

Dendrochronological reconstruction of spruce budworm outbreaks in northern Maine, USA

Shawn Fraver, Robert S. Seymour, James H. Speer, and Alan S. White

Abstract: Using dendrochronological analyses, we reconstructed a 300 year history of eastern spruce budworm (*Choristoneura fumiferana* (Clem.)) outbreaks in northern interior Maine. By analyzing radial growth patterns from the budworm host, red spruce (*Picea rubens* Sarg.), and nonhost, northern white cedar (*Thuja occidentalis* L.), we identified five outbreaks beginning ca. 1709, 1762, 1808, 1914, and 1976, all of which have been documented from eastern Canada. However, little or no evidence was found in our study for the 1830s, 1870s, or 1940s outbreaks also documented there. The mean outbreak return interval in our study (67 years) was roughly twice that postulated for eastern Canada. Differences in forest types, and associated stand dynamics, between the regions may explain the longer return intervals, and consequently the absence of these three outbreaks in Maine. Results also indicate that small, slow-growing trees exhibit a budworm signal very similar to that of overstory trees, once tree-ring series have been properly standardized.

Résumé : À l'aide d'analyses dendrochronologiques, nous avons reconstitué l'historique des épidémies de tordeuse des bourgeons de l'épinette (*Choristoneura fumiferana* (Clem.)) sur une période de 300 ans à l'intérieur des terres dans le nord du Maine. En analysant les patrons de croissance radiale d'un hôte de la tordeuse, l'épinette rouge (*Picea rubens* Sarg.), et d'une espèce non hôte, le thuya occidental (*Thuja occidentalis* L.), nous avons identifié cinq épidémies qui ont débuté vers 1709, 1762, 1808, 1914 et 1976, toutes répertoriées dans l'est du Canada. Cependant, aucun ou peu d'indices ont été trouvés au sujet des épidémies de 1830, 1870 ou 1940, également rapportées dans cette région. L'intervalle moyen entre les épidémies (67 ans) était en gros le double de celui qui a été avancé pour l'est du Canada. Les différences entre les régions quant aux types de forêt et la dynamique des peuplements qui leur est associée peuvent expliquer les intervalles plus longs entre les épidémies et par conséquent l'absence de ces trois épidémies dans le Maine. Les résultats indiquent également que le signal produit par la tordeuse chez les petits arbres à croissance lente est très semblable à celui qui est observé chez les arbres de l'étage dominant, une fois les séries dendrochronologiques correctement standardisées.

[Traduit par la Rédaction]

Introduction

Periodic outbreaks of the eastern spruce budworm (*Choristoneura fumiferana* (Clem.), Lepidoptera, Tortricidae) strongly influence forest structure and species composition in many forest types in northeastern North America. The insect feeds on buds and developing foliage of mature conifers, principally balsam fir (*Abies balsamea* (L.) Mill.) and spruce (*Picea*) species, causing dramatic growth reductions and widespread mortality. Despite its common name, the spruce budworm causes greatest mortality to balsam fir (Swaine and Craighead 1924). The area affected by major outbreaks can exceed 50 million hectares (Westveld 1946; Blais 1983; MacLean 1984), making the budworm one of the foremost disturbance agents in the region.

A thorough understanding of this disturbance agent requires long-term historical information on outbreak frequency, severity, and extent. Although such information is documented for parts of eastern Canada, it is lacking for the northeastern USA. In eastern Canada, major outbreaks began ca. 1577, 1642, 1678, 1710, 1752, 1805, 1832, 1868, 1914, 1947, and 1975 (Blais 1983; Boulanger and Arseneault 2004; and citations within), with return intervals estimated at 29–34 years (Jardon et al. 2003), 34 years (Royama 1984; Royama et al. 2005) and 40 years (Baskerville 1975; Boulanger and Arseneault 2004). Given the differences in dominant forest types, it is not known to what extent the historical information from Canada can be extrapolated to the northeastern USA. Balsam fir is common in both regions; however, unlike eastern Canada, extensive balsam-fir dominated forests were historically uncommon in Maine. Dominance by white and black spruces (*Picea glauca* (Moench) Voss and *P. mariana* (Mill. BSP) in eastern Canada shifts to red spruce (*P. rubens* Sarg.) in northern New England (Seymour 1992). Further, the northeastern USA supports more complex, mixed-species forests than does eastern Canada.

Methods of dendrochronology provide a reliable means of reconstructing the history of spruce budworm outbreaks, visible as abrupt and prolonged radial growth reductions in surviving trees. Host–nonhost analyses aid the identification and interpretation of such growth reductions (e.g., Blais 1965; Swetnam and Lynch 1989; Morin et al. 1993; Krause

Received 6 March 2006. Accepted 8 September 2006. Published on the NRC Research Press Web site at cjfr.nrc.ca on 16 May 2007.

S. Fraver.¹ Department of Natural Sciences, Mid Sweden University, SE-851 70, Sundsvall, Sweden.

R.S. Seymour and A.S. White. Department of Forest Ecosystem Science, 5755 Nutting Hall, University of Maine, Orono, ME 04469, USA.

J.H. Speer. Department of Geography, Geology and Anthropology, Indiana State University, Terre Haute, IN 47809, USA.

¹Corresponding author (e-mail: Shawn.Fraver@miun.se).

1997; Fillion et al. 1998; Speer et al. 2001; Boulanger and Arseneault 2004). If a host tree species shows an abrupt and prolonged growth reduction while the concurrent growth in a nonhost species shows no such reduction, the host's response can be attributed to a host-specific agent. Applying these methods to the history of spruce budworm outbreaks requires relatively long tree-ring chronologies for both host and nonhost species. This has been a limitation in eastern North America, because forest harvesting has eliminated most of the old-growth forests that contain this biological archive. Krause (1997) and Boulanger and Arseneault (2004) overcame this limitation by constructing chronologies from spruce beams of old buildings in Quebec, supplemented by, in the latter study, chronologies from living trees.

An additional limitation of dendrochronological methods, as applied to this topic, is the possibility that small trees, such as those predominant in the early portions of the chronology, might be less affected by budworm defoliation than larger canopy trees predominant in the latter portion. For example, spruce and balsam fir seedlings (Baskerville 1975) and small suppressed balsam fir trees (Reams et al. 1988) are known to be less affected by budworm defoliation than are overtopping trees. Markedly different responses would clearly confound the interpretation of results, causing poor resolution in the early portions of reconstructed outbreak chronologies (Boulanger and Arseneault 2004).

Thus, the objectives of this study were to (1) reconstruct the history of major spruce budworm outbreaks in northern interior Maine using host–nonhost dendrochronological analyses, with red spruce as the host and northern white cedar (*Thuja occidentalis* L.) as the nonhost species; (2) contrast the outbreaks detected in this region to those of eastern Canada; and (3) evaluate the efficacy of using radial growth patterns of small spruce trees for the purpose of detecting outbreaks. Where necessary we augment our dendrochronological analyses with relevant historical documentation. The dendrochronological data were collected from an extensive old-growth forest reserve that supports relatively old red spruce and northern white cedar, thereby offering a unique opportunity to reconstruct budworm outbreaks for the last 300 years. Further, fire is not a confounding factor in these chronologies, given its absence in recent centuries (Fraver 2004). This is the first detailed retrospective study of spruce budworm outbreaks for the northeastern USA.

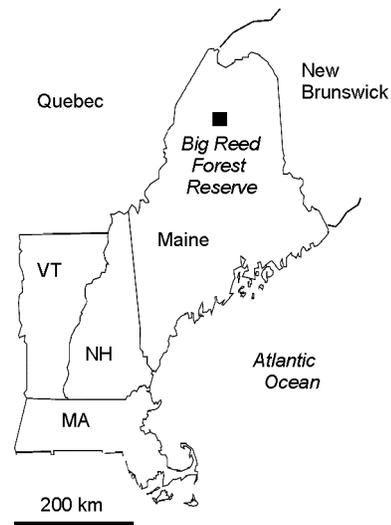
Material and methods

Study area

This work was conducted within the Big Reed Forest Reserve (hereafter referred to as the Reserve) of northern Piscataquis County, Maine (centered at 46°20'N, 69°5'W; Fig. 1). The Reserve is owned by The Nature Conservancy. At approximately 2000 ha, it is one of the largest remaining tracts of old-growth forest in the northeastern USA. Historical records and field observations reveal minimal evidence of timber harvesting in the Reserve (Chokkalingam and White 2001). Mean annual precipitation is 1058 mm, and temperature 5.3 °C (Baron et al. 1980; Millinocket station). The Reserve supports forest communities, soils, elevation ranges, and topographic settings typical of northern Maine.

The following five forest community types are found in

Fig. 1. Regional map showing the location of the Big Reed Forest Reserve (not to scale) in north-central Maine.



the Reserve (listed here in order of decreasing aerial extent): mixed hardwood – conifer forests, northern white cedar seepage forests, red spruce forests, northern white cedar swamps, and northern hardwood forests (community nomenclature generally follows that of the Maine Natural Areas Program 1991). Red spruce is present in varying abundance in all community types, ranging from 3% basal area (northern white cedar swamps) to 90% (red spruce forests). Northern white cedar is present in all but the northern hardwood type, ranging from 3% basal area (red spruce forests) to 87% (northern white cedar swamps). Balsam fir, though present in all community types, is never dominant; it reaches only 12% basal area (mixed hardwood–conifer forests) to 13% (northern white cedar seepage forests) (Fraver 2004). Detailed reconstructions of disturbance histories for the Reserve reveal no evidence of stand-replacing disturbance in recent centuries; all stands studied show multi-aged structures (Chokkalingam 1998; Fraver 2004; Fraver and White 2005).

Field and laboratory procedures

The dendrochronological material used in this study was collected for a larger, ongoing project addressing patterns of natural disturbance throughout the Reserve (see Fraver 2004). That project includes thirty-seven plots (30 m × 50 m) whose locations were selected in a stratified (by forest community type) random manner. Mean plot basal areas (31.2 m²/ha) and stem densities (521 trees per hectare) are typical for old-growth forests of the region (Lutz 1930; Leopold et al. 1988). Plot elevations range from 330 m to 520 m above sea level. On each plot, we extracted increment cores (one per tree) at breast height (1.37 m) from all living canopy trees with diameters at breast height (dbh) ≥ 10 cm. Cores were mounted and sanded to a fine polish using standard methods. Ring widths were measured on a Velmex sliding-stage stereomicroscope to the nearest 0.01 mm. Cross-dating was conducted following the pointer-year method (Yamaguchi 1991), with subsequent verification by COFECHA (Holmes 1983). To increase sample size prior to

1750, we augmented the above data with six archived red spruce cores collected from the Reserve in 1990 and 1999 by members of our laboratory.

Analyses

We produced a standardized chronology for host (red spruce, $N = 772$ trees) and nonhost (northern white cedar, $N = 249$) species to remove unwanted long-term radial-growth trends and homogenize the variance, using the ARSTAN program (Cook and Krusic 2005). Individual tree-ring series with questionable dating were eliminated prior to standardization. Each tree-ring series was standardized by first fitting a cubic spline, then dividing ring widths by the fitted values, producing a unit-less index for each year in the series (Fritts 1978). For both species we selected a cubic spline length of 100 years with a 50% frequency response cutoff. Indexed series were then averaged for each species using a biweight robust mean (Cook et al. 1990) to produce the standardized chronologies.

The host–nonhost analysis assumes the host and nonhost species respond similarly to climate. Deviations between the chronologies can thus be more safely attributed to a host-specific agent. This assumption is reasonable for these species. Working in Quebec, Tardif et al. (2001) found radial growth of northern white cedar, black spruce, white spruce, and balsam fir all to be positively correlated with warm spring and cool, moist July conditions. Though red spruce was not evaluated, it is reasonable to assume that its growth response is similar to the two sympatric spruces. Further, Conkey (1986) found the maximum ring density of red spruce to be positively correlated with early growing-season temperature. Nevertheless, northern white cedar from the Reserve shows a ca. 40 year, quasi-periodic growth cycle (not evident in red spruce), the cause of which is unknown.

We tested whether small-diameter, slow-growing red spruces, such as those predominant in the early decades of the chronology, responded differently to outbreaks than the free-growing canopy trees predominant in the latter portion. By back calculating diameters (as per Frelich 2002) and growth rates, we determined that the sixteen trees alive in the early 1700s were quite small (dbh < 5 cm) and all but one had slow growth (mean ring width 0.44 mm in the 10 years prior to 1709), suggesting they were overtopped saplings at that time. To determine whether the response of overtopped saplings differed from that of canopy trees, we created a data set containing only those individuals with similarly small diameters and slow growth in the 10 years prior to the 1808 outbreak ($N = 14$ series). From these overtopped trees, we developed a standardized chronology (as above), and visually compared it to a chronology developed from the remaining trees. We repeated this same data subsetting and standardization for the period prior to the 1914 outbreak ($N = 34$ series). We could not use data from the most recent outbreak for this purpose because of limited numbers of small diameter trees (i.e., too small for coring in 2000).

Previously undocumented outbreaks were identified by use of the OUTBREAK computer program (Holmes and Swetnam 1996). The program evaluates negative deviations in each standardized host tree-ring series by subtracting from it the indexed values from the standardized nonhost

chronology, once the two have been scaled to the same variance (Swetnam and Lynch 1989). Negative deviations evident in the host chronology can be evaluated by a combination of user-defined parameters to determine whether they are likely attributable to spruce budworm outbreaks. Using the response of red spruce during the two documented outbreaks, we define an outbreak as having indices 1.4 standard deviations below the mean index, a 50% or greater reduction in index values at the onset of the reduction period, and reductions lasting at least four years. To suppress the effect of positive deviations in the nonhost chronology due to its cyclic growth, we raised nonhost index values greater than 1.0 to the power of 0.3 before subtraction (as per Holmes and Swetnam 1996).

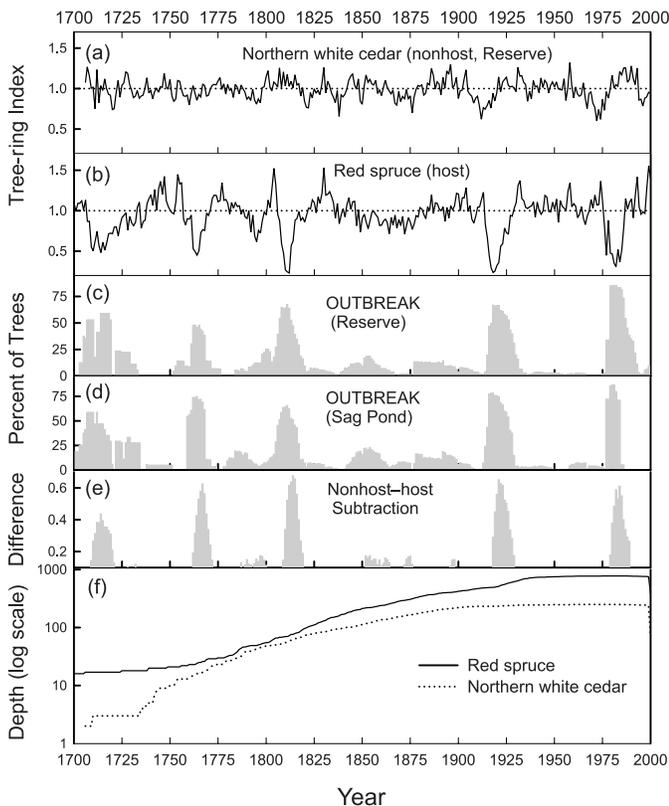
Concerned that the ca. 40 year cycle in the local northern white cedar chronology might confound the OUTBREAK analysis, we used a published northern white cedar chronology from Sag Pond, Maine (46°46'N, 69°10'W; Cook 2005), which does not show the 40 year cycle, in an additional OUTBREAK analysis. Further, to enhance the visual interpretation of putative outbreaks, we simply subtracted the standardized host chronology from the standardized nonhost chronology (from Sag Pond) and plotted the positive differences (after smoothing with a 6 year running mean).

Results and discussion

A visual inspection of the standardized red spruce chronology, coupled with the results from the host–nonhost analyses, corroborates the well-documented outbreak beginning ca. 1976 and strongly suggests outbreaks beginning ca. 1914, 1808, 1762, with slightly weaker evidence for an outbreak beginning ca. 1709 (Fig. 2*b*). A visual inspection of the nonhost–host subtraction (Fig. 2*e*) provides additional strong supporting evidence for all five outbreaks. The growth reduction beginning ca. 1790 is discounted as an outbreak because of a concomitant reduction in both northern white cedar and sugar maple (*Acer saccharum* Marsh., not shown), as well as the lack of evidence from the host–nonhost analysis. The strength and relative consistency of the budworm signal (i.e., an 8–12 year period of markedly slow growth; Fig. 2*b*), suggests that we have not generated false positives (inferred outbreaks that did not occur) or false negatives (undetected major outbreaks) in our analyses. Further, given the large sample sizes used in this study, the random placements of plots within the Reserve, and the fact that the Reserve represents forest communities and topographic settings typical of the region, we consider the results to be representative of northern interior Maine over the last 300 years.

As stated above, our analyses were meant to detect major spruce budworm outbreaks, similar to the documented outbreaks of 1976 and 1914, and similar to those typically identified in dendrochronological reconstructions (e.g., Krause 1997; Boulanger and Arseneault 2004; Morin et al. 1993). We recognize that minor outbreaks, largely undetected by our methods, may have occurred intermittently. Such outbreaks may account for some of the "noise" in our results (Fig. 2). In addition, other moderate-severity disturbances are known to have occurred in the Reserve: hurricanes in 1788, 1869, 1874, 1893, and 1896 likely reached northern

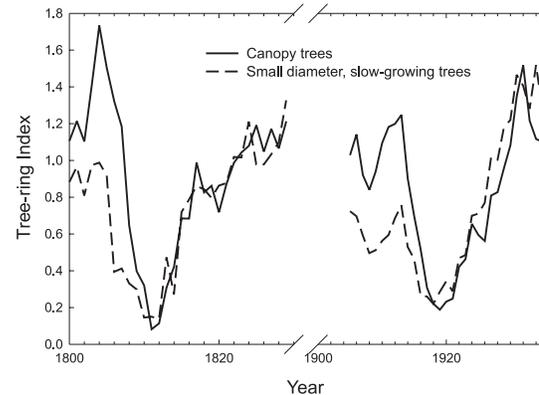
Fig. 2. (a) Standardized chronology for northern white cedar (non-host) derived from the Big Reed Forest Reserve; (b) standardized chronology for red spruce (host) from the Reserve, suggesting five spruce budworm outbreaks as dramatic growth reductions beginning 1709, 1762, 1808, 1914, 1976; (c) results of the OUTBREAK (host–nonhost) analysis, using the nonhost chronology from the Reserve, showing the percent of trees in each year meeting predefined criteria for budworm outbreak detection, with peaks indicating budworm outbreaks; (d) results of the OUTBREAK analysis using the nonhost chronology from Sag Pond; (e) subtraction of the host standardized chronology from the nonhost chronology, after smoothing with a 6 year running mean; (f) sample depth (number of tree-ring series) used in the chronologies and analyses, based on material from the Reserve.



Maine (Ludlum 1963; Neuman et al. 1978; Boose et al. 2001); a spruce bark beetle outbreak occurred ca. 1874 (Packard 1881; Hopkins 1901); and thunderstorm downbursts are known to have been relatively common (Fraver and White 2005). Such events may cause abrupt growth increases (from reduced competition as neighboring trees are killed), or perhaps growth reductions (from canopy damage), thereby creating noise in the host–nonhost analyses, even after standardization of individual tree-ring series. Consequently, though our results convincingly show a sequence of five major outbreaks, they shed little light on budworm population dynamics in intervening periods.

We found that small-diameter, slow-growing red spruces (likely overtopped saplings at the time of the outbreak) clearly express the typical budworm signal once ring-width data have been properly standardized (Fig. 3). This finding may allay concerns that early outbreaks have been overlooked in this and previous work, in part because small indi-

Fig. 3. Comparison of indexed growth reductions between upper-canopy and small-diameter, slow-growing red spruce trees (presumably overtopped saplings) for the periods 1800–1830 and 1900–1935.



viduals may be less affected than larger ones (Boulanger and Arseneault 2004). Though this may be true for spruce and balsam fir seedlings in even-aged fir-dominated stands (Baskerville 1975), it does not appear to be the case in the uneven-aged, non-fir-dominated forests analyzed here.

Following the convention established by previous authors (e.g., Blais 1965, 1968; Morin et al. 1993; Krause 1997; Boulanger and Arseneault 2004) we address details of each outbreak individually, beginning with the most recent.

The 1976 outbreak

During this episode, the host–nonhost analyses indicated that 85% (Reserve nonhost chronology, Fig. 2c) and 87% (Sag Pond nonhost chronology, Fig. 2d) of trees living at that time met the detection criteria at its peak in 1980–1981. This outbreak is extremely well documented in Maine and eastern Canada (e.g., Irland et al. 1988; Boulanger and Arseneault 2004). The outbreak reached epidemic status by 1975 when virtually all the spruce–fir region of northern Maine was severely defoliated (Irland et al. 1988). Severely infested, conifer-dominated forest types within Baxter State Park (the only large continuously unsprayed area in Maine), only 40 km to the south, experienced nearly complete mortality of mature balsam fir and 40%–59% mortality of mature red spruce by 1985 (Osawa et al. 1986; Solomon et al. 2003).

The 1914 outbreak

During this episode, the host–nonhost analyses indicated that 67% (Reserve nonhost chronology, Fig. 2c) and 79% (Sag Pond nonhost chronology, Fig. 2d) of trees living at that time met the detection criteria at its peak in 1918. A visual inspection of the nonhost–host subtraction (Fig. 2e) provides additional strong supporting evidence. This outbreak is well documented in Quebec and New Brunswick (Swaine and Craighead 1924). Although prominent foresters in the USA referred to this outbreak as if it were common knowledge (e.g., Westveld 1946), reliable documentation on its extent and severity in the USA is scanty. Blais (1968) reported this outbreak in Maine, based on a small sample from four locations (see also Blais 1964). Colby (1919) confirmed that the budworm was first observed in western Maine in

1911, and by 1917, had reached epidemic status throughout northern and eastern regions. Seymour (1980) reported balsam fir mortality from 57%–89% of the merchantable volume, with red spruce mortality ranging from 17%–43% in 11 townships that lie within 40 km of the Reserve (see table 16 in Seymour (1980)).

The 1808 outbreak

During this episode, the host–nonhost analyses indicated that 67% (Reserve nonhost chronology, Fig. 2c) and 65% (Sag Pond nonhost chronology, Fig. 2d) of trees living at that time met the detection criteria at its apparent peak in 1811. A visual inspection of the nonhost–host subtraction (Fig. 2e) provides additional strong supporting evidence. This outbreak has been reported from various locations in eastern Canada (e.g., Blais 1983; Krause 1997; Boulanger and Arseneault 2004). Prior to this study, the only evidence from Maine came from 20 red spruce trees sampled as logs from sawmills in southern Quebec (Blais 1964). Historic corroboration comes from observations by Cary (1894) of growth reductions between 1810 and 1814 on spruce logs from Maine.

The 1762 outbreak

During this episode, the host–nonhost analyses indicated that 48% (Reserve chronology, Fig. 2c) and 75% (Sag Pond, Fig. 2d) trees met the criteria at its peak in 1765. A visual inspection of the nonhost–host subtraction (Fig. 2e) provides additional strong supporting evidence. Based on white spruce trees from central Quebec and red and white spruce logs from southern Quebec and northern Maine, Blais (1964, 1965) concluded that two outbreaks had occurred in this period, one in Quebec (1748) and one in Maine (1762). Krause's (1997) outbreak reconstruction shows an unmistakable budworm signal beginning in 1753 in Quebec. This outbreak is also evident in all six of Boulanger and Arseneault's (2004) sites in Quebec. Our chronology shows an unmistakable growth-reduction signal (Fig. 2b), corresponding precisely with Blais' 1762 onset date.

The 1709 outbreak

During this episode, the host–nonhost analyses indicated that 58% (both Reserve and Sag Pond nonhost chronologies, Fig. 2c, d) of trees met the detection criteria. A visual inspection of the nonhost–host subtraction (Fig. 2e) provides supporting evidence, though not as strong as in other outbreaks. This outbreak shows an abrupt growth reduction, as seen in other outbreaks, but exhibits an uncharacteristically long recovery phase (Fig. 2b). Evidence for an early 1700s outbreak has also been reported from Quebec (Blais 1965; Krause 1997; Boulanger and Arseneault 2004). We had suspected that the prolonged recovery seen in our chronology was simply an artifact of the predominance of small, overtopped trees (more appropriately, saplings) in the early portion of the chronology; however, as stated above, results clearly show that sapling response did not differ in any appreciable way from that of canopy trees. A similar contemporaneous prolongation can be seen in Krause's (1997) chronology, as well as Boulanger and Arseneault's (2004) St. Fabien Church chronology. Krause describes this prolongation as a "second wave of reduction" from 1718–1721.

Blais (1962) and Gray et al. (2000) also report similar double-wave outbreaks.

"Missing" outbreaks

All five outbreaks discussed above have been reported from some region of eastern Canada. Perhaps of equal interest are three major outbreaks, namely those of the 1940s, 1870s, and 1830s, that are well documented in Canada, but have not been detected in northern interior Maine. The possible reasons for their absence are discussed in the Outbreak periodicity section that follows.

During the late 1940s, budworm populations had reached epidemic status in Quebec and the Adirondack region of New York (Westveld 1946; Peirson 1950; Boulanger and Arseneault 2004). Annual maps from this period show "light–negligible" defoliation from 1945–1951 near our study location (Weed 1977). Throughout the 1950s, the infestation in Maine was restricted to the very northeastern portion of the state (Irland et al. 1988). Careful examination of our chronologies during this period shows no growth reduction, even for balsam fir, the species most likely to experience modest defoliation in a light outbreak.

The absence of a major outbreak in the 1870s (Fig. 2) is noteworthy, considering that Blais (1968) rated this outbreak as "severe" in southern Quebec, New Brunswick, and Maine, and Etheridge et al. (2005) attributed forest age structures in northwestern New Brunswick to an 1870s outbreak. However, close scrutiny of Blais' (1964) unindexed tree-ring series shows no growth reduction during this period in the Ross Lake site closest to our study area (50 km west–northwest). Swaine and Craighead (1924) found budworm-caused growth reduction beginning ca. 1878 in southeastern Quebec (but not in other Quebec locations) and northeastern New Brunswick. Boulanger and Arseneault (2004) show the outbreak in three of the eight studies reviewed in Quebec. Thus, this outbreak appears to have been quite variable throughout the region. Further, the interpretation of events during the late 1800s has long been confounded by extensive red spruce mortality in areas such as northern interior Maine that were not infested by budworm. Packard (1884) concluded that the mortality found there was attributed to "borers," not the spruce budworm. Hopkins (1901) later conclusively attributed this mortality to the spruce bark beetle (*Dendroctonus piceaperda*, now *D. rufipenis*). Outbreaks of this species avoid detection by host–nonhost analyses because affected trees very rarely recover to record the evidence (Hopkins 1901).

A further outbreak occurred the 1830s in eastern Canada (Blais 1965; Morin et al. 1993; Krause 1997; Boulanger and Arseneault 2004). Blais (1965) regards this outbreak as having a "relatively short duration" and not particularly extensive throughout Quebec; however, Boulanger and Arseneault (2004) found evidence on all their sites in eastern Quebec. Blais's (1964) results show no evidence of this outbreak from four sites in Maine. Similarly, our chronologies show no evidence of an outbreak at this time, nor does historical evidence exist for this outbreak in Maine.

Outbreak periodicity

Assuming the 1709 episode is a bona fide budworm outbreak, northern Maine has experienced five major outbreaks

over a 267 year period, a return interval of 67 years. Superficial inspection suggests no cyclical pattern; only one of the four inter-outbreak periods, the 62 year interval in the 20th century, is close to the long-term average. Interestingly, our return interval is approximately twice the 29–34 year periodicity suggested by Jardon et al. (2003), the 34 year cycle postulated by Royama (1984) and Royama et al. (2005), and the 40 year cycle illustrated by Baskerville (1975) and reconstructed from tree rings by Boulanger and Arseneault (2004). Some authors have speculated that before significant human influence, red spruce – balsam fir forests were historically more resistant to budworm outbreaks than more northerly balsam fir – white spruce forests (Mott 1980; Seymour 1992). This assertion was based largely on the observation (confirmed by this study) that Maine escaped a major budworm outbreak for over 100 years during the 19th century, in contrast to Quebec, which experienced outbreaks in the 1870s and 1830s.

Although spatial variability in the outbreak dynamics could explain the occasional lack of evidence in northern Maine of the major outbreaks reported from eastern Canada, it likely falls short of explaining the apparent absence of three major outbreaks and the resulting longer return interval. We believe the longer return interval can be explained in part by differences in forest types — and the attendant differences in stand dynamics and species longevity — between northern Maine and eastern Canada. In balsam fir-dominated forests of eastern Canada, budworm outbreaks act as stand-replacing disturbances for balsam fir cohorts over age 50–60 years (Baskerville 1975), owing to the well-known increased vulnerability of balsam fir with age (MacLean 1984). In contrast, extensive balsam-fir dominated forests were historically uncommon in Maine. In the natural forest types found here, balsam fir coexists with various longer-lived species that dominate the mixed hardwood-conifer forests, northern white cedar seepage forests, and red spruce or spruce–fir forests. Here, much balsam fir is killed during major outbreaks, but nonhost species as well as many or most spruces survive, given spruce's much lower vulnerability to budworm mortality when compared with balsam fir (Swaine and Craighead 1924; MacLean 1984). Without such extensive stand-wide mortality, new cohorts of highly susceptible even-aged balsam fir do not develop. Although advance regeneration of balsam fir is often abundant in the mixed-species forest types of Maine (Osawa 1994; Chokkalingam and White 2001; Fraver and White 2005), seedlings develop in canopy gaps and lower strata beneath irregular canopies dominated by longer-lived spruces and nonhost species (Seymour 1992; Fraver and White 2005) and are thus delayed in reaching the main canopy.

Acknowledgements

This work benefited from discussions with Charlie Cogbill, Erika Rowland, and Tom Royama. The manuscript has been substantially improved following reviews by two anonymous referees. We thank Brittany Armstrong-Gordon, Charlie Cogbill, Rick Dyer, and Duane Fraver for assistance in the field, and Erika Rowland and Morten Moesswilde for contributing several old spruce cores. Funding was provided by the US Environmental Protection Agency (STAR Fellowship to S.F.), The Nature Conservancy's Ecosystem Re-

search Program (to A.S.W.), and McIntire-Stennis funds. We thank the Maine Chapter of The Nature Conservancy for permission to conduct this work in the Big Reed Forest Reserve. This is Maine Agricultural and Forest Experiment Station Publication 2906.

References

- Baron, W.R., Smith, D.C., Borns, H.W., Jr., Fastook, J., and Bridges, A.E. 1980. Long-time series temperature and precipitation records for Maine, 1808–1978. Life Sciences and Agricultural Experiment Station, University of Maine, Orono, Maine.
- Baskerville, G.L. 1975. Spruce budworm: super silviculturist. *For. Chron.* **51**: 138–140.
- 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. Dept. Forestry, Entom., and Pathol. Branch Bimonthly Prog. Rep.* **20**: 1–2.
- 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. 1968. Regional variation in susceptibility of eastern North American forests to budworm attack based on history of outbreaks. *For. Chron.* **44**: 17–23.
- 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.
- Boose, E.R., Chamberlin, K.E., and Foster, D.R. 2001. Landscape and regional impacts of hurricanes in New England. *Ecol. Monogr.* **71**: 27–48. doi:10.2307/3100043.
- Boulanger, Y., and Arseneault, D. 2004. Spruce budworm outbreaks in eastern Quebec over the last 450 years. *Can. J. For. Res.* **34**: 1035–1043. doi:10.1139/x03-269.
- Cary, A. 1894. On the growth of spruce. Second annual report of the Forest Commissioner of the State of Maine, Augusta, Maine.
- Chokkalingam, U. 1998. Spatial and temporal patterns and dynamics in old-growth northern hardwood and mixed forests of northern Maine. Ph.D. dissertation, University of Maine, Orono, Maine.
- Chokkalingam, U., and White, A. 2001. Structure and spatial patterns of trees in old-growth northern hardwood and mixed forests of northern Maine. *Plant Ecol.* **156**: 139–160. doi:10.1023/A:1012639109366.
- Colby, F.H. 1919. Forest protection and conservation in Maine. Forest Commissioner's Report, Augusta, Maine.
- Conkey, L.E. 1986. Red spruce tree-ring widths and densities in Eastern North America as indicators of past climate. *Quat. Res.* **26**: 232–243. doi:10.1016/0033-5894(86)90107-9.
- Cook, E.R. 2005. Standardized *Thuja occidentalis* chronology for Sag Pond, Maine. IGBP PAGES / World Data Center for Paleoclimatology Data. NOAA / NCDC Paleoclimatology Program, Boulder, Colo.
- Cook, E.R., and Krusic, P.J. 2005. Program ARSTAN: A tree-ring standardization program based on detrending and autoregressive time series modeling, with interactive graphics. Lamont-Doherty Earth Observatory, Columbia University, Palisades, N.Y.
- Cook, E.R., Shiyatov, S., and Mazepa, V. 1990. Estimation of the mean chronology. *In* Methods of dendrochronology: applications in the environmental sciences. Edited by E.R. Cook and L.A. Kairiukstis. Kluwer Academic Publishers, Dordrecht, Netherlands. pp. 123–132.
- Etheridge, D.A., MacLean, D.A., Wagner, R.G., and Wilson, J.S.

2005. Changes in landscape composition and stand structure from 1945–2002 on an industrial forest in New Brunswick. *Can. J. For. Res.* **35**: 1965–1977. doi:10.1139/x05-110.
- Filion, L., Payette, S., Delwaide, A., and Bhiry, N. 1998. Insect defoliators as major disturbance factors in the high-altitude balsam fir forest of Mount Mégantic, southern Quebec. *Can. J. For. Res.* **28**: 1832–1842. doi:10.1139/cjfr-28-12-1832.
- Fraver, S. 2004. Spatial and temporal patterns of natural disturbance in old-growth forests of northern Maine, USA. Ph.D. dissertation, University of Maine, Orono, Maine.
- Fraver, S., and White, A.S. 2005. Disturbance dynamics of old growth *Picea rubens* forests of northern Maine. *J. Veg. Sci.* **16**: 597–610. doi:10.1658/1100-9233(2005)16[597:DDOOPR]2.0.CO;2.
- Frelich, L.E. 2002. Forest dynamics and disturbance regimes. Cambridge University Press, Cambridge, UK.
- Fritts, H.C. 1978. Tree rings and climate. Academic Press, New York.
- 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. doi:10.1016/S0378-1127(99)00134-6.
- Holmes, R.L. 1983. Computer-assisted quality control in tree-ring dating and measurements. *Tree-Ring Bull.* **44**: 69–75.
- Holmes, R.L., and Swetnam, T.W. 1996. Program OUTBREAK Users Manual. Laboratory of Tree-Ring Research. University of Arizona, Tucson, Ariz.
- Hopkins, A.D. 1901. Insect enemies of the spruce in the northeast. USDA Division of Entomology Bull. 28.
- Ireland, L.C., Dimond, J.B., Stone, J.L., Falk, J., and Baum, E. 1988. The spruce budworm outbreak in Maine in the 1970's – assessment and directions for the future. *Maine Agric. Exp. Stn. Bull.* 819.
- 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. doi:10.1139/x03-108.
- 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. doi:10.1139/cjfr-27-1-69.
- Leopold, D.J., Reschke, C., and Smith, D.S. 1988. Old-growth forests of Adirondack Park, New York. *Nat. Areas J.* **8**: 166–189.
- Ludlum, D.M. 1963. Early American hurricanes 1492–1870. American Meteorological Society, Boston, Mass.
- Lutz, H.J. 1930. The vegetation of Heart's Content, a virgin forest in northwestern Pennsylvania. *Ecology*, **11**: 1–29. doi:10.2307/1930778.
- MacLean, D.A. 1984. Effects of spruce budworm outbreaks on the productivity and stability of balsam fir forests. *For. Chron.* **60**: 273–279.
- Maine Natural Areas Program. 1991. Natural landscapes of Maine: a classification of ecosystems and natural communities. Department of Economic and Community Development, Augusta, Maine.
- 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. 1980. Spruce budworm protection management in Maine. *Maine Forest Review*, **13**: 26–33.
- Neuman, C.J., Cry, G.E., Caso, E.L., and Jarvinen, B.R. 1978. Tropical cyclones of the North Atlantic 1871–1977. National Climatic Center, Asheville, N.C.
- Osawa, A. 1994. Seedling responses to forest canopy disturbance following a spruce budworm outbreak in Maine. *Can. J. For. Res.* **24**: 850–859.
- Osawa, A., Spies, C.J., and Dimond, J.B. 1986. Patterns of tree mortality during an uncontrolled spruce budworm outbreak in Baxter State Park, 1983. *Maine Agric. Exp. Stn. Tech. Bull.* 121.
- Packard, A.S. 1881. Insects injurious to forest and shade trees. U.S. Entomol. Comm. Bull. 7. U.S. Department of the Interior, Washington, D.C.
- Packard, A.S. 1884. Second report on the causes of the destruction of the evergreen and other forest trees in northern New England and New York. In Report of the Commissioner of Agriculture for the year 1884. U.S. Government Printing Office, Washington, D.C. pp. 374–377.
- Peirson, H.B. 1950. Spruce budworm control: a cooperative project in Maine. *Maine Forest Service Circular*, 8, Augusta, Maine.
- Reams, G.A., Brann, T.B., and Halteman, W.A. 1988. A nonparametric survival model for balsam fir during a spruce budworm outbreak. *Can. J. For. Res.* **18**: 787–793.
- Royama, T. 1984. Population dynamics of the spruce budworm *Choristoneura fumiferana*. *Ecol. Monogr.* **54**: 429–462. doi:10.2307/1942595.
- Royama, T., MacKinnon, W.E., Kettela, E.G., Carter, N.E., and Hartling, L.K. 2005. Analysis of spruce budworm outbreak cycles in New Brunswick, Canada, since 1952. *Ecology*, **86**: 1212–1224.
- Seymour, R.S. 1980. Vulnerability to spruce budworm damage and 100-year development of mixed red spruce – fir forests in north central Maine. Ph.D. dissertation, Yale University, New Haven, Conn.
- Seymour, R.S. 1992. The red spruce–balsam fir forest of Maine: evolution of silvicultural practice in response to stand development patterns and disturbances. In *The ecology and silviculture of mixed-species forests*. Edited by M.J. Kelty, B.C. Larson, and C.D. Oliver. Kluwer Publishers, Norwell, Mass. pp. 217–244.
- Solomon, D.S., Zhang, L., Brann, T.B., and Larrick, D.S. 2003. Mortality patterns following spruce budworm infestation in unprotected spruce-fir forests in Maine. *North. J. Appl. For.* **20**: 148–153.
- 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. doi:10.2307/2680188.
- Swaine, J.M., and Craighead, F.C. 1924. Studies on the spruce budworm (*Cacoecia fumiferana* Clem.). *Can. Dep. Agric. Tech. Bull.* 37 (New Ser.). Canada Department of Agriculture, Ottawa, Ont.
- 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.
- Tardif, J., Conciatori, F., and Bergeron, Y. 2001. Comparative analysis of the climate response of seven boreal tree species from northwestern Quebec, Canada. *Tree-Ring Res.*, **57**: 169–181.
- Weed, D. 1977. Spruce budworm in Maine, 1910–1976. Maine Department of Conservation, Maine Forest Service, Augusta, Maine.
- Westveld, M. 1946. Forest management as a means of controlling the spruce budworm. *J. For.* **44**: 949–953.
- Yamaguchi, D.K. 1991. A simple method for cross-dating increment cores from living trees. *Can. J. For. Res.* **21**: 414–416.