Holocene occurrence of *Lophodermium piceae*, a black spruce needle endophyte and possible paleoindicator of boreal forest health

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Abstract

Holocene occurrences of conifer needle endophytes have not previously been reported. We report the fossil remains of *Lophodermium piceae* (Fckl.) Hoehn., a fungal endophyte of black spruce (*Picea mariana* (Mill.) B.S.P.) needles, in macrofossils dating back to 8000 cal yr BP. Spruce budworm head capsules and *L. piceae* remains were found preceding charcoal layers delineating the transformation of four spruce−moss forest sites to spruce−lichen woodland. As *L. piceae* is found solely on senescent needles, its increased presence during these transformation periods likely indicates that the forests were in decline due to the spruce budworm (*Choristoneura fumiferana* (Clem.)) when they burned. Future paleoecological studies incorporating needle fungi observations could be used to investigate the historical occurrence of tree disease and the role of fungi in forest health and decline.
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Keywords: Forest decline; Forest health; Endophytic fungi; Tree diseases; Spruce budworm; Paleoecology

Introduction

Disturbance dynamics play a major role in all ecosystems (Pickett and White, 1985). In the boreal forest, fire and insect epidemics are considered the major disturbance factors (Blais, 1983; Heinselman, 1981; Johnson, 1992; MacLean, 1990; Martineau, 1985; Morin, 1998; Payette, 1992; Sanders et al., 1985). However, fungi also play an important, but less studied, role as forest pathogens (Hansen and Lewis, 1997; Myren, 1994). In addition, there is considerable interest in endophytic fungi that convey insect resistance to conifers (Clark et al., 1989; Findlay, 1996; Findlay et al., 1995b; Johnson and Whitney, 1992; Miller et al., 2002).

Reconstructions of past forest vegetation and disturbance dynamics have focused primarily on the role of climate, fire, and insect dynamics, insofar as Holocene paleofungal indicators, apart from mycorrhizal fungi such as *Cenococcum graniforme*, have been elusive. Indeed, erroneous inferences have been made regarding their presence; the mid-Holocene hemlock decline was attributed to a possible fungal pathogen due to the similarities with modern-day Dutch Elm disease and Chestnut blight caused by *Ophiostoma ulmi* (Buisman) Nannf. and *Cryphonectria parasitica* (Murrill) Barr, respectively (Allison et al., 1986; Davis, 1981). However, an increase in microlepidopteran larval head capsules found in pond sediments corresponding with the time of the decline suggested that phytophagous insect activity may have played a role (Anderson et al., 1986). The decline was later attributed to the hemlock looper (*Lambdina fiscellaria* (Gn.)) when positively identified head capsules were obtained from a peat record corresponding with the stratigraphic levels of the decline (Bhiry and Filion, 1996a,b).

Here we report the Holocene occurrence of *Lophodermium piceae*, a needle endophyte found on black spruce in the Parc national des Grands-Jardins, Québec (Fig. 1). We infer that increases in the abundance of this species may be related to spruce budworm epidemics and/or drought, with tree stress and premature needle loss augmenting *L. piceae* infection and/or fructification rates. This study is part of a larger research project investigating the role of changing disturbance regimes in this

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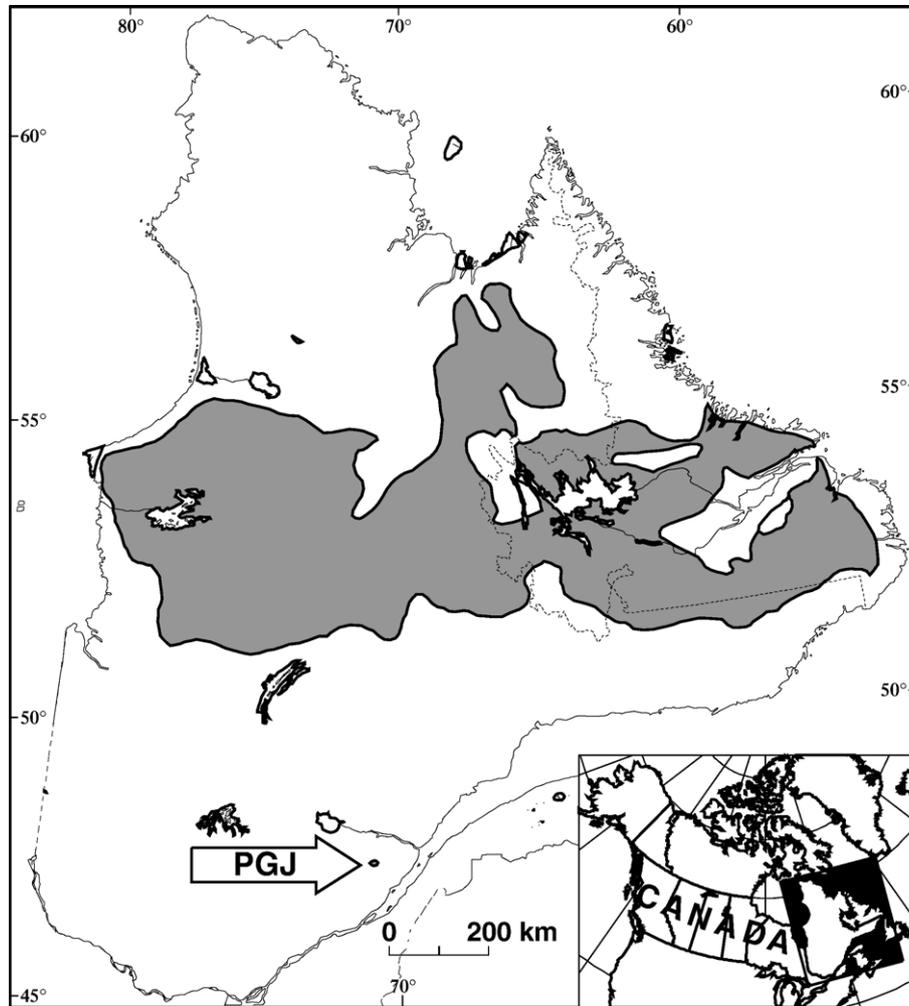*E-mail address:* pauljasinski@alumni.uwaterloo.ca (J.P.P. Jasinski).

Figure 1. The location of the study site in the Parc national des Grands-Jardins, Quebec, Canada. The grey shading indicates lichen woodland.

part of the boreal forest, particularly the role that compounded spruce budworm and fire disturbances play in the transformation of spruce moss forests to spruce lichen woodlands.

Ecology of Lophodermium piceae

L. piceae is a needle fungus found on several different spruce and fir (*Abies*) species (Darker, 1932; Gourbière et al., 1986; Magan and Smith, 1996; Osario and Stephan, 1991b; Sharma and Sharma, 1981; Whitney and Ip, 1990). The life cycle of *L. piceae* has been described by Osario and Stephan (1991b) in 6 stages: (1) spruce needles are infected with ascospores, (2) the fungus lives as an endophyte in the green needle for several years, (3) conidiomata and conidia form but are not relevant for further infection of needles, (4) ascomata form on retained and fallen needles, (5) ascomata ripen and release spores infecting more needles, and (6) empty fruit bodies and needles decompose in the forest litter.

An interesting trait of most *L. piceae* varieties is their ability to make "zone lines" on the needle. These are transversal walls ("disks") that are formed by several layers of hyphae and melanized parenchyma cells (Gourbière et al., 1986; Stephan and Osorio, 1995). These disks, which are used in this study to quantify *L. piceae* abundance, are likely created in an antagonistic reaction against other species of fungi and/or other individuals of *L. piceae* (Stephan and Osorio, 1995). Figure 2 displays *L. piceae* ascomata, conidiomata, zonal lines, and disks. Photographs and illustrations of *L. piceae* are also found in Darker (1932); Osario and Stephan (1991a,b) and Gourbière et al. (1986).

The pathogenicity of *L. piceae* in contemporary populations is still uncertain. In North America it is usually found living as a foliar endophyte in black spruce (Jean Bérubé, Canadian Forest Service, personal communication, 2004). Whereas Sinclair et al. (1987) list the species as a pathogen that causes browning and casting of old spruce needles, this relationship is not clear in the literature. In Europe, the pathogenicity of *L. piceae* is still being debated, with some considering it to be a cause of tree death and general forest decline, particularly for Norway spruce (*Picea abies* (L.) Karst.) (Coutts, 1995; Rehfuess and Rodenkirchen, 1984; Rose, 2001), while others consider it to be saprophytic, colonizing only senescent needles (Barklund, 1987; Butin and Wagner, 1985; Gourbière et al., 1986; Osario and Stephan, 1991b; Schutt, 1985). Identification techniques using both chemotaxonomical analysis and scanning electron microscopy have found *L. piceae* in symptomless
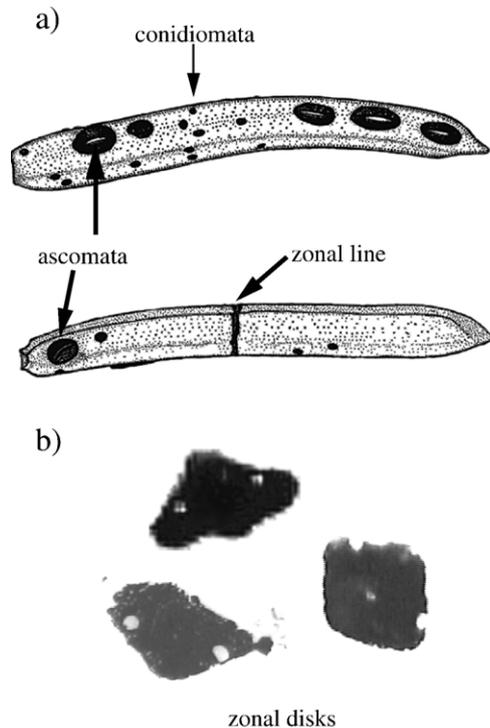
a)

b)

zonal disks

Figure 2. (a) Illustration of *Lophodermium piceae* ascomata, conidiomata, and zonal line from Darker (1932), Copyright © President and Fellows of Harvard College Archives of the Arnold Arboretum. (b) Macrofossil zonal "disks" resulting from needle decomposition.

green needles, further suggesting that its pathogenicity is limited (Magan and Smith, 1996; Müller and Hallaksela, 1998; Müller et al., 2001; Suske and Acker, 1990).

Study area

The Parc national des Grands-Jardins ("Park"; 47°49′N, 70°59′W) is located 120 km northeast of Quebec City, Québec, in the Charlevoix Highlands. It contains the southernmost spruce−lichen woodlands in eastern Canada, which are situated ∼ 500 km south of the northern spruce−lichen woodland zone (Fig. 1). These open forests are embedded within the closed boreal forest and are characterized by well-spaced black spruce, a lichen groundcover (*Cladina* and *Cladonia* species), and a shrub layer that often includes dwarf birch (*Betula glandulosa* Michx.), and ericoid shrubs (*Vaccinium*, *Kalmia*, and *Ledum*). The Park's forests are a mixture of black spruce feathermoss forests and black spruce−lichen woodlands. Fire and spruce budworm epidemics are the main disturbance factors in the Park. The sites in this study, Lac des Iles, Lac Arthabasca, La Roche, and Km 20 are located within lichen woodlands.

Methods

Peat monoliths (approximately 15 by 15 cm and cut in subsequent blocks down to the mineral contact) were obtained from four small peatlands adjacent to spruce−lichen woodlands in the Park and transported to the laboratory for macrofossil analysis. In the laboratory, a lamp equipped with a magnifying

lens was used to note the peat stratigraphy and charcoal layers. The close proximity of the sampling sites to their respective peatland borders and adjacent forests maximized the possibility that the peatland surfaces would burn during fire events, thus allowing the fire history of the forest to be reconstructed using stratigraphic charcoal layers (Pitkanen et al., 2002; Jasinski and Payette, 2005). For macrofossil analysis, the peat monoliths were cut into 1-cm-thick sections and volumes of 25 cm^3 (100 cm^3 were used for some Lac des Iles samples) were measured by water displacement and passed through a stacked nest of sieves (2, 1.5, 0.8, 0.5, and 0.18 mm).

Agglomerated samples were separated by briefly boiling them in a dilute KOH solution. The retained residues were sorted in water with the aid of a binocular microscope. Plant macrofossils were identified using a modern reference collection and published references (Lévesque et al., 1988; Martin and Barkley, 1961; Montgomery, 1977). Spruce needle counts are comprised of whole (including charred) needles, needle points or bases (with the one possessing a greater abundance being included in the total count), and needle epidermi (needles that have decomposed leaving only their "skin"). Insect head capsules were identified using a modern reference collection and scanning electron microscope photographs of previously identified insects. *L. piceae* abundance was quantified by counting both individual disks (the host needle having been previously decomposed) and zonal lines still embedded within the needles. Bulk radiocarbon samples were analyzed at Université Laval's ^{14}C laboratory, while AMS samples were analyzed at both IsoTrace and Beta Analytical Radiocarbon Dating laboratories. All dates were calibrated using CALIB 4.4html (Stuiver et al., 2003).

Results

Holocene remains of *L. piceae* were found at all sites and included fossil needles containing ascomata, conidiomata, and zonal lines, as well as individual zonal disks devoid of needles. Some needles contained multiple infections, as evident by the presence of 2 or 3 zonal lines. The zonal disks appear to be the structure most resistant to decomposition, as they were often found in highly decomposed stratigraphic layers that did not contain any of the other fructifications. Thus, only needle zonal lines and zonal disks isolated from decomposed needles were counted, in order to provide a consistent measure of *L. piceae* abundance. The zonal disks likely came from black spruce needles, as the morphology of the needle preserved in the disks always displayed two resin ducts; black spruce needles contain two continuous resin ducts while white spruce (*Picea glauca* (Moench) Voss) possesses discontinuous resin ducts (Weng and Jackson, 2000). The needle fungi *Rhizospaera kalkhofii* and *Lirula macrospora* were also observed on occasion but were not quantified.

Abbreviated macrofossil diagrams showing results pertinent to *L. piceae* are shown in Figure 3. The diagrams have been separated into moss forest and lichen woodland zones (full diagrams, vegetation interpretations, and explanations for radiocarbon date discrepancies are found in Jasinski and
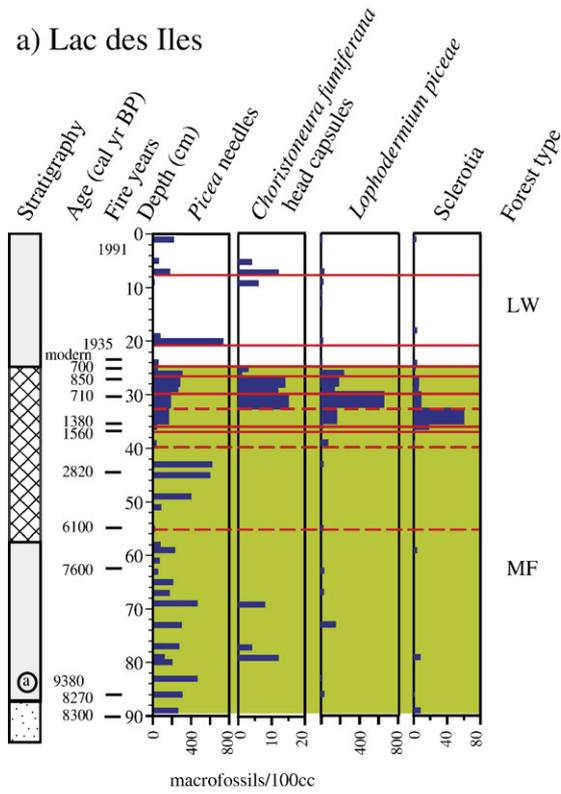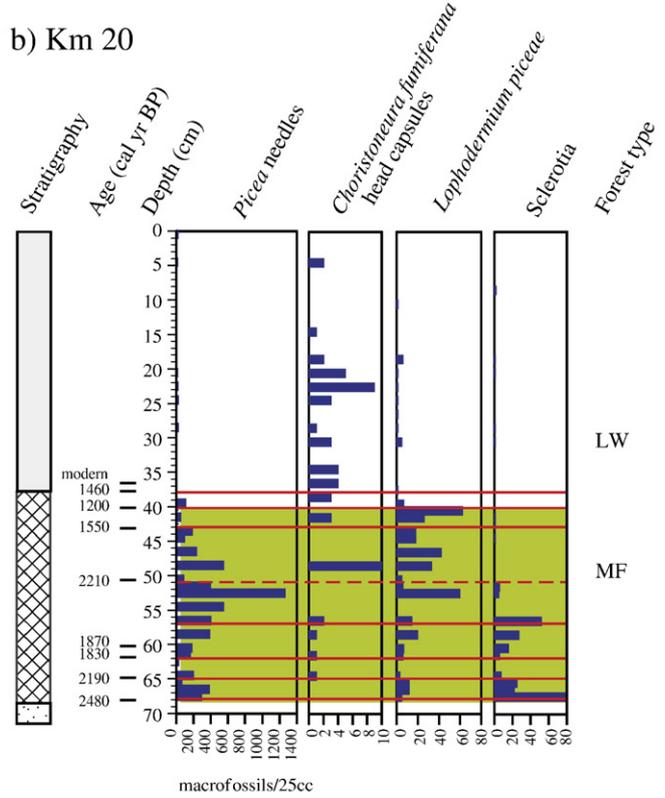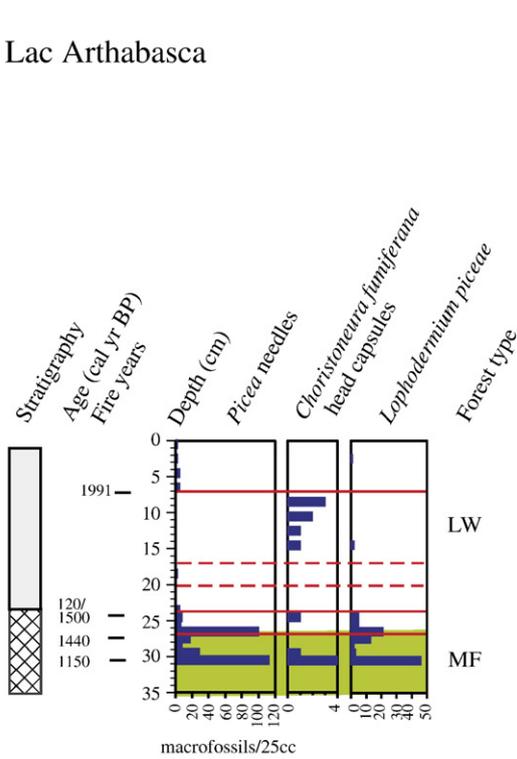
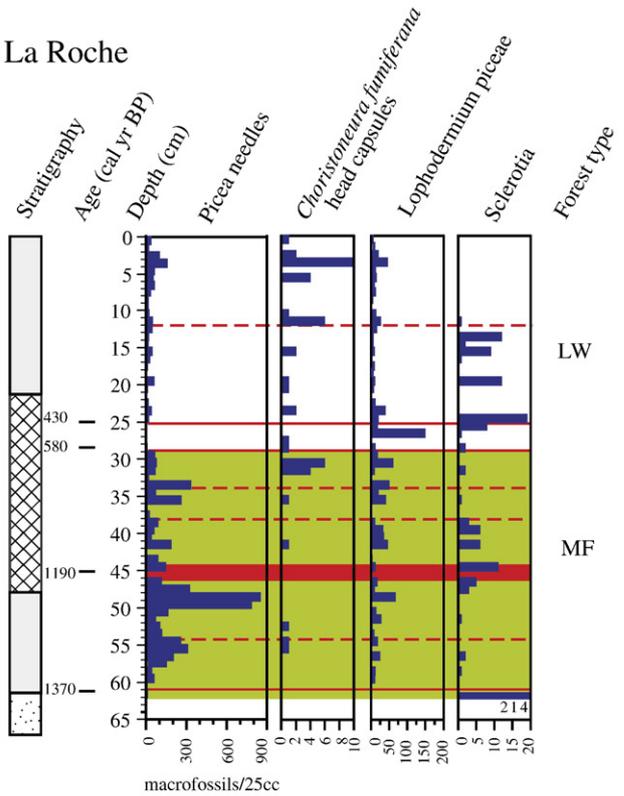Figure 3. Abbreviated macrofossil diagrams depicting forest type transformations at the study sites. Note that fire was present in the early LDI diagram but no distinct charcoal layers were found.

Payette, 2005). *L. piceae* remains were found at all sites with the earliest occurring around 8000 cal yr BP at Lac des Iles. An abrupt increase in its abundance at this site occurs at around 1380 cal yr BP concurrently with an increase in fire events, sclerotia of *Cenococcum graniforme*, and, in the subsequent stratigraphic level, spruce budworm head capsules. At both Lac Arthabasca and Km 20, *L. piceae* peaks were found along with spruce budworm head capsules before the fire events (∼1150 and ∼1200 cal yr BP, respectively) that initiated the shift from moss forests to lichen woodlands. At La Roche a *L. piceae* peak is observed before the delineating fire event (∼580 cal yr BP) but it is not as clear as the previous two sites. A larger *L. piceae* peak is found before the next fire event (430 cal yr BP) along with spruce budworm head capsules.

Discussion and conclusions

Increases in the abundance of *L. piceae* remains in the site profiles may be related to spruce budworm epidemics and/or drought. Spruce budworm head capsules were found in the stratigraphic layers preceding the fire events delineating the shifts from moss forest to spruce−lichen woodland forest types, which suggests that the mechanism for these shifts was the combined impacts of a defoliating insect epidemic followed by a fire (Payette et al., 2000; Jasinski and Payette, 2005).

The general presence of *L. piceae* at these times may be a direct result of needle damage by the spruce budworm. In balsam fir, an increased infection rate and diversity of fungi were noted for needles affected by the spruce budworm compared to unaffected needles (Miller et al., 1985). Needles of Norway spruce killed by the gall mite, *Sacchiphantes abietis* L., and the spruce needle miner, *Epinotia tedella* Cl., were observed to have *L. piceae* fruiting bodies that were "forced" to develop with the premature death of the needle (Stephan and Osorio, 1995). However, an inverse relationship has also been reported between insect damaged *Picea abies* needles and *L. piceae* abundance (Livsey and Barklund, 1992). Although the insect in question was not noted in the Livsey and Barklund (1992) study, it suggests a possible inhibitory effect between the fungus and some insect types. While certain endophytes have been reported to be toxic to defoliating insects (Clark et al., 1989; Findlay, 1996; Findlay et al., 1995a,b; Miller et al., 2002), it does not appear that *L. piceae* has been investigated in this regard. Another possibility is that a tree weakened (or killed) from insect damage would be more likely to become infected and/or possess premature needle death, thus initiating fungus fructification. Lehtijarvi and Barklund (1999) hypothesized that *L. piceae* colonization may be increased in trees with less photosynthetic activity and growth, both of which are found in spruce budworm affected trees.

Drought has elsewhere been found to be a trigger for *L. piceae* infection or fructification by reducing tree health (Lehtijarvi and Barklund, 1999; Rose, 2001). High abundances of *L. piceae* were observed on Sitka spruce (*Picea sitchensis* (Bong.) Carr.) growing in peaty soils during a drought (Rose, 2001). The rise in *L. piceae* remains at Lac des Iles occurs concurrently with an increase in fire events, suggesting that

climate may have been drier at this time. In addition, an abrupt increase in the presence of *Cenococcum graniforme* fungal sclerotia was also observed during this time period and increases in their abundance have previously been attributed to drought or the drying of a peatland surface (Lavoie et al., 1995; Van Geel et al., 1983). However, interpreting the presence of *C. graniforme* sclerotia is difficult because it is a cosmopolitan species that colonizes all trees and ericaceous species found in bogs and fens (Thormann et al., 1999). Furthermore, being a mycorrhizal fungus, it establishes itself beneath the surface and thus does not belong to the stratigraphic layer in which it is found. Thus, it could only be used for general time periods. In addition, the presence of the species in wet phases of bog development indicates that it is not a reliable drought indicator (Lavoie and Payette, 1995). More likely, there may be a relationship between fire and *C. graniforme*. Torres and Honrubia (1997) found that areas affected by fire had higher levels of *C. graniforme* than areas that had not burned. Indeed sclerotia abundance in peat cores is often associated with an increase in charcoal (Jasinski et al., 1998; Lavoie et al., 1995; Peteet et al., 1998). Increases in sclerotia values were also associated with fire events at Lac des Iles, Km 20, and La Roche, but they were not associated with *L. piceae*. It is likely that fire acts as trigger for the development of sclerotia (Johnson, 1995; Miller et al., 1994; Visser, 1995) by inducing environmental stress (Massicotte and Trappe, 1991). The sclerotia should therefore not be used a drought indicator. While the increase in late-Holocene fires in the Park (Bussières et al., 1996; Lavoie, 2001; Lavoie and Richard, 2000; Zimmermann and Lavoie, 2001; Jasinski and Payette, 2005) suggests drier summers than those of the mid-Holocene, it is difficult to determine with the available data if there were episodes dry enough to initiate needle mortality and *L. piceae* fructification.

A definitive interpretation of the fossil *L. piceae* remains is limited by both methodological considerations (i.e. differing peat accumulation and decomposition rates) and the general paucity of ecological knowledge of the species. However, the association between *L. piceae* abundance and spruce budworm head capsules in our data suggests that damage by the spruce budworm may initiate increases in *L. piceae* infection and/or fructification. Drought, although difficult to detect in the paleoecological record, may also be a means to initiate fructification. As *L. piceae* produces its reproductive structures on dying and dead needles, increases in its remains in the paleoecological record may indirectly indicate the distressed state of forest trees, thus permitting its use as a paleoindicator of forest health. It may be particularly useful in investigating conifer forest decline (Coutts, 1995; Rehfuess and Rodenkirchen, 1984; Rose, 2001; Schutt, 1985). Other fungi with diagnostic features (e.g., other *Lophodermium* species, *Rhizosphaera kalkhofii*, *Lirula macrospora*) could also be studied in this manner.

Acknowledgments

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