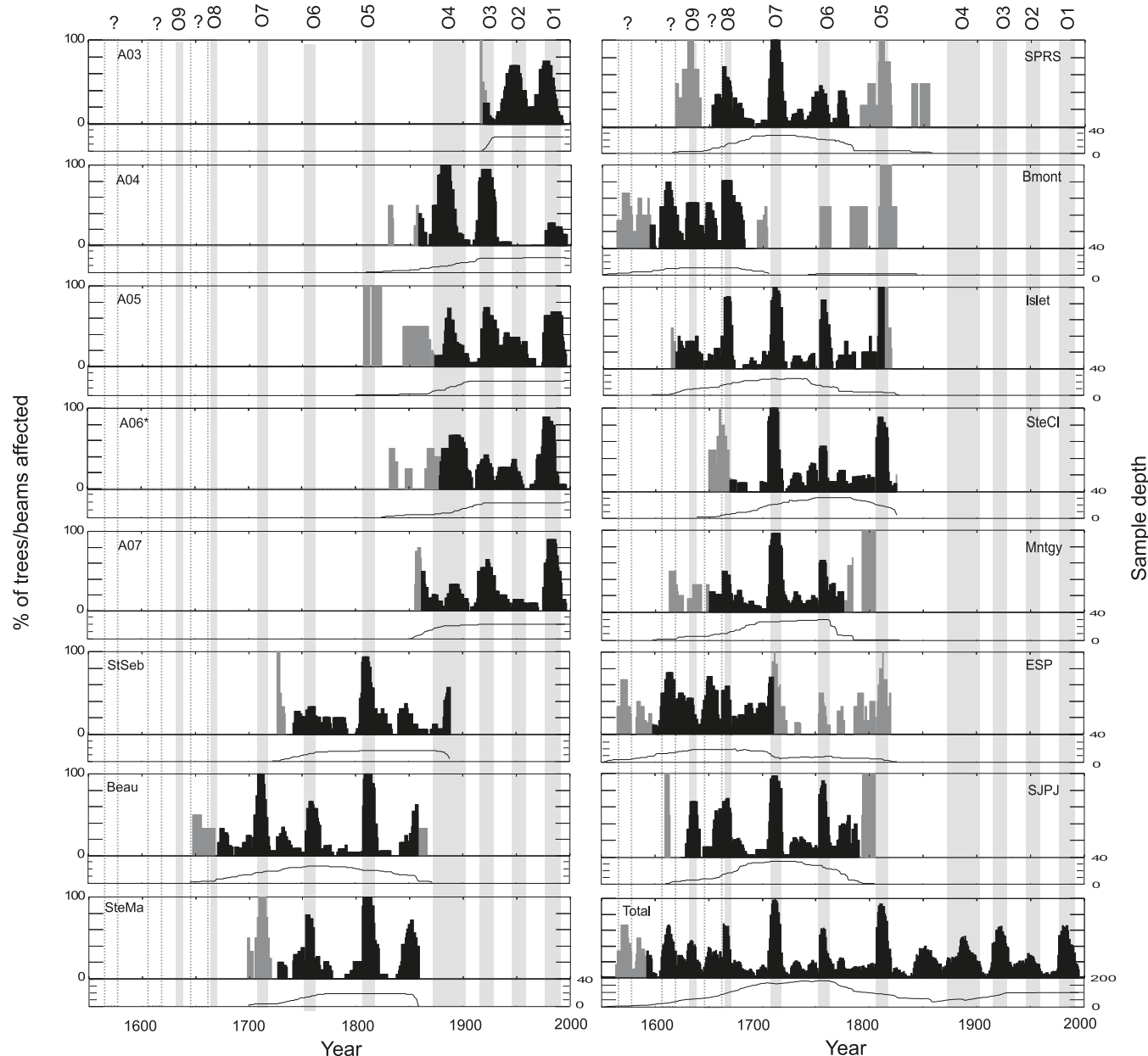


The average outbreak recurrence cycle estimated here (approximately 37.1–44.8 years) was only slightly longer than generally reported in host-dominated forests (Blais 1983; Morin 1998; Jardon et al. 2003) yet within the range (25–45 years) proposed by Royama (1984) and Boulanger and Arseneault (2004). In addition, the outbreak history that we reconstructed for the northern temperate forest of Quebec is synchronous to the one observed in more boreal ecosystems. Indeed, slight differences in outbreak frequency mostly re-

sulted from one supraregional outbreak (ca. 1830–1840) reported from neighboring areas (Fig. 4) that was absent in the present study (Fig. 3). When excluding the pre-1700 period (which is covered by only one additional study with a very limited number of samples (Boulanger and Arseneault 2004)), this means that outbreaks were strongly in phase with those recorded from different bioclimatic domains (Fig. 4).

Similar outbreak frequency and synchrony between our study area and the more northern locations where balsam fir

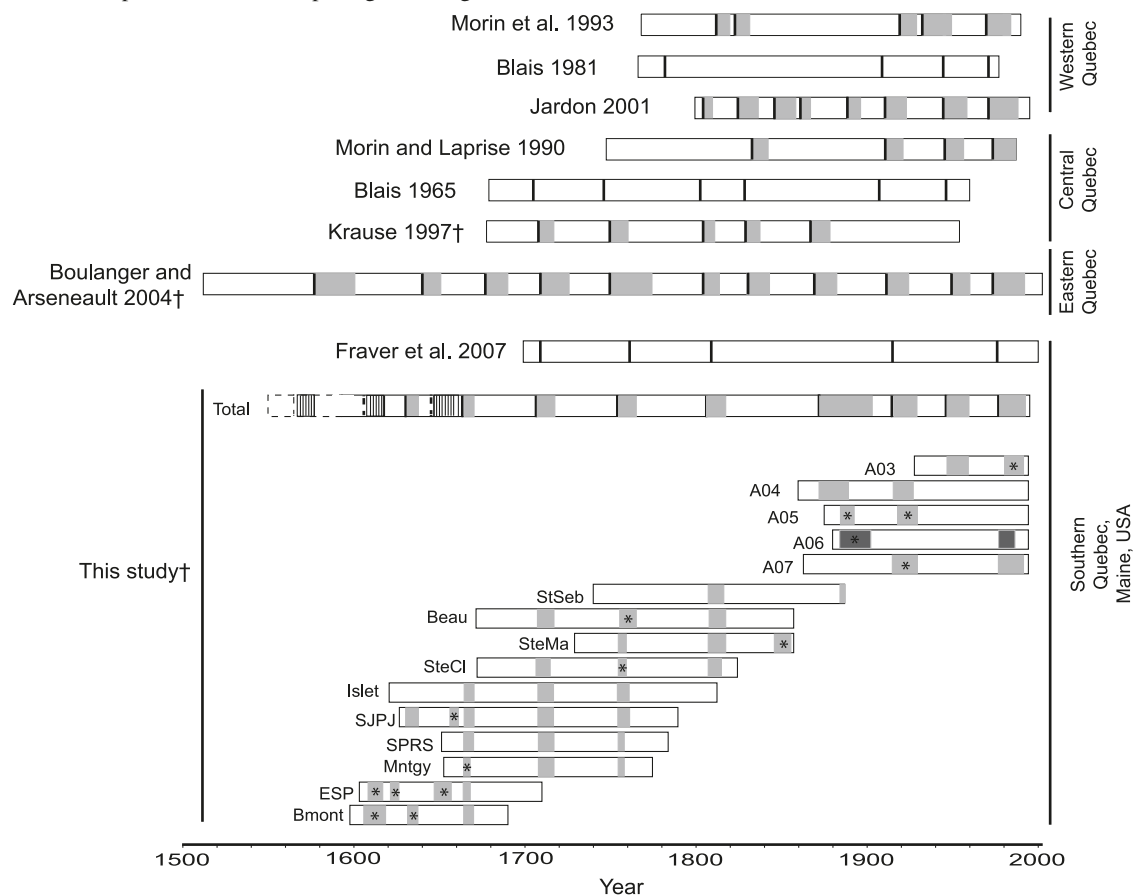
Fig. 3. Proportion of trees/beams showing a significant growth reduction after the host–non-host correction. For A06, significant growth reductions were assessed from uncorrected series. Sample depth along with the time period covered in each sampling site are also given (right-hand axis). Identification number (O) and the interval covered by each potential outbreak (light gray) are shown. Time intervals covered by uncertain outbreaks are shown by broken rectangles.



is more abundant may seem surprising. Indeed, it was proposed that non-host-dominated regions (Blais 1983; Fraver et al. 2007) or those with marginally suitable climate conditions for SBW development (Gray 2008; Bouchard and Pothier 2010) should be less vulnerable to SBW or even escape large-scale outbreaks, leading to lower regional outbreak frequency (Blais 1983; Fraver et al. 2007). For example, relatively long return intervals (approximately 67 years) of SBW outbreaks in northern Maine were associated with low regional abundance of the preferred host, i.e., balsam fir (Fraver et al. 2007). Although our sampling design including

several sites distributed over a relatively large area may have allowed the detection of patchy outbreaks, our results indicate that differences in regional forest composition between northern temperate and adjacent southern boreal forests are not sufficient to trigger a completely “out-of-phase” outbreak dynamics. Whatever the causes of synchrony and associated periodicity, between the two zones, exogenous and endogenous factors affecting these parameters clearly extended well beyond the spatial scale considered in our study (Williams and Liebhold 2000; Peltonen et al. 2002; Jardon et al. 2003; Boulanger and Arseneault 2004).

Fig. 4. Timing of outbreaks reported from additional studies in adjacent areas (see also Fig. 1) in comparison with this study. The onset of outbreak (black line) and time interval covered (gray area) when available are shown for each study. †Studies based on dendroarcheological material. Potential outbreaks identified in this study are also depicted (broken line, onset; hatched area, interval). Spruce budworm (*Choristoneura fumiferana*) outbreaks identified in each site are also shown. Identification number (O) and the interval covered by each outbreak are also shown for the time period with subsample signal strength >0.85. Shaded areas marked with an asterisk concerned uncertain outbreaks.



A stable SBW regional dynamic?

Unlike other studies held in the boreal forest, we did not find any evidence that the regional outbreak periodicity (Blais 1983) or supraregional synchrony (Jardon et al. 2003) observed during the 20th century was unprecedented during the last 400 years. In fact, the data suggest that small temporal variations in outbreak dynamics were observed in southern Quebec during the last 400 years. While analyses suggested higher regional outbreak frequency since O3 (30.3 years between onsets of potential outbreaks) when compared with the 1706–1915 period (52.0 years), similar or even higher outbreak frequency might have occurred prior to 1706 (28.4 years). In addition, the timing of potential outbreaks suggested little change in supraregional synchrony after 1700. Outbreak severity, i.e., its impact on host mortality, is difficult to interpret from dendrochronological data. Nevertheless, the results suggested that several outbreaks prior to the 20th century, especially O5 and O7 that were recorded in 93.4% and 98.8% of all samples, respectively (Fig. 3), might have affected a larger proportion of host trees than O1, which is recognized as one of the most severe out-

breaks of recent times. However, how these outbreaks might have affected the composition and the structure of the landscape is unknown.

Several authors argued for more severe (Jardon 2001), synchronized (Jardon et al. 2003), and frequent (Blais 1983) outbreaks in the southern boreal forest since the beginning of the 20th century. A recent shift in outbreak dynamics was also reported for various insects in North America (e.g., larch sawfly: Jardon et al. 1994; western spruce budworm: Swetnam and Lynch 1993; Pandora moth: Speer et al. 2001) and in Europe (larch budmoth: Esper et al. 2007). Authors argued that the recent shift in SBW outbreak dynamics in the southern part of the boreal forest mostly resulted from a climatically and (or) a logging-induced increase in balsam fir relative abundance (Blais 1983; Bergeron and Leduc 1998; Jardon et al. 2003; Bouchard and Pothier 2010). The relative multicentennial stability that we report for southern Quebec is puzzling. Indeed, along with similar studies conducted in neighboring areas (Boucher et al. 2006; Dupuis et al. 2011), recent analyses based on early land surveys (A. De Römer et al., in preparation) indicate that the study area went through

major logging-induced changes in forest composition and structure within the past two centuries. Balsam fir has become more frequent and dominant today than in presettlement forests, suggesting increased forest vulnerability to SBW outbreaks. However, strong concurrent decline in secondary host abundance, i.e., spruce in favor of non-host species (e.g., *Acer* spp., *Populus* spp.), as well as the important forest fragmentation through extensive land-clearing for agriculture and urban development might both have negatively affected, to a certain extent, the vulnerability of the regional forest to SBW. As a result, it is still difficult to assess how these potential additive shifts in forest composition and landscape configuration might have affected the regional vulnerability to SBW outbreaks and hence the outbreak regime.

The hypothesis of a recent shift in the SBW outbreak synchrony and (or) frequency has been challenged in the last decade (Jardon et al. 2003; Boulanger and Arseneault 2004). Many studies suggesting such a shift were based on growth patterns of living trees. As such, they covered a relatively short time interval (none included outbreaks prior to 1800, except in Blais 1965) and hence very few completed outbreak cycles (at most six). Such a technique prevents the consideration of potential long-term variability in the SBW outbreak dynamics. Moreover, the sole use of living trees may further amplify the perception that outbreaks were more frequent and synchronized in recent times, as sapling or subcanopy trees are less susceptible to record the outbreak signal (Baskerville 1975; but see Fraver et al. 2007). Indeed, this may partly explained the relative asynchronous patterns of growth reductions observed in hosts between 1860 and 1900 in our study, as this period is mostly covered by living trees (except for samples coming from the Saint-Sébastien church). Using a similar sampling strategy as in the present study, Boulanger and Arseneault (2004) estimated that outbreak frequency and synchrony have remained relatively stable for the last 450 years in eastern Quebec. Although we observed changes in outbreak frequency, the present study gives further weight to the hypothesis that the recent SBW outbreak dynamic is not outside its historical range, at least considering the last 400 years.

Limitations

Dendrochronological data are considered to represent a good proxy to identify past insect outbreaks. However, they do not provide direct evidence of past insect activity. Considering that we used a host–non-host correction procedure, we consider that growth reductions identified in host samples mostly represent a non-climatic signal. Nevertheless, we cannot exclude that other disturbance agents, including other pests (e.g., hemlock looper, spruce bark beetle), may have influenced spruce growth. Yet, these insects rarely affect large portions (supraregional) of the territory, contrary to SBW. It is also worth mentioning that our data set is not homogeneous in space and time. Outbreaks prior to O7 were only reconstructed from sites located along the St. Lawrence River, whereas the 20th century SBW history was only assessed from old-growth stands located in the southernmost part of the study area. As a result, spatiotemporal trends in SBW outbreak dynamics may have occurred without being detected by our sampling design.

Conclusions

This study brings further evidence that long dendrochronological reconstructions encompassing several complete outbreak cycles and based on several and well spatially distributed host chronologies are needed to assess the long-term spatiotemporal variability in the SBW outbreak dynamic. Although variations were observed in outbreak frequency, results suggest that outbreak synchrony in the study area has been relatively stable over the last 400 years. Along with other studies (Krause 1997; Boulanger and Arseneault 2004; Esper et al. 2007), we believe that dendroarcheological material from old buildings, especially old churches, provides high-quality data to study the historical dynamics of SBW outbreaks. This material may overcome to a certain extent the problems associated with the sole use of living trees. Further investigations should be conducted throughout the SBW range where such material is available to broaden the spatial and temporal extent of SBW outbreak time series.

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