

Long-term spruce budworm outbreak dynamics reconstructed from subfossil trees

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ABSTRACT: We reconstructed the long-term spruce budworm (SBW) (*Choristoneura fumiferana* Clem.) outbreak dynamics in the boreal forest of Quebec (Canada) using a dendrochronological approach with subfossil trees. Although the majority of the excavated wood belonging to the genus *Picea* could potentially reveal the past activity of spruce budworms in the tree rings, very few were cross-dated due to a lack of marker rings. All cross-dated trees were found within a particular zone of the peat bogs and the floating chronology was radiocarbon dated to ca. 5.1 cal ka BP. The results presented in this study suggest that the dynamics of SBW outbreaks in the studied area fluctuated during the last millennia and that severe outbreaks as observed during the 20th century seldom occurred in that part of the boreal forest since the end of the last glaciation. These results are in agreement with observations from other parts of eastern North America. Copyright © 2011 John Wiley & Sons, Ltd.

KEYWORDS: *Choristoneura fumiferana*; Holocene; insect outbreak; subfossil wood; tree rings.

Introduction

Other than forest fires, insect outbreaks are one of the most important disturbances in the eastern North American boreal forest. The spruce budworm (SBW) (*Choristoneura fumiferana* Clem.) defoliates balsam fir (*Abies balsamea* [L.] Mill.) as its favourite host, followed by white spruce (*Picea glauca* [Moench] Voss), red spruce (*Picea rubens* Sarg.) and black spruce (*Picea mariana* [Mill.] B.S.P.) (MacLean, 1980; Blais, 1983; Morin *et al.*, 2007; Hennigar *et al.*, 2008). Outbreaks have occurred at an approximate 30- to 40-year cycle over the last 300–400 years (Royama, 1984; Jardon *et al.*, 2003; Boulanger and Arseneault, 2004; Royama *et al.*, 2005). This insect can cause severe damage to the forest, often leading to massive tree mortality during severe SBW outbreaks, especially in fir stands (Blais, 1962; MacLean, 1980; Morin, 1994).

Recent studies have quantified the relationship between forest composition and SBW-induced mortality at the stand and the landscape level (MacLean, 1980; MacLean and Ostaff, 1989; Bergeron *et al.*, 1995; Cappuccino *et al.*, 1998; MacKinnon and MacLean, 2004). Stands dominated by balsam fir have been shown to be more vulnerable to budworm outbreaks than stands dominated by spruce, for example, or stands mixed with non-host softwoods (Harper *et al.*, 2003; Bouchard *et al.*, 2005). The density of hardwoods is also related to lower SBW impact (Bergeron *et al.*, 1995; Campbell *et al.*, 2008).

Fire is a powerful agent enabling rapid changes in stand composition over large areas. At the regional scale, regions with long mean fire return intervals (MFRIs) are generally associated with higher abundance of balsam fir whereas regions with short MFRIs show a higher abundance of pioneer species not susceptible to SBW defoliation (Bouchard and Pothier, 2008, and references therein). Shifts from shorter to longer MFRIs were observed throughout the Holocene. Accordingly, we hypothesized that the impact of SBW outbreaks in the studied area varied during the last millennia as a result of the modification of the forest structure and composition.

To verify this hypothesis, past insect activity was reconstructed using a dendrochronological proxy, tree-ring width (TRW), from subfossil trees excavated from peat bogs. Subfossil

trees were used to extend TRW chronologies back in time, as the age of living forests limits long-term reconstructions.

Study area

The study area, known to be very susceptible to severe SBW outbreaks in the 20th century, is located in the hilly Mont-Valin region, approximately 100 km north of Saguenay, Québec, Canada (48°N, 71°W), within the eastern balsam fir/white birch bioclimatic domain of the continuous boreal forest (Saucier *et al.*, 1998). Balsam fir and black spruce are the dominant canopy species whereas white spruce, paper birch (*Betula papyrifera* Marsh.) and trembling aspen (*Populus tremuloides* Michx.) are less common. Eastern larch (*Larix laricina* [Du Roi] K. Koch) is present on peatlands.

Regional climatic conditions for 1942–1990 (Bagotville A meteorological station, 48°20'N, 71°00'W, 159 m asl), ~120 km south of the study area, are characterized by a mean annual temperature of 2.3°C and mean annual precipitation of 950.8 mm (36% as snow) (Environnement Canada, 2010). All sites were located at an elevation of approximately 600 m asl. The primary disturbances affecting the forest in this environment consist of insect outbreaks and fires (Morin, 1994).

Methods

Peatlands in the studied areas were investigated to evaluate their potential of containing buried wood. Three small peat bogs surrounded by forested slopes were selected. The adjacent forest was composed of balsam fir and black spruce. Prior to excavation, the surface of the bogs was mapped using a theodolite. Excavation was done using a mini-excavator and shovels and water was pumped out of the excavation site regularly using a gas pump. Each piece of wood sufficiently well preserved to show tree rings in transverse cross-section was numbered, sampled and mapped to assess the depth at which it laid. A mean burial depth was computed from peat thickness measured above the base and tip of stems. Transverse sections were taken at the largest end of the stem for dendrochronological analysis. Samples were stored frozen. Peat bogs were excavated down to the mineral horizon.

All wood remains were identified to species or genus using anatomical features (Schweingruber, 1982; Hoadley, 1990). Although most tree species likely to be encountered can be distinguished using wood anatomy parameters, there is no absolute criterion to differentiate black spruce from white

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spruce (Hoadley, 1990; Marguerie *et al.*, 2000). Spruce was consequently identified at the genus level. Black spruce is, however, the species most likely to be found in this environment. Both spruce species are affected by SBW, black spruce to a lesser extent (Hennigar *et al.*, 2008). *Picea* sp. were used to build the chronology as they were the most abundant host species recovered from the peat bogs. The percentage of subfossil balsam firs was limited and consequently that species could not be used to build tree-ring chronologies.

The surface of each section was either prepared with a razor blade or sanded frozen to 200 or 400 grit to count the maximal number of tree rings present. TRWs were measured using a sliding-stage incremental micrometer (Henson, CA, USA) with a precision of 0.01 mm (Cook and Kairiukstis, 1990).

Groups of samples were established based on their location in the peat vertical profile to facilitate cross-dating. Layers of 50 cm overlapping by 25 cm were selected to test trees against one another to find a possible match. Cross-dating was verified using the COFECHA program (Holmes, 1983) and TSAP-Win™ (Rinntech, Germany) software, but also by visual inspection of the growth curves. Samples containing fewer than 55 rings were not considered. Standardization with the ARSTAN program was done using a 66% n year cubic smoothing spline with a fixed 50% cutoff without removing the autocorrelation to preserve the outbreak signal throughout the defoliation period (Cook, 1985). Once all possible trees were assembled, radiocarbon dating of wood from five trees distributed in different parts of the chronology was carried out by accelerator mass spectrometry (Stuiver *et al.*, 1998). ^{14}C dates were calibrated to calendar years using INTCAL04 and are expressed as cal ka BP (BP indicating before AD 1950).

The program OUTBREAK was used to identify possible SBW outbreaks (Holmes and Swetnam, 1996). It allows the identification of growth reduction periods according to defined criteria. The criteria used for SBW-related growth reductions were: growth reductions last a minimum of 5 years and the maximal growth decrease has to be equal to or 1.28 times greater than the standard deviation of the chronology (Jardon, 2001).

The same dendrochronological methods as for subfossil woods (preparation, TRW measurements, detrending, OUTBREAK analysis) were applied on basal transverse sections of 57 living *Picea mariana* sampled in a 20 × 20-m plot in the forest adjacent to the peat bog in site 1, in order to build a reference chronology for the living trees.

Results

The thickness of the organic horizon was variable among the studied peat bogs, from 1.40 to 3.10 m (Fig. 1). More than 500 pieces of wood were excavated; the majority (61%) belonged to the genus *Picea*. Other species such as larch, balsam fir and some deciduous trees, most likely paper birch, were also found.

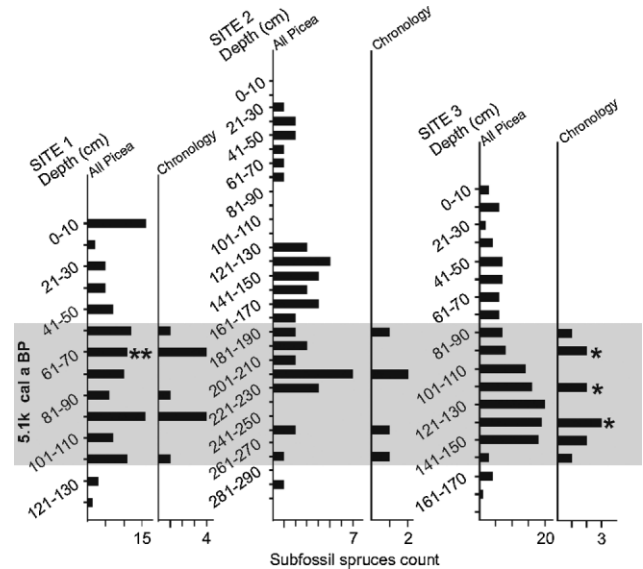


Figure 1. Vertical distribution in the three organic profiles of the excavated subfossil *Picea* sp. having more than 55 rings. The shaded area indicates the location where trees were cross-dated to build the chronology. Stars indicate radiocarbon dates obtained from the wood.

Nearly 30% of the samples were not analysed due to having too few rings (10%), the minimal number having been set at 55 rings for cross-dating, heavy rot (5%) or for other reasons (roots, branches, presence of reaction wood, etc.) (12%).

Despite considerable efforts made at the sampling and cross-dating steps, and even with relatively well-distributed samples across the organic profile of the three peat bogs (Fig. 1), less than 10% of the spruces could be combined to form a 364-year floating chronology (Fig. 2). The chronology was radiocarbon dated to ca. 5.1 ka BP.

Sample size remained low throughout the chronology, reaching 14 individuals at maximum for a short time period (Fig. 2). Within the 364-year floating chronology, 14 growth reductions possibly associated with SBW outbreaks were highlighted by the program OUTBREAK. Based on observations from living trees (Fig. 3), the threshold of affected trees to be considered a potential outbreak was set at 30%.

A 250-year-long chronology from living black spruces sampled in sites surrounding the peat bogs was also built (Fig. 3). The number of trees within the chronology remains above 40, reaching a maximum of 57 during the 20th century, constantly decreasing while going back in time in the 19th century (from 40 to 15 trees). The chronology spans 1754–2005 and includes all known outbreaks that occurred in the 19th and 20th centuries in the area (1810–1813, 1835–1841, 1870–1880, 1906–1922, 1942–1954, 1974–1980) (Blais, 1965; Morin and Laprise, 1990; Krause, 1997). These outbreaks,

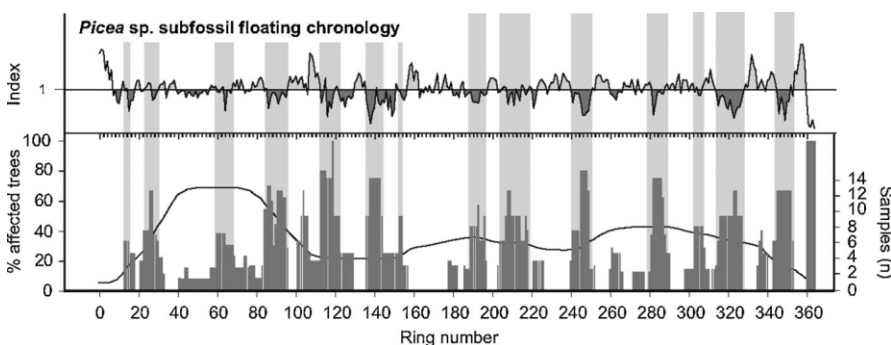


Figure 2. Indexed tree-ring floating chronology, OUTBREAK analysis of growth reductions and number of subfossil *Picea* sp. samples included in the chronology. Shaded areas indicate possible outbreak periods.

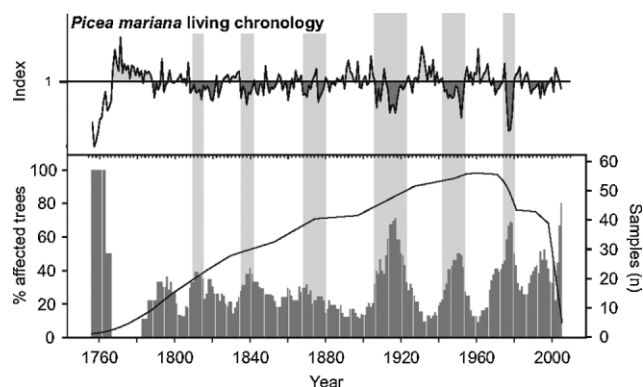


Figure 3. Indexed tree-ring chronologies, OUTBREAK analysis of growth reductions and number of *Picea mariana* samples included in the chronology. Shaded areas indicate known SBW outbreaks.

particularly from the 20th century, were well recorded in tree rings and detected with the program OUTBREAK (Fig. 3). Around 60–80% of trees recorded simultaneously the growth decrease. Outbreaks from the 19th century apparently were less severe, as can be seen in the chronology and from OUTBREAK results. Less than 40% of the analysed trees presented simultaneously a maximal growth reduction during the three known outbreak periods of the 19th century. Compared with outbreaks from the 20th century, the results suggest a more diffuse and relatively constant impact of the insect on tree growth rather than clear pulses of defoliation affecting most of the trees at the same time.

Discussion

Despite a relatively consistent vertical distribution of wood in the studied peat bog, most of the excavated subfossils trees could not be incorporated into a chronology. Only 28 wood pieces located within a particular layer, corresponding to ca. 5.1 cal ka BP, had distinctive tree-ring patterns, allowing us to cross-date radial growth series confidently. Many growth reductions were detected by the program OUTBREAK. This analysis has been very efficient at detecting known SBW outbreaks of the 19th and 20th centuries, suggesting that growth reductions observed in subfossil woods were probably a result of budworm defoliation activity. Although a frequency of growth decrease similar to that observed in modern times (~30–40 years) has been observed, it remains difficult to draw definite conclusions on that particular aspect of the SBW outbreak dynamics due to the very low number of samples at any given time covered by the floating chronology. In recent time, outbreaks of the 20th century considered severe clearly decreased TRW of black spruces in this area.

An extensive overview of the palaeoecological studies conducted to reconstruct the long-term natural variability of insect activity in eastern North America's balsam fir/spruce forest was presented by Lavoie *et al.* (2009). Besides the period of modern insect activity documented from tree rings and insect survey, two main periods during the Holocene with a high presence of insect remains such as head capsules were detected in organic profiles. The first peak of the budworm activity occurred between 1.7 and 0.6 cal ka BP (~300–1330 AD), a period partly corresponding to the Medieval Warm Period (~800–1300 AD; Cronin *et al.*, 2003). This period of high insect activity was detected in different parts of the province of Quebec, specifically in the Charlevoix Highlands (Jasinski and Payette, 2005), in Saguenay (Simard *et al.*, 2006), on Anticosti Island (Lavoie *et al.*, 2009) and in the Mingan Archipelago (Simard *et al.*, 2002). Although head capsules were retrieved in

the Saguenay area within that period (Simard *et al.*, 2006), no tree-ring chronology covering this time frame could be produced, as no marker rings were present to match radial growth patterns. Among the host species, black spruce is the least defoliated for a given density of budworm and could have not registered this outbreak if the SBW population was lower (Hennigar *et al.*, 2008; Nealis and Régnière, 2004). On the other hand, although successive outbreaks may look reasonably regular and predictable over large spatiotemporal scales (Gray *et al.*, 2000), patterns in terms of forest dynamics at the regional scale linked to the severity and mortality associated with SBW outbreaks may be highly variable (Bouchard *et al.*, 2007; Bouchard and Pothier, 2010).

The results of this study suggest more intense SBW activity ca. 5.1 cal ka BP corresponding to the second important period of this insect activity observed in Maine (Anderson *et al.*, 1986) and the St Lawrence Lowlands (Bhury and Filion, 1996) (ca. 5.5–4.5 cal ka BP). Simard *et al.* (2006) observed an increased amount of SBW frass in the Saguenay area at an earlier time, ca. 6.0 cal ka BP. The environmental conditions during this extended period were probably favourable to SBW larvae survival.

The lack of distinctive features in the rings of trees located in the peat bog profile above and below those used to construct the floating chronology, together with observations of a small amount of insect remains in the above-mentioned studies, suggests environmental conditions leading to low interannual variation in tree growth. Although severe SBW outbreaks result in distinct ring patterns in terms of radial growth reduction, as observed in living black spruces from the 20th century, moderate to light defoliation periods are not well captured in TRWs (Nealis and Régnière, 2004; Hennigar *et al.*, 2008). Although black spruce is less susceptible to defoliation than balsam fir (the favourite host of SBW; Nealis and Régnière, 2004; Hennigar *et al.*, 2008), it proved to be a proxy comparable with firs at recording SBW outbreaks of the last century in TRW. The absence of growth reduction in TRW of black spruces is not interpreted here as an absence of SBW outbreaks in the studied area but perhaps as outbreaks of lower severity than those observed in the 20th century. Under lower budworm population, balsam fir would probably sustain more defoliation than black spruces and might be a better indicator of moderate outbreaks (Hennigar *et al.*, 2008).

SBW outbreak severity increases in forests with greater presence of balsam fir (MacLean, 1980; MacLean and Ostaff, 1989). Balsam fir abundance is very closely and positively related to the time elapsed since fire, and this is why several authors have suggested that SBW outbreak severity should be higher in regions in the boreal forest of eastern Canada presenting a longer MFRI (Bergeron and Leduc, 1998; Morin *et al.*, 2007). The relationship between fire occurrence and climate throughout the Holocene in the eastern boreal forest has been demonstrated in palaeoecological reconstructions (Carcaillat and Richard, 2000; Ali *et al.*, 2009). The hypothesis of a change in MFRI and associated forest composition to explain the more severe and synchronized outbreaks observed in the 20th century as compared with the 19th century has been proposed by several researchers (Bergeron and Leduc, 1998; Jardon *et al.*, 2003; Bouchard *et al.*, 2006) although this hypothesis was not completely supported by simulation models (Bouchard and Pothier, 2008).

Even if a link between forest structure and composition and the severity of SBW outbreaks has been demonstrated in earlier studies, the link between the SBW outbreak dynamics during the Holocene and the changing environment (climate and MFRI) inferred from palaeoecological research does not seem to be straightforward. Some authors have suggested that the

early part of the Holocene was characterized by high fire incidence in eastern Canada followed by a low fire frequency between 8 and 3.2 cal ka BP and an increase after 3 cal ka BP (Carcaillet and Richard, 2000; Ali *et al.*, 2009; Cyr *et al.*, 2009). However, Hély *et al.* (2010) suggested the occurrence of a dry period from 7 to 4 cal ka BP followed by a millennial trend toward wetter conditions. It appears to be difficult to draw conclusions based on large-scale climate and fire frequency reconstructions while results from the SBW outbreak dynamics were obtained at the local scale. Other possible reasons might also help explain an increased SBW outbreak impact in relation to changes in climatic conditions. Climate change can act at different levels and has the potential to shift rates of phenological development of either tree host species, of the budworm itself or of its natural enemies, possibly disrupting these trophic relationships (Fleming and Candau, 1998). The climate influence increases toward both cold and warm extremes of the SBW population distribution (Régnière *et al.*, 2010).

Although it is not yet possible to explain the change in the SBW outbreak dynamics during the last millennia, our reconstruction still remains consistent with other SBW reconstructions based on different proxies.

Conclusions

The results presented here suggest that the dynamics of SBW outbreaks fluctuated during the last millennia and that severe outbreak as reflected in the radial growth of black spruce during the 20th century seldom occurred in the studied area since the end of the last glaciation. These results are in agreement with observations from researches using various proxies that covered different parts of eastern North America (Anderson *et al.*, 1986; Bhiry and Filion, 1996; Jasinski and Payette, 2005; Simard *et al.*, 2006; Lavoie *et al.*, 2009).

Regardless of a significant sampling effort, few trees could be cross-dated and the number of samples along the floating chronology remained low. The amount and localization of subfossil wood used to build the chronology suggest that the budworm population in the study area was rarely high enough during the Holocene to lead to important radial growth reduction of black spruces. Nevertheless, lower SBW population levels might have had an impact on the growth of more susceptible species as balsam fir.

Although black spruce is the least susceptible species to SBW defoliation and certainly did not record all SBW outbreaks of the last millennia, the results presented here, in agreement with earlier work from other authors, suggest that the natural variability of the impact of SBW outbreaks during the Holocene was higher than what could be expected when looking at the recent century only. In a context where forest management approaches aim at maintaining healthy and resilient ecosystems by diminishing the gap between natural and managed landscapes, this information is of importance for forest management strategies. Light outbreaks resulting in lower mortality compared with severe outbreaks create more complex forest structures in contrast to those produced by forest management practices (Bouchard and Pothier, 2010). Basing the spatial pattern and rate of harvesting on exceptional severe outbreaks as observed in the last century might not be a sound ecosystem management plan.

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Abbreviations MFRI, mean fire return interval; SBW, spruce budworm; TRW, tree-ring width.

References

- Ali AA, Carcaillet C, Bergeron Y. 2009. Long-term fire frequency variability in the eastern Canadian boreal forest: the influences of climate vs. local factors. *Global Change Biology* **15**: 1230–1241.
- Anderson RS, Davis RB, Miller NG, Stuckenrath R. 1986. History of late- and post-glacial vegetation and disturbance around Upper South Branch Pound, northern Maine. *Canadian Journal of Botany* **64**: 1977–1986.
- Bergeron Y, Leduc A, Morin H, Joyal C. 1995. Balsam fir mortality following the last spruce budworm outbreak in north western Québec. *Canadian Journal of Forest Research* **25**: 1375–1384.
- Bergeron Y, Leduc A. 1998. Relationship between change in fire frequency and mortality due to spruce budworm outbreak in the southeastern Canadian boreal forest. *Journal of Vegetation Science* **9**: 493–500.
- Blais JR. 1962. Collection and analysis of radial growth data from trees for evidence of past spruce budworm outbreaks. *Forestry Chronicles* **38**: 474–483.
- Blais JR. 1965. Spruce budworm outbreaks in the past three centuries in the Laurentide Park, Québec. *Forest Science* **11**: 130–138.
- Blais JR. 1983. Trends in the frequency extent and severity of spruce budworm outbreaks in the eastern Canada. *Canadian Journal of Forest Research* **13**: 539–547.
- Bhiry N, Filion L. 1996. Mid-Holocene hemlock decline in eastern North America linked with phytophagous insect activity. *Quaternary Research* **45**: 312–320.
- Bouchard M, Kneeshaw D, Bergeron Y. 2005. Mortality and stand renewal patterns following the last spruce budworm outbreak in mixed forests of western Quebec. *Forest Ecology and Management* **204**: 297–313.
- Bouchard M, Kneeshaw D, Bergeron Y. 2006. Forest dynamics after successive spruce budworm outbreaks in mixedwood forests. *Ecology* **87**: 2319–2329.
- Bouchard M, Kneeshaw D, Messier C. 2007. Forest dynamics following spruce budworm outbreaks in the northern and southern mixed-woods of central Quebec. *Canadian Journal of Forest Research* **37**: 763–772.
- Bouchard M, Pothier D. 2008. Simulations of the effects of change in mean fire return intervals on balsam fir abundance, and implications for spruce budworm outbreaks. *Ecological Modelling* **218**: 207–218.
- Bouchard M, Pothier D. 2010. Spatiotemporal variability in tree and stand mortality caused by spruce budworm outbreaks in eastern Quebec. *Canadian Journal of Forest Research* **40**: 86–94.
- Boulanger Y, Arsenault D. 2004. Spruce budworm outbreaks in eastern Quebec over the last 450 years. *Canadian Journal of Forest Research* **34**: 1035–1043.
- Campbell EM, MacLean DA, Bergeron Y. 2008. The severity of budworm-caused growth reductions in balsam fir/spruce stands varies with the hardwood content of surrounding forest landscapes. *Forest Science* **54**: 195–205.
- Cappuccino N, Lavertu D, Bergeron Y, Régnière J. 1998. Spruce budworm impact, abundance and parasitism rate in a patchy landscape. *Oecologia* **114**: 236–242.
- Carcaillet C, Richard PJH. 2000. Holocene changes in seasonal precipitation highlighted by fire incidence in eastern Canada. *Climate Dynamics* **16**: 549–559.
- Cook ER. 1985. *A time-series analysis approach to tree-ring standardization*. PhD dissertation, University of Arizona, Tucson.
- Cook ER, Kairiukstis LA. 1990. *Methods of Dendrochronology. Applications in the Environmental Sciences*. Kluwer Academic Publishers, Dordrecht.
- Cronin TM, Dwyer GS, Kamia T, Schwede S, Willard DA. 2003. Medieval Warm Period, Little Ice Age and 20th century temperature variability from Chesapeake Bay. *Global and Planetary Change* **36**: 17–29.
- Cyr D, Gauthier S, Bergeron Y, Carcaillet C. 2009. Forest management is driving the eastern North American boreal forest outside its natural range of variability. *Frontiers in Ecology and the Environment* **7**: 519–524.

- Environnement Canada. 2010. Normales et moyennes climatiques au Canada 1971–2000. <http://climate.weatheroffice.gc.ca/> [accessed 1 May 2010].
- Fleming RA, Candau JN. 1998. Influences of climatic change on some ecological processes of an insect outbreak system in Canada's boreal forests and the implications for biodiversity. *Environmental Monitoring and Assessment* **49**: 235–249.
- Gray DR, Régnière J, Boulet B. 2000. Analysis and use of historical patterns of spruce budworm defoliation to forecast outbreaks patterns in Quebec. *Forest Ecology and Management* **127**: 217–231.
- Harper K, Boudreault C, DeGranpré L, Drapeau P, Gauthier S, Bergeron Y. 2003. Structure, composition and diversity of old-growth black spruce forest of the Clay Belt region in Quebec and Ontario. *Environmental Reviews* **11**: S79–S98.
- Hély C, Girardin MP, Ali AA, Carcaillet C, Brewer S, Bergeron Y. 2010. Eastern boreal North American wildfire risk of the past 7000 years: a model comparison. *Geophysical Research Letters* **37**: L14709. DOI: 10.1029/2010GL043706.
- Hennigar CR, MacLean DA, Quiring DT, Kershaw JA Jr. 2008. Differences in spruce budworm defoliation among balsam fir and white, red and black spruces. *Forest Sciences* **54**: 158–166.
- Hoadley RB. 1990. *Identifying Wood: Accurate Results with Simple Tools*. The Tautin Press: Connecticut.
- Holmes RL. 1983. Computer-assisted quality control in tree-ring dating and measurement. *Tree-ring Bulletin* **43**: 69–78.
- Holmes RL, Swetnam T. 1996. *Program OUTBREAK Users Manual, Dendrochronology Program Library*. Laboratory of Tree-Ring Research, University of Arizona, Tucson, Arizona.
- Jardon Y. 2001. *Analyses temporelles et spatiales des épidémies de la tordeuse des bourgeons de l'épinette au Québec*. PhD thesis, Université du Québec à Montréal, Montréal, Québec.
- Jardon Y, Morin H, Dutilleul P. 2003. Périodicité et synchronisme des épidémies de la tordeuse des bourgeons de l'épinette au Québec. *Canadian Journal of Forest Research* **33**: 1947–1961.
- Jasinski JPP, Payette S. 2005. The creation of alternative stable states in the southern boreal forest, Québec, Canada. *Ecological Monographs* **75**: 561–583.
- Krause C. 1997. The use of dendrochronological material from buildings to get information about past spruce budworm outbreaks. *Canadian Journal of Forest Research* **27**: 69–75.
- Lavoie M, Fillion L, Robert EC. 2009. Boreal peatland margins as repository sites of long-term natural disturbances of balsam fir/spruce forests. *Quaternary Research* **71**: 295–306.
- MacKinnon WE, MacLean DA. 2004. Effects of surrounding forest and site conditions on growth reduction of balsam fir and spruce caused by spruce budworm defoliation. *Canadian Journal of Forest Research* **34**: 2351–2362.
- MacLean DA. 1980. Vulnerability of fir–spruce stands during uncontrolled spruce budworm outbreaks: a review and discussion. *Forestry Chronicles* **56**: 213–221.
- MacLean DA, Ostaff DP. 1989. Patterns of balsam fir mortality caused by an uncontrolled spruce budworm outbreak. *Canadian Journal of Forest Research* **19**: 1087–1095.
- Marguerie D, Bégin Y, Cournoyer L. 2000. Wood anatomy distinction among tamarack (*Larix laricina* [Du Roi] K. Koch), white spruce (*Picea glauca* [Moench.] Voss), and black spruce (*Picea mariana* [Mill.] B.S.P.) from macroremains analysis. *Géographie Physique et Quaternaire* **54**: 317–325.
- Morin H. 1994. Dynamics of balsam fir forest in relation to spruce budworm outbreaks in the Boreal zone of Quebec. *Canadian Journal of Forest Research* **24**: 730–741.
- Morin H, Laprise D. 1990. Histoire récente des épidémies de la tordeuse des bourgeons de l'épinette au nord du lac St-Jean (Québec): une analyse dendrochronologique. *Canadian Journal of Forest Research* **20**: 1–8.
- Morin H, Jardon Y, Gagnon R. 2007. Relationship between spruce budworm outbreaks and forest dynamics in eastern North America. In *Plant Disturbance Ecology. The Process and the Response*, Jonhson EA, Miyanishi K (eds). Academic Press, Elsevier: London; 555–577.
- Nealis VG, Régnière J. 2004. Insect–host relationships influencing disturbance by the spruce budworm in a boreal mixedwood forest. *Canadian Journal of Forest Research* **34**: 1870–1882.
- Régnière J, St-Amant R, Duval P. 2010. Predicting insect distribution under climate change from physiological responses: spruce budworm as an example. *Biological Invasions* doi 10.1007/s10530-010-9918-1.
- Royama T. 1984. Population dynamics of the spruce budworm *Choristoneura fumiferana*. *Ecological Monographs* **54**: 429–462.
- Royama T, MacKinnon WE, Kettela EG, Carter NE, Harting L. 2005. Analysis of spruce budworm outbreak cycles in New Brunswick, Canada, since 1952. *Ecology* **86**: 1212–1224.
- Saucier JP, Bergeron JF, Grondin P, Robitaille A. 1998. *Les régions écologiques du Québec méridional (3e version): un des éléments du système hiérarchique de classification écologique du territoire mis au point par le ministère des Ressources naturelles du Québec*. Supplément de l'Aubelle, no 124. Ministère des ressources naturelles et de la faune, Québec.
- Schweingruber FH. 1982. *Anatomie microscopique du bois*, 2nd edn. Kommissionsverlad: Teufen AR.
- Simard I, Morin H, Potelle B. 2002. A new paleoecological approach to reconstruct long-term history of spruce budworm outbreaks. *Canadian Journal of Forest Research* **32**: 428–438.
- Simard I, Morin H, Lavoie C. 2006. A millennial-scale reconstruction of spruce budworm abundance in Saguenay, Québec, Canada. *The Holocene* **16**: 313–37.
- Stuiver M, Reimer PJ, Beck JW, Burr GS, Hughen KA, Kromer B, McCormac FG, van der Plicht J, Spurk M. 1998. INTCAL98 radiocarbon age calibration, 24 000–0 cal BP. *Radiocarbon* **40**: 1041–1083.