A millennial-scale reconstruction of spruce budworm abundance in Saguenay, Québec, Canada

Isabelle Simard,[1]* Hubert Morin[1] and Claude Lavoie[2]

([1]Département des Sciences fondamentales, Université du Québec à Chicoutimi, 555, boulevard de l'Université, Chicoutimi Québec G7H 2B1, Canada; [2]Centre de recherche en aménagement et développement, Université Laval, Québec G1K 7P4, Canada)

Received 24 January 2005; revised manuscript accepted 22 July 2005

A HOLOCENE RESEARCH PAPER

Abstract: A high-resolution macrofossil analysis was conducted to reconstruct spruce budworm abundance in an 8600-year-old mire in Saguenay, Québec, Canada. Abundant spruce budworm (*Choristoneura fumiferana* [Clem.]) faeces recovered in the peat profile suggested endemic and epidemic presence of the insect in the study site since 8240 cal. BP. Important variations in the abundance of faeces were observed, and two exceptional periods of insect activity were delineated, from 6815 to 6480 cal. BP and during the twentieth century. Lepidoptera head capsules were also found in the Lac des Îlets peat profile. They were less abundant and more altered than spruce budworm faeces, but they offered complementary information on insect activity. The long-term perspective achieved with this macrofossil analysis strongly suggests that intense periods of spruce budworm activity were rare events during the Holocene.

Key words: Insect faeces, Lepidoptera head capsule, macrofossil analysis, mire, outbreak, spruce budworm, Québec, Canada, Holocene.

Introduction

Disturbances such as fire and insect outbreaks have a major influence on the dynamics of boreal ecosystems, more particularly on forest composition and structure (Payette, 1992; Bergeron *et al.*, 1998; McCullough *et al.*, 1998). Insect outbreaks have been studied worldwide to understand their impacts on forest dynamics. Dendroecological and palaeoecological techniques have been used to reconstruct insect outbreak history (Elkinton and Liebhold, 1990; Veblen *et al.* 1991, 1994; Swetnam and Lynch, 1993). Spruce budworm (*Choristoneura fumiferana* [Clem.]) has been widely studied in this respect because it is the main insect affecting coniferous forests in eastern North America (Hardy *et al.*, 1985). Periodic increases in budworm populations to epidemic levels cause extensive mortality and growth reduction in balsam fir (*Abies balsamea* [L.] Mill.) and black spruce (*Picea mariana* [Mill.] B.S.P.) populations (Blais, 1983; Miller and Rusnock, 1993). Using tree rings, it is possible to reconstruct 300–400 years of spruce budworm activity (Blais, 1965, 1983; Morin and Laprise, 1990; Morin *et al.*, 1993; Morin, 1994, 1998; Krause, 1997). However, the timeframe of tree-ring studies is limited by the age of trees, and it is rare to find living balsam fir or black spruce older than 300 years. A millennial-scale perspective is nevertheless essential to achieve a better understanding of natural disturbance cycles and to evaluate the impacts of recent forest management strategies.

A long-term perspective can be achieved with the help of palaeoecological proxies. Most palaeoecological reconstructions of insect outbreaks used head capsules as indicator of the presence of the insect. By using head capsules of hemlock looper (*Lambdina fiscellaria fiscellaria* [Guen.]) and hemlock needles showing chewing damage as indicators, Bhiry and Filion (1996) were able to associate the mid-Holocene hemlock decline in eastern North America with phytophagous insect activity. Head capsules were also tentatively used to reconstruct spruce budworm outbreaks (Davis *et al.*, 1980), but they were too scarce and fragmented to provide a valuable long-term history of insect infestations. Spruce budworm faeces recovered from thick boreal forest humus were also used as a palaeoecological indicator to reconstruct recent outbreak history. The discovery of 1500-year-old faeces in thick humus deposits suggests that this proxy could be used for the long-term reconstruction of insect outbreaks (Simard *et al.*, 2002). The objective of this research was to reconstruct spruce budworm

*Author for correspondence: Centre de recherche en aménagement et développement, Université Laval, Sainte-Foy, Quebec G1K 7P4, Canada (e-mail: I1simard@uqc.ca)

 10.1191/0959683606hl904rp

outbreaks and vegetation history of an 8600-year-old ombrotrophic mire in Saguenay, Québec, Canada.

Study area

The study area is located in the Laurentides Wildlife Reserve (48°11′50″N, 71°14′34″W, 120 m a.s.l.), approximately 30 km south of Saguenay, Québec, Canada (Figure 1). It is included in the Laurentides–Onatchiway forest region (Rowe, 1972) and the balsam fir–white birch (*Betula papyrifera* Marsh.) ecological region 8e (Thibault, 1987). The relief is undulating to mountainous and the area lies on Precambrian crystalline rocks (Rowe, 1972). Regional climatic conditions at the study area for AD 1961–90 (Bagotville station A, 48°20′N, 71°00′W, 159 m a.s.l.) are characterized by a mean annual temperature of 2.2°C and mean annual precipitation of 930 mm, 37% of which falling as snow (Environnement Canada, 1993). The main natural disturbances affecting the forests of the Laurentides Wildlife Reserve are spruce budworm outbreaks and fires. The most recent spruce budworm outbreaks affecting the study area were registered around AD 1748, 1808, 1834, 1910, 1947 and 1972 (Blais, 1965; Lussier *et al.*, 2002). The fire history of the study area is not known. The study site is located in the forested area of the Lac des Îlets mire, approximately 500 m away from the open ombrotrophic part of the mire, in a dense black spruce stand growing on a thick peat deposit (Figure 1). The vegetation is dominated by black spruce and mosses, mainly *Sphagnum* spp. and *Pleurozium schreberi* (Brid.) Mitt.

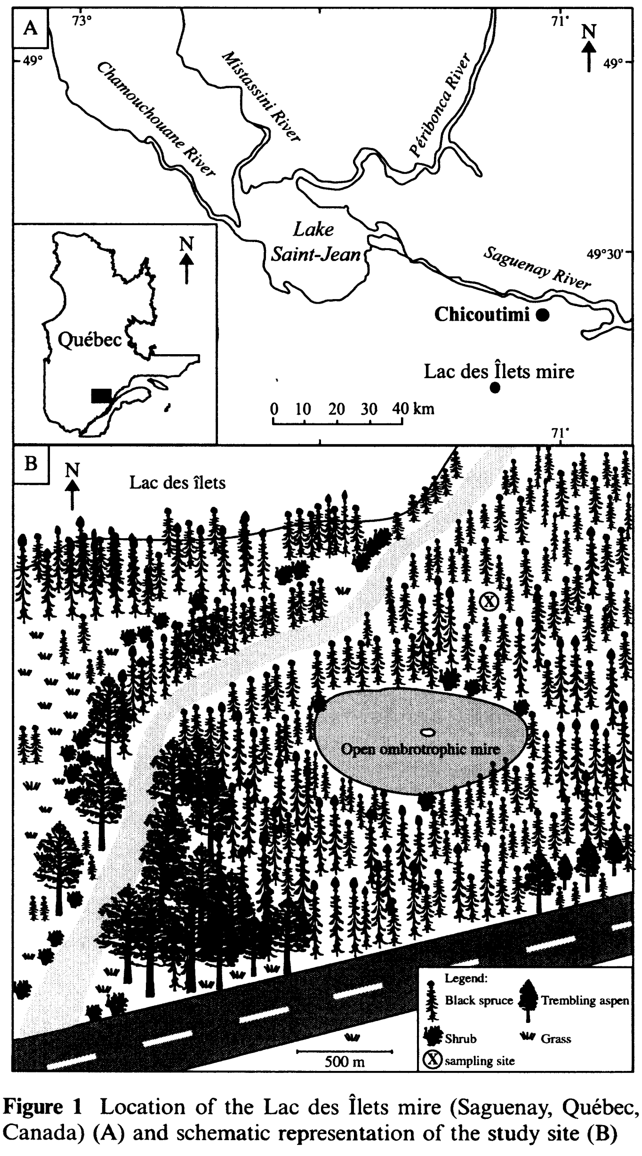

Figure 1 Location of the Lac des Îlets mire (Saguenay, Québec, Canada) (A) and schematic representation of the study site (B)

Methods

A 258-cm core, covering the entire peat deposit and the upper part of the underlying clay deposit, was extracted in the forest area of the mire. The first 40 cm of the profile were extracted with a shovel (10 × 10 × 40-cm monolith). A Coûteau corer (Coûteau, 1962) with a 10-cm diameter was used to sample peat from 40 to 207 cm. The bottom part of the core (207–258 cm) was sampled using a 4.5-cm diameter side-wall peat corer (Jowsey, 1966). The peat was wrapped in plastic and aluminium foil and placed in plastic tubes for transportation to the laboratory where it was kept frozen.

The entire profile was cut into continuous 1-cm-thick slices for macrofossil analysis. No chemical treatment was applied to the samples. Samples were washed through a series of sieves (2, 1, 0.5-mm meshes). Macrofossils recovered (charcoal, spruce budworm faeces, Lepidoptera head capsules, vascular plant, moss and other animal remains) were identified and counted at 60× under a binocular microscope. Plant macrofossils were identified using Montgomery (1977) and Lévesque *et al.* (1988) illustrated guides. A reference collection of seeds, fruits, leaves and stems was also used to identify macrofossils. Nomenclature follows Marie-Victorin (1995) for vascular plants, except Farrar (1996) for trees, and Anderson *et al.* (1990) for mosses. Spruce budworm faeces (Figure 2) were identified according to Simard *et al.* (2002). They were compared with reference faeces (1) of spruce budworm produced by reared larvae feeding on balsam fir and black spruce trees, (2) of spruce budworm collected on the ground during the last outbreak, and (3) collected in a site presently affected by moderate defoliation by spruce budworm. The faeces found in the peat profile were also compared with reference faeces of four other defoliating insects found in boreal forests of Québec: hemlock looper (*Lambdina fiscellaria fiscellaria* [Guen.]), eastern blackheaded budworm (*Acleris variana* [Fern.]), yellowheaded spruce sawfly (*Pikonema alaskensis* [Rohwer]) and Swaine jack pine sawfly (*Neodiprion swainei* Midd.). Larvae of these four species were also reared in laboratory to obtain faeces. When the identification of the faeces found in the Lac des Îlets profile was uncertain, they were labelled 'unidentified' faeces.

Volumes and data were standardized to obtain the number of pieces corresponding to a uniform sampling volume of

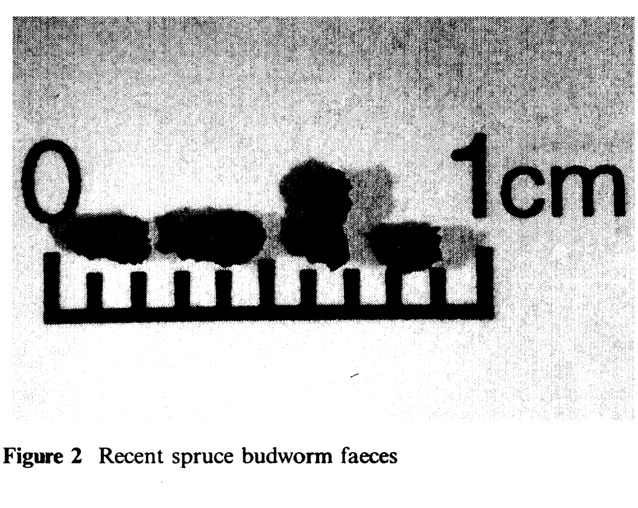

Figure 2 Recent spruce budworm faeces

100 cm^3. When moss and *Sphagnum* stems were too numerous in a fraction to be easily counted ($n > 200$), the number of stems contained in a subsample of 0.3 g was counted. The real number of stems was then extrapolated for the total weight of the fraction. Once the macrofossil analyses were completed, plant remains were extracted from five samples (76–77, 102–103, 151–152, 212–213 and 257–258 cm) for accelerator mass spectrometry radiocarbon dating. Calibrated radiocarbon dates (Stuiver *et al.*, 1998) were used to calculate the peat accumulation rate by linear interpolation. Macrofossil zones were delineated according to changes observed in the relative abundance of taxa and species composition throughout the peat profile.

The identification of fire events was not possible because the charcoal fragments did not form distinct layers that can be associated with single fire events. Statistical procedures developed to identify individual fire events in lake sediments (Clark and Royall, 1996; Whitlock and Millspaugh, 1996; Carcaillet and Richard, 2000; Carcaillet *et al.*, 2001) did not apply well on this peat material since there is no or little transport of charcoal fragments in a mire environment (Whitlock and Millspaugh, 1996; Clark and Patterson, 1997; Clark *et al.*, 1998; Ohlson and Tryterud, 2000). Furthermore, the great abundance of charcoal fragments retrieved in the surface (0–80 cm) peat samples suggests that part of the peat deposit was probably burned and material lost, complicating fire reconstruction.

Results

Peat accumulation rate and stratigraphy

Plant material in the basal section of the soil profile was dated 8600 cal. BP (Figure 3, Table 1). The basal section (258–236 cm) was composed of lacustrine clay containing mollusk shells (Figure 4). The clay was overlain by 34 cm of brown gyttja. Peat accumulation was initiated about 7700 cal. BP. The peat accumulation rate was relatively constant between 8600 and 5185 cal. BP, varying from 0.44 to 0.67 mm/yr (Figure 3). The peat accumulation curve suggests a very slow accumulation rate during the last 5000 years, but it is likely that part of the surface (0–80 cm) peat material was burned and lost because of the intense fire activity that occurred during this period.

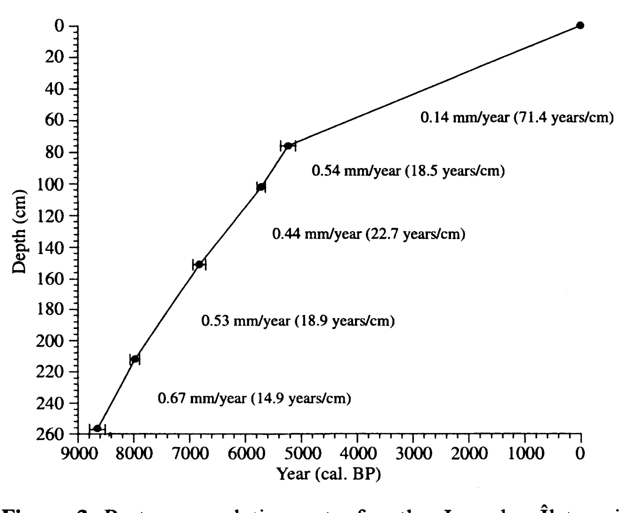

Figure 3 Peat accumulation rate for the Lac des Îlets mire (Saguenay, Québec, Canada). Horizontal bar: 2 sigma calibrated age range

Vegetation reconstruction

According to changes observed in species composition through the Lac des Îlets profile (Figure 4, Table 2), six macrofossil zones were delineated to reconstruct vegetation history. Between 8600 and 8287 cal. BP (Zone I), the study site was a small lake. The vegetation composition was dominated by trees and aquatic plants. Abundant macrofossil remains of organisms such as Bivalva spp. and Gasteropoda spp. were observed in that zone. Macrofossil Zone II (8287–7873 cal. BP–shallow pond stage) is characterized by the disappearance of Bivalva and Gastropoda shells and a rise in the number of ericaceous shrub, sedge and moss remains. Abundant charcoal fragments were recovered in that section of the profile. A transition from pond to minerotrophic mire was observed in Zone III (7873–6850 cal. BP). A first important decrease in tree macrofossils abundance occurred at the beginning of this period, while mosses, ericaceous shrubs and sedge species were abundant. The vegetation history of Zone IV (6850–5609 cal. BP) reflects a transition from minerotrophic to ombrotrophic mire with a second drastic decline in tree composition and abundance. A major decrease in the abundance of ericaceous shrub and sedge remains was also registered in Zone IV, whereas abundant *Sphagnum* spp. and *Pleurozium schreberi* stems were recovered. Between 5609 and 269 cal. BP (Zone V), the study site was an open ombrotrophic mire. Very abundant charcoal fragments were retrieved in that zone, while plant macrofossil remains were very scarce. Macrofossil Zone VI (269 cal. BP to present) corresponds to the treed ombrotrophic stage of the Lac des Îlets mire. *Picea mariana*, ericaceous shrubs and mosses dominated the vegetation during that period. The highest number of charcoal fragments of the Lac des Îlets mire was observed at 14 cm.

Spruce budworm macrofossil remains abundance

Spruce budworm faeces started accumulating in the study site about 8240 cal. BP (Figure 4). The faeces were observed throughout the peat profile, but were particularly abundant around 150 cm (6775 cal. BP), 140 cm (6550 cal. BP) and in the surface peat layer corresponding approximately to the last two centuries. A few Lepidoptera head capsules were also collected in the peat core, but they were too altered or fragmented to be correctly identified to the species level. Peaks in head capsules were observed near 170, 160, 140 and 30–20 cm, which sometimes corresponded with, but was most often out of phase with, the peaks in spruce budworm faeces. No head capsules were recovered in the surface (20 cm) peat layer.

Discussion

Development of the Lac des Îlets mire and vegetation history

The major changes observed in the vegetation composition of the Lac des Îlets site (Table 2) are the result of the typical transition occurring in a mire environment: from a pond to a minerotrophic mire to an ombrotrophic mire (Zobel, 1988; Kuhry *et al.*, 1993; Hu and Davis, 1995; Hughes and Dumayne-Peaty, 2002). The vegetation succession was mainly induced by autogenic processes, including peat buildup, oligotrophication and acidification, mediated by the mire ecosystem itself (Kuhry *et al.*, 1993). The most drastic changes observed in the abundance of tree macrofossil remains are also attributable to the autogenic evolution of the mire. The first important reduction of the number of tree macrofossils occurred around 7800 cal. BP. *Abies balsamea* disappeared from the study site while the abundance of the other tree

Table 1 Radiocarbon dates of Lac des Îlets mire (Saguenay, Québec, Canada)

Depth (cm)	Laboratory number	Conventional radiocarbon age (BP)	Calibrated age (cal. BP)	Material used for datation
76–77	Beta-159827	4540±40	5185	Leaves, seeds and wood fragments
102–103	Beta-161780	4920±50	5665	Leaves and wood fragments
151–152	Beta-159828	5950±50	6775	Leaves, seeds and wood fragments
212–213	Beta-159829	7120±50	7925	Leaves, seeds and wood fragments
257–258	Beta-159830	7830±50	8600	Leaves and seeds

species greatly diminished. The second major tree decline occurred around 6800 cal. BP. The decline of tree species such as *Larix laricina* [Du Roi] K. Koch and *Betula papyrifera* is probably attributable to the thickness of the peat deposit, which was respectively 50 cm (7800 cal. BP) and 100 cm (6800 cal. BP) thick; tree roots no longer had access to the nutrients from the underlying mineral soil (Montague and Givnish, 1996; Lavoie *et al.*, 2001). Tree macrofossil declines were also observed at similar depths in other mires of eastern Québec (Lavoie *et al.*, 2001; Zimmermann and Lavoie, 2001). However, the decline in the number of *Picea mariana* remains did not appear at the same level as the other tree species. Furthermore, the present-day black spruce stand is growing on a 237-cm-thick deposit, suggesting that the thickness of the peat deposit does not prevent the establishment and growth of the species. On the other hand, the decline in the number of black spruce macrofossils coincided with an exceptional peak of spruce budworm faeces around 6800 cal. BP, suggesting that insect activity may have had a major influence on the vegetation structure of the mire.

Spruce budworm abundance

Spruce budworm faeces were recovered in almost the entire profile, suggesting endemic or epidemic presence of the insect at the study site since 8240 cal. BP. This is the earliest recorded date of spruce budworm presence in North America. Important variations in the abundance of faeces were observed in the Lac des Îlets profile, with two periods of presumably intense spruce budworm activity (Figure 4). The first peak, which also yielded the highest number of spruce budworm faeces, was registered between 6815 and 6480 cal. BP. This exceptional period of spruce budworm activity occurred while balsam fir (*Abies balsamea*), the preferred host species of spruce budworm, was absent from the study site, although it was probably present in the forests surrounding the mire. This high number of faeces in an ecosystem without fir (the Lac des Îlets mire) suggests that the a high density population of spruce budworm larvae had to feed on a secondary host (*Picea mariana)* to survive (Stillwell, 1956; Blais, 1981, 1984; Mattson *et al.*, 1988). Such a phenomenon was observed during recent high intensity outbreaks.

The second period of high spruce budworm activity in the Lac des Îlets mire was observed in the top 15 cm of the profile, corresponding approximately with the spruce budworm outbreaks that occurred in the Laurentides Wildlife Reserve during the last two centuries (Blais, 1965; Lussier *et al.*, 2002). Those outbreaks cannot be precisely pin-pointed in the faeces distribution. The peat accumulation rate was too low during that period and outbreaks too frequent to allow the formation of distinct layers of spruce budworm faeces. The rest of the faeces distribution fluctuated more or less regularly but never reached the abundance described for the two periods of

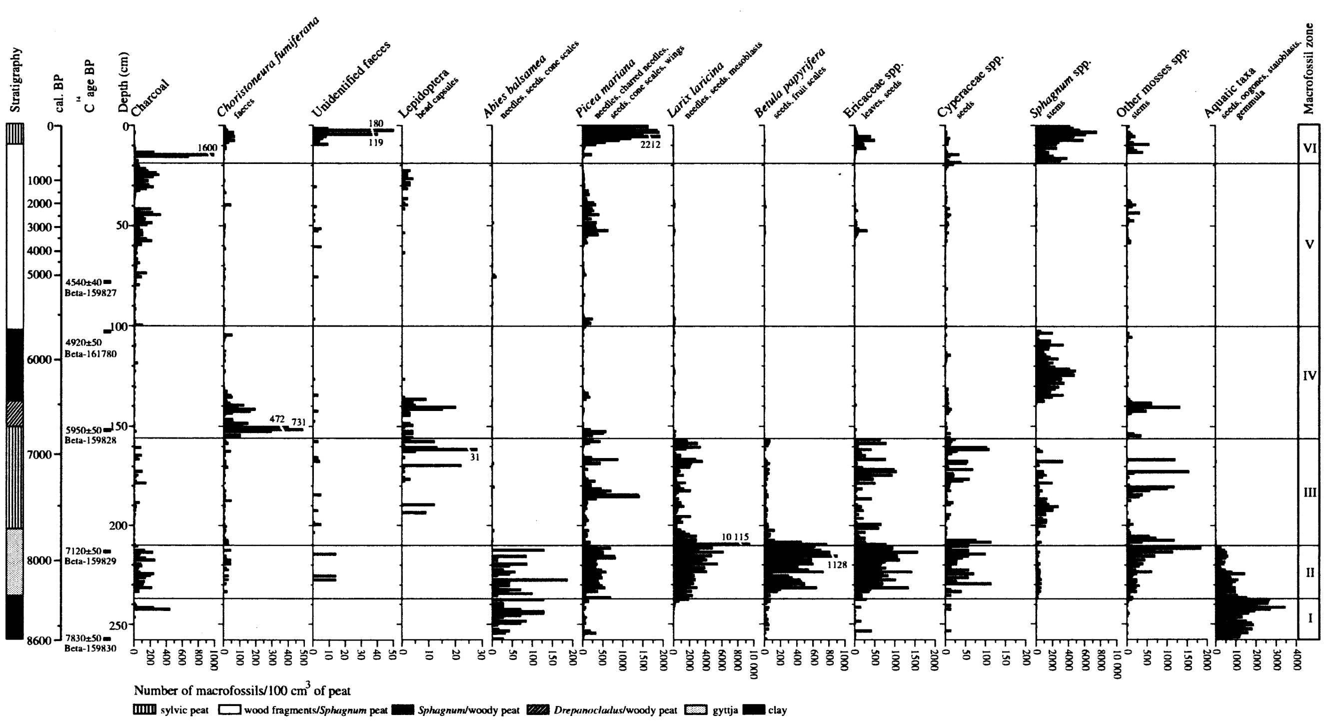

Figure 4 Macrofossil diagram (selected taxa) for the Lac des Îlets mire (Saguenay, Québec, Canada)

Table 2 Dominant species and developmental stages of the Lac des Îlets mire observed for each macrofossil zone

Macrofossil zone	Depth (cm)	Age (cal. BP)	Dominant species	Developmental stage
VI	0–18	0–269	*Picea mariana, Carex trisperma, Sphagnum* spp., *Pleurozium schreberi, Kalmia angustifolia, Rhododendron groenlandicum*	Treed ericaceous mire
V	18–100	269–5609	*Picea mariana, Carex trisperma, Pleurozium schreberi,* ericaceous shrubs	Ombrotrophic mire
IV	100–156	5609–6850	*Picea mariana, Carex trisperma, Carex disperma, Viola* spp., *Sphagnum* spp., *Pleurozium schreberi*	Transition from a minerotrophic to an ombrotrophic mire
III	156–210	6850–7873	*Picea mariana, Larix laricina, Cyperaceae* spp., *Chamaedaphne calyculata, Calla palustris, Hypericum virginicum, Menyanthes trifoliata, Myrica gale, Sparganium* spp., *Sphagnum* spp., *Tomenthypnum falcifolium, Drepanocladus* spp.	Transition from a pond to a treed minerotrophic mire
II	210–237	7873–8287	*Chara* spp., *Naja flexilis, Potamogeton* spp., *Abies balsamea, Betula papyrifera, Larix laricina, Picea mariana, Chamaedaphne calyculata, Myrica gale, Drepanocladus* spp., *Pleurozium schreberi*	Shallow pond
I	237–258	8287–8600	Bivalva spp., Gasteropoda spp., *Daphnia* spp., *Chara* spp., *Naja flexilis, Potamogeton* spp. Porifera spp. *Abies balsamea, Betula papyrifera, Picea mariana*	Small lake

high budworm activity. Not every outbreak can be registered in one location, even with dendrochronological techniques, so it is possible that some outbreaks were missed. Nevertheless, the faeces distribution suggests that intense periods of spruce budworm activity were rare events during the Holocene. They may indicate important changes in the dynamics of spruce budworm outbreaks. Low fire activity, associated with other factors such as the presence of susceptible stands and climatic conditions favourable to larval development, were possibly responsible for the major spruce budworm outbreaks that occurred in the Lac des Îlets mire between 6815 and 6480 cal. BP and during the last century (Greenbank, 1956; Pilon and Blais, 1961; Lucuik, 1984; Blais, 1985; Bergeron and Archambault, 1993; Bergeron and Leduc, 1998). Conversely, the absence or the low abundance of susceptible stands may have contributed to less budworm activity between 5000 and 2000 cal. BP.

Faeces are a new palaeoecological proxy of the presence of spruce budworm. Lepidoptera head capsules were also used to reconstruct outbreak history (Davis *et al.*, 1980; Filion *et al.*, 1998). In the Lac des Îlets profile, faeces were much more abundant than head capsules. Faeces were also better preserved and easier to identify. Noticeable mismatches were observed between peaks of spruce budworm faeces and those of head capsules. In addition, no head capsules were collected in the upper 15 cm of the core, corresponding to the outbreaks that occurred during the two last centuries in the study area. Consequently, spruce budworm faeces appear to be a more suitable palaeoecological indicator to reconstruct past outbreaks. Faeces are often characteristic in size and form for larvae of different ages and species (Morris, 1949; Fridén, 1958). The identification of faeces indicates the presence of the insect *in situ* and may be the only apparent clue to identify the defoliator (Morris, 1942). However, head capsules should not be discarded as palaeoecological indicators for insect defoliation. A few of the peaks in Lepidoptera head capsules found in the Lac des Îlets peat core were observed where no or few spruce budworm faeces were recovered. Those peaks may represent spruce budworm activity that was not clearly detected in the faeces reconstruction. It appears that in order to collect as much information as possible on spruce budworm activity, both head capsules and faeces should be used simultaneously as complementary indicators of the presence of the insect.

Conclusion

This study revealed that spruce budworm was endemic in the Lac des Îlets mire during the last 8240 years. Furthermore, the long-term perspective achieved with this macrofossil analysis strongly suggests that very intense periods of spruce budworm activity were exceptional events during the Holocene. Outbreaks are natural phenomena, but human interventions and a change in fire frequency might have modified the forest structure and increased the abundance of spruce budworm during the twentieth century. Fire recurrence may also have had an impact on spruce budworm activity, as the two major defoliation periods at the study site occurred while fire activity was low. Low fire recurrence might have favoured the development of mature host stands highly susceptible to spruce budworm outbreaks. The link between fire and spruce budworm outbreaks should be investigated more thoroughly in order to obtain more information on the dynamics of the boreal forest. A possible relation between warm climatic conditions and intense periods of spruce budworm activity should also be investigated since the highest abundances of spruce budworm faeces were observed during the two warmest periods of the Holocene, ie, between 7000 and 6000 cal. BP and during the twentieth century (Richard, 1994, 1998; Sawada *et al.*, 1999).

Acknowledgements

This project was financially supported (grants to H. Morin and C. Lavoie) by the Natural Sciences and Engineering Research Council of Canada (NSERC) and the Consortium de recherche sur la forêt boréale commerciale. The Fonds pour la Formation de chercheurs et l'aide à la recherche du Québec (FCAR) and NSERC provided doctoral scholarships to I. Simard. We thank the Ministère des Ressources naturelles and Abitibi-Consolidated for providing forest maps. We are grateful to A.C. Larouche for his help with macrofossil identification and to L. Dieumegarde, G. Dallaire, N. Fantin, F. Girard, J.-G. Girard, A. Saint-Louis, and G. Savard for laboratory and field assistance.

References

Anderson, L.E., Crum, H.A. and **Buck, W.R.** 1990: List of the mosses of North America north of Mexico. *Bryologist* 93, 448–99.

Bergeron, Y. and **Archambault, S.** 1993: Decreasing frequency of forest fires in the southern boreal zone of Québec and its relation to global warming since the end of the 'Little Ice Age'. *The Holocene* 3, 255–59.

Bergeron, Y. and **Leduc, A.** 1998: Relationships between change in fire frequency and mortality due to spruce budworm outbreak in the southeastern Canadian boreal forest. *Journal of Vegetation Science* 9, 492–500.

Bergeron, Y., Engelmark, O., Harvey, B., Morin, H. and **Sirois, L.** 1998: Key issues in disturbance dynamics in boreal forests: introduction. *Journal of Vegetation Science* 9, 464–68.

Bhiry, N. and **Filion, L.** 1996: Mid-Holocene hemlock decline in eastern North America linked with phytophagous insect activity. *Quaternary Research* 45, 312–20.

Blais, J.R. 1965: Spruce budworm outbreaks in the past three centuries in the Laurentides Park, Quebec. *Forest Science* 11, 130–38.

—— 1981: Mortality of balsam fir and white spruce following a spruce budworm outbreak in the Ottawa River watershed in Quebec. *Canadian Journal of Forest Research* 11, 620–29.

—— 1983: Trends in the frequency, extent, and severity of spruce budworm outbreaks in eastern Canada. *Canadian Journal of Forest Research* 13, 539–47.

—— 1984: Réflexions sur l'épidémiologie de la tordeuse des bourgeons de l'épinette (*Choristoneura fumiferana* [Clem.]) suite à 40 années d'études. *Revue d'entomologie du Québec* 29, 27–33.

—— 1985: The ecology of the eastern spruce budworm: a review and discussion. In Sanders, C.J., Stark, R.W., Mullins, E.J. and Murphy, J., editors, *Recent advances in spruce budworm research: proceedings of the CANUSA spruce budworm research symposium*. Canadian Forestry Service, 49–59.

Carcaillet, C. and **Richard, P.J.H.** 2000: Holocene changes in seasonal precipitation highlighted by fire incidence in eastern Canada. *Climate Dynamics* 16, 549–59.

Carcaillet, C., Bergeron, Y., Richard, P.J.H., Fréchette, B., Gauthier, S. and **Prairie, Y.T.** 2001: Change of fire frequency in the eastern Canadian boreal forests during the Holocene: does vegetation composition or climate trigger the fire regime? *Journal of Ecology* 89, 930–46.

Clark, J.S. and **Patterson, W.A., III** 1997: Background and local charcoal in sediments: scales of fire evidence in the paleorecord. In Clark, J.S., Cachier, H., Goldammer, J.G. and Stocks, B.J., editors, *Sediment records of biomass burning and global change, NATO ASI series volume I: Global environmental change*. Springer, 23–48.

Clark, J.S. and **Royall, P.D.** 1996: Local and regional sediment charcoal evidence for fire regimes in presettlement northeastern North America. *Journal of Ecology* 84, 365–82.

Clark, J.S., Lynch, J., Stocks, B.J. and **Goldammer, J.G.** 1998: Relationships between charcoal particles in air and sediments in west-central Siberia. *The Holocene* 8, 19–29.

Coûteau, M. 1962: Notes sur le prélèvement et la préparation de certains sédiments. *Pollen et Spores* 4, 317–22.

Davis, R.B., Anderson, R.S. and **Hoskins, B.R.** 1980: A new parameter for paleoecological reconstruction: head capsules of forest-tree-defoliator microlepidopterans in lake sediment. In *Abstracts and program of the 6th biennial meeting of the American Quaternary Association*. Institute of Quaternary Studies, University of Maine, 62 (Abstract).

Elkinton, J.S. and **Liebhold, A.M.** 1990: Population dynamics of gypsy moth in North America. *Annual Review of Entomology* 35, 571–96.

Environnement Canada 1993: *Normales climatiques au Canada: 1961–1990, Québec*. Service de l'environnement atmosphérique, Environnement Canada.

Farrar, J.L. 1996: *Les arbres du Canada*. Fides and Service canadien des forêts.

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. *Canadian Journal of Forest Research* 28, 1832–42.

Fridén, F. 1958: *Frass-drop frequency in Lepidoptera*. Almqvist & Wiksells Boktryckeri AB.

Greenbank, D.O. 1956: The role of climate and dispersal in the initiation of outbreaks of the spruce budworm in New Brunswick. I. The role of climate. *Canadian Journal of Zoology* 34, 453–76.

Hardy, Y., Mainville, M. and **Schmitt, D.M.** 1985: *Atlas de la défoliation causée par la tordeuse des bourgeons de l'épinette dans la nord-est de l'Amérique du Nord de 1938 à 1980*. Service canadien des forêts.

Hu, F.S. and **Davis, R.B.** 1995: Postglacial development of a Maine bog and paleoenvironmental implications. *Canadian Journal of Botany* 73, 638–49.

Hughes, P.M.D. and **Dumayne-Peaty, L.** 2002: Testing theories of mire development using multiple successions at Crymlyn Bog, West Glamorgan, South Wales, UK. *Journal of Ecology* 90, 456–71.

Jowsey, P.C. 1966: An improved peat sampler. *New Phytologist* 65, 245–48.

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.

Kuhry, P., Nicholson, B.J., Gignac, L.D., Vitt, D.H. and **Bayley, S.E.** 1993: Development of *Sphagnum*-dominated peatlands in boreal continental Canada. *Canadian Journal of Botany* 71, 10–22.

Lavoie, C., Zimmermann, C. and **Pellerin, S.** 2001: Peatland restoration in southern Québec (Canada): a paleoecological perspective. *Écoscience* 8, 247–58.

Lévesque, P.E.M., Dinel, H. and **Larouche, A.** 1988: *Guide illustré des macrofossiles végétaux des tourbières du Canada*. Publication No. 1817. Agriculture Canada.

Lucuik, G.S. 1984: Effect of climatic factors on post-diapause emergence and survival of spruce budworm larvae (Lepidoptera: Tortricidae). *Canadian Entomologist* 116, 1077–83.

Lussier, J.M., Morin, H. and **Gagnon, R.** 2002: Mortality in black spruce stands of fire or clear-cut origin. *Canadian Journal of Forest Research* 32, 539–47.

Marie-Victorin, F. 1995: *Flore Laurentienne*. 3rd edition. Presses de l'Université de Montréal.

Mattson, W.J., Simmons, G.A. and **Witter, J.A.** 1988: The spruce budworm in eastern North America. In Berryman, A.A., editor, *Dynamics of forest insect populations: patterns, causes, implications*. Plenum Press, 309–30.

McCullough, D.G., Werner, R.A. and **Neumann, D.** 1998: Fire and insects in northern and boreal forest ecosystems of North America. *Annual Review of Entomology* 43, 107–27.

Miller, A. and **Rusnock, P.** 1993: The rise and fall of the silvicultural hypothesis in spruce budworm (*Choristoneura fumiferana*) management in eastern Canada. *Forest Ecology and Management* 61, 171–89.

Montague, T.G. and **Givnish, T.J.** 1996: Distribution of black spruce versus eastern larch along peatland gradients: relationship to relative structure, growth rate, and shade tolerance. *Canadian Journal of Botany* 74, 1514–32.

Montgomery, F.H. 1977: *Seeds and fruits of plants of eastern Canada and northern United States*. University of Toronto Press.

Morin, H. 1994: Dynamics of balsam fir forests in relation to spruce budworm outbreaks in the boreal zone of Quebec. *Canadian Journal of Forest Research* 24, 730–41.

—— 1998: Importance et évolution des épidémies de la tordeuse des bourgeons de l'épinette dans l'est du Canada: l'apport de la dendrochronologie. *Géographie physique et Quaternaire* 52, 237–44.

Morin, H. and **Laprise, D.** 1990: Histoire récente des épidémies de la tordeuse des bourgeons de l'épinette au nord du lac Saint-Jean:

une analyse dendrochronologique. *Canadian Journal of Forest Research* 20, 1–8.
Morin, H., **Laprise, D.** and **Bergeron, Y.** 1993: Chronology of spruce budworm outbreaks near Lake Duparquet, Abitibi region, Quebec. *Canadian Journal of Forest Research* 23, 1497–506.
Morris, R.F. 1942: The use of frass in the identification of forest insect damage. *Canadian Entomologist* 74, 164–67.
—— 1949: *Frass-drop measurement in studies of the European spruce sawfly.* University of Michigan Press.
Ohlson, M. and **Tryterud, E.** 2000: Interpretation of the charcoal record in forest soils: forest fires and their production and deposition of macroscopic charcoal. *The Holocene* 10, 519–25.
Payette, S. 1992: Fire as a controlling process in the North American boreal forest. In Shugart, H.H., Leemans, R. and Bonan, G.B., editors, *A systems analysis of the global boreal forest*. Cambridge University Press, 145–69.
Pilon, J.G. and **Blais, J.R.** 1961. Weather and outbreaks of the spruce budworm in the province of Quebec from 1939 to 1956. *Canadian Entomologist* 93, 118–23.
Richard, P.J.H. 1994: Postglacial palaeophytogeography of the eastern St. Lawrence River Watershed and the climatic signal of the pollen record. *Palaeogeography, Palaeoclimatology, Palaeoecology* 109, 137–61.
—— 1998: Les changements climatiques: regard vers le passé pour mieux voir l'avenir. *Interface* 19, 36–44.
Rowe, J.S. 1972: *Forests regions of Canada.* Information Canada.
Sawada, M., **Gajewski, K.**, **de Vernal, A.** and **Richard, P.** 1999: Comparison of marine and terrestrial Holocene climatic reconstructions from northeastern North America. *The Holocene* 9, 267–77.
Simard, I., **Morin, H.** and **Potelle, B.** 2002: A new paleoecological approach to reconstruct long-term history of spruce budworm outbreaks. *Canadian Journal of Forest Research* 32, 428–38.
Stillwell, M.A. 1956: Pathological aspects of severe spruce budworm attack. *Forest Science* 2, 174–80.
Stuiver, M., **Reimer, P.J.**, **Beck, J.W.**, **Burr, G.S.**, **Hughen, K.A.**, **Kromer, B.**, **McCormac, F.G.**, **van der Plicht, J.** and **Spurk, M.** 1998: INTCAL98 radiocarbon age calibration, 24 000–0 cal BP. *Radiocarbon* 40, 1041–83.
Swetnam, T.W. and **Lynch, A.M.** 1993: Multicentury, regional-scale patterns of western spruce budworm outbreaks. *Ecological Monographs* 63, 399–424.
Thibault, M. 1987: *Les régions écologiques du Québec méridional. Deuxième approximation*. Service de la recherche, Ministère de l'Énergie et des Ressources.
Veblen, T.T., **Hadley, K.S.**, **Reid, M.S.** and **Rebertus, A.J.** 1991: Methods of detecting past spruce beetle outbreaks in Rocky Mountains subalpine forests. *Canadian Journal of Forest Research* 21, 242–54.
Veblen, T.T., **Hadley, K.S.**, **Nel, E.M.**, **Kitzberger, T.**, **Reid, M.** and **Villalba, R.** 1994: Disturbance regime and disturbance interactions in a Rocky Mountain subalpine forest. *Journal of Ecology* 82, 125–35.
Whitlock, C. and **Millspaugh, S.H.** 1996: Testing the assumptions of fire-history studies: an examination of modern charcoal accumulation in Yellowstone National Park, USA. *The Holocene* 6, 7–15.
Zimmermann, C. and **Lavoie C.** 2001: A paleoecological analysis of a southern permafrost peatland, Charlevoix, Quebec. *Canadian Journal of Earth Sciences* 38, 909–19.
Zobel, M. 1988: Autogenic succession in boreal mires: a review. *Folia Geobotanica et Phytotaxonomica* 23, 417–45.