

Differential Development of Two Palsa Fields in a Peatland Located Near Whapmagoostui-Kuujjuarapik, Northern Québec, Canada

Authors: Fillion, Marie-Ève, Bhiry, Najat, and Touazi, Mustapha

Source: Arctic, Antarctic, and Alpine Research, 46(1): 40-54

Published By: Institute of Arctic and Alpine Research (INSTAAR),

University of Colorado

URL: https://doi.org/10.1657/1938-4246-46.1.40

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Differential Development of Two Palsa Fields in a Peatland Located near Whapmagoostui-Kuujjuarapik, Northern Québec, Canada

Marie-Ève Fillion* Najat Bhiry*‡ and Mustapha Touazi*†

*Centre d'études nordiques (CEN) and Département de géographie, Université Laval, Québec, QC, G1V 0A6, Canada †Present address: Trifide Group, 771, St-Joseph Est, Bureau 204, Québec, QC, G1K 3C7, Canada ‡Corresponding author: najat.bhiry@cen.ulaval.ca

Abstract

Macrofossil analysis of the peat and topographic surveys of two palsa fields (Fields 3 and 4) within a permafrost peatland located in subarctic Québec was conducted to trace the factors that contributed to their differential development. The two palsa fields are visibly different in terms of their geomorphology, ecology, and hydrology. According to our results, the evolution of the two fields was largely synchronous in terms of the respective trophic conditions. Moreover, the climate certainly played a significant role in the evolution of this ecosystem. For example, the cooling of the Neoglacial period would have favored the ombrotrophication of both sites, whereas the Little Ice Age conditions would have contributed to palsa formation. Despite the synchronous changes within the two fields, significant differences were also noted. These include the rate of peat accumulation, the number of species found in the peat monoliths, and the presence or absence of forest cover during the ombrotrophic phase. The topography of the underlying substrate would also have influenced the hydrological conditions. For example, a light slope toward the northwest engendered a faster trophic impoverishment in Field 4. In addition, streaming water in Field 3 favored the preservation of wet and rich conditions that triggered the following changes: more diverse vegetation, the significant accumulation of peat, and the formation of higher palsas.

DOI: http://dx.doi.org/10.1657/1938-4246-46.1.40

Introduction

Palsa peatlands are commonly found in regions where permafrost is discontinuous or sporadic. A palsa consists of a mound of peat rising out of mire 1 to 7 m and containing a permafrost core of peat or silt. Palsa formation is triggered by several persistent dry and cold winters that cause ice lenses to form in the underlying sediment (Zoltai, 1971; An and Allard, 1995). In addition, coverage by moss facilitates the maintenance of permafrost in the peat. The moss dries during the summer and insulates the ground from summer heat, while in the winter it conducts the cold into the interior of the palsa (e.g., Couillard and Payette, 1985; Zoltai et al., 1988; Bhiry and Robert, 2006; Kuhry, 2008). In subarctic Québec, the formation of palsas at the tree line can be traced to the beginning of the Neoglacial period (3000 yr BP), while palsas formed south of this subarctic zone during the Little Ice Age (LIA) (Payette, 2001; Arlen-Pouliot and Bhiry, 2005; Bhiry and Robert, 2006).

Since the end of the LIA, and especially during the past century, the permafrost has begun to thaw in the peatlands of northern Canada as well as in Alaska and Eurasia (e.g., Dionne, 1984; Allard and Séguin, 1987a, 1987b; Laprise and Payette, 1988; Laberge and Payette, 1995; Matthews et al., 1997; Sollid and Sørbel, 1998; Payette et al., 2004; Camill, 2005; Parsekian et al., 2011). As a result of the permafrost thaw in the peatlands in subarctic Québec, many palsas have collapsed and have been replaced by thermokarst ponds, which then fill with peat. However, very few studies have examined the evolution of such ponds. The primary characteristic of these filled thermokarst ponds (FTP) is that they are initially colonized by hygrophilic vegetation and subsequently by mesic vegetation. The latter change occurs once water levels have lowered sufficiently through evaporation and once peat has established itself in the pond depressions (Arlen-Pouliot and Bhiry, 2005).

In addition to climate, autogenic factors have had a significant impact on the development of palsas. In fact, the height of palsas and the vegetation on their surface mediates the impact of snow and wind. For example, a very high palsa without vegetation on its surface is commonly exposed to the wind. In turn, this prevents snow accumulation over the surface of the peat. While snow limits the transmission of cold by isolating the peat from winter cooling, the absence of snow makes the permafrost more likely to persist (Seppälä, 1990; An and Allard, 1995).

The permafrost in the peatlands is also susceptible to the effects of hydrological change and fire. Following the studies of Zoltai (1993), fire may be regarded as a key trigger for thaw/ regeneration cycles in the permafrost. In the interior of Alaska, fire seems to exacerbate permafrost thawing in addition to the role played by global warming (Jones et al., 2012). Furthermore, Kuhry (2008) demonstrated that the creation of palsas in one very specific location was primarily due to hydrological changes caused by the construction of a nearby railroad that modified the drainage conditions at the site.

Synchronous changes within a very large peatland or within several peatlands in the same region are typically the result of climate processes. However, the following question remains unresolved: Are differential variations observed in the same peatland linked to internal or autogenous factors? To answer this question, we studied a 5 km² palsa peatland located 8 km south of Whapmagoostui-Kuujjuarapik (northern Québec, Canada) that bears distinct traces of differential evolution. This peatland is subdivided into seven principal palsa fields that exhibit significant differences in terms of their respective geomorphology and ecology (Bhiry, 2008). Two palsa fields in particular are visibly different in terms of their geomorphology, ecology, and hydrology. One of these fields (Field 3) was studied previously by Arlen-Pouliot and Bhiry (2005), while the other (Field 4) is studied here for the first time.

The aim of this study is thus to identify the allogenic and autogenic factors that caused the differential development of two very distinct sectors (i.e., Field 3 and Field 4) of the same palsa peatland. The study includes the macrofossil analysis of the palsa fields and thermokarst ponds (FTP) in Field 4 and a topographical analysis of the surface of the fields.

Region and Study Site

The study site is located in northern Québec on the east coast of Hudson Bay (Fig. 1) close to the village of Whapmagoostui-Kuujjuaraapik (55°13′N, 77°41′W). It lies on granite-gneiss rocks of the Precambrian Shield. The region consists of a series of depressions and low hills oriented eastwest. Deglaciation occurred at approximately 8000 yr BP (Hillaire-Marcel, 1976), after which the Tyrrell Sea submerged the area at around 7900–7800 yr BP to a maximum altitude of 270 m (Vincent, 1989). Isostatic rebound here is one of the highest in the world, with an estimated rate of 1.2 to 1.5 m per century (Allard and Tremblay, 1983).

The climate is subarctic, with a mean annual temperature of $-4.4\,^{\circ}\text{C}$ (between 1971 and 2000) (Environment Canada, 2010). The month of January is the coldest, with a mean temperature of $-23.4\,^{\circ}\text{C}$, while the mean temperature is 11.4 °C during the warmest month (August). The mean average precipitation is 656 mm, of which 37% falls as snow (Environment Canada, 2010). It is noteworthy that for the past 10 years the region has been much warmer than expected (Bhiry et al., 2011). In fact, mean annual air temperatures for the period 2001–2010 averaged $-2.6\,^{\circ}$ ± 1.2 °C, significantly above that for 1960–2000 ($-4.3\,^{\circ}$ ± 1.6 °C; t=3.78, P<0.001).

The Whapmagoostui-Kuujjuarapik area lies in the discontinuous and scattered permafrost zone (Allard and Séguin, 1987b). Permafrost can be found in rocky hills near the shore of Hudson Bay and in peatlands located in depressions filled by marine sediments. Modern vegetation in the study area belongs to the forest tundra zone. Lichen-moss and shrub tundra vegetation dominate the landscape, and forest patches are restricted to sites sheltered from the wind. Lichen-spruce forests grow in well-drained sites, and moss-spruce forests grow in wetter sites. Major tree species are *Picea mariana*, *P. glauca*, and *Larix laricina*. Ericaceous shrubs and *Betula glandulosa* occupy well-drained sites. Other shrubs such as *Salix*, *Alnus*, and *Myrica gale* are common in poorly drained sites and along bodies of water.

The study site is a permafrost peatland (known by its unofficial name, Sasapimakwananistikw peatland) located 8 km southeast of Whapmagoostui-Kuujjuarapik (Fig. 1), covering approximately 5 km2 at a mean altitude of 110 m a.s.l. The two palsa fields in this study (Fields 3 and 4) are approximately 100 m apart. The palsas in Field 3 (of which there are approximately 20) have an average height of 3 to 5 m (Fig. 1, part a). Patches devoid of vegetation are common on the top of the palsas, while the sides are covered with sparse vegetation consisting of, for example, lichens, Ledum, Betula, and Vaccinium. The filled (by organic material) thermokarst ponds (FTP) between the palsas are oval in shape, have very little vegetation, and are very damp on the surface. Field 4, in the northeast of the peatland, comprises upwards of 30 palsas between 1 and 3 m high (Fig. 1, part b). These palsas are separated by 35 FTP, which are generally elongated, less damp at the surface, and contain more vegetation than is found in Field 3.

Methods

SAMPLING, MACROFOSSIL ANALYSIS, AND DATING

A palsa and an adjacent FTP in Field 4 were sampled. The FTP was doubtless a part of the palsa that was transformed into a pond after it degraded and was then filled with vegetation. By studying this neighboring milieu, we will be able to reconstruct a continuous history of the site from the initial establishment of the peat to the present.

A peat monolith 1.72 m thick was excavated from the eroding edge of a palsa within Field 4. The mollisol was approximately 70 cm deep. Once thawed, the thickness of the monolith decreased to 1.60 m. A stratigraphic analysis was also conducted, studying the decomposition rate and color of the peat. The decomposition rate of the peat was determined in the field according to its macrofossil content: If the peat contains several macrofossils that are visible to the naked eye and using the magnifying glass ($10\times$), then the peat is considered to be poorly decomposed (or non-decomposed); if very few macrofossils are visible, then the peat is considered to be highly decomposed; if the samples are between both these extremes, then the peat is moderately decomposed. Several units were identified and measured. The peat monolith was cut into several blocks ($30\times20\times30$ cm) and the samples were stored at 4 °C for further processing.

The transition from the peat found in the ancient, degraded palsa (i.e., dark and decomposed peat) to recent peat (i.e., orange non-decomposed peat) was tracked by removing five peat cores using a Russian peat corer from an FTP located near the palsa we sampled. One of the cores was then subdivided into 1-cm-thick subsamples that were kept at a temperature of 4 °C until the time of analysis. The four other cores were observed and then returned to the holes.

The core subsamples were treated following the protocol outlined by Bhiry and Filion (2001). The remaining material was analyzed under binocular and light microscopy. Plant macrofossils were identified with the aid of the Centre d'études nordiques (CEN) reference collection of northern Québec vascular and nonvascular plants and the following references: Ireland (1982), Porsild and Cody (1980), and Crum and Anderson (1981). The results of the macrofossil analysis were compiled into macrofossil diagrams using the Palaeo Data Plotter (Juggins, 2002).

Seven samples were dated using the AMS radiocarbon method at CEN's ¹⁴C laboratory in Québec City. These samples consisted of identifiable macrofossils such as leaves, needles of the vascular plants, leaves of the brown mosses, and seeds. Six samples were taken from the palsa monolith and one sample from the transition between the old and new peat in the core taken from the FTP. Radiocarbon dates were calibrated with the CALIB 6.0 program (Stuiver et al., 1998). While we always use calibrated dates in the text and for the calculation of the peat accumulation rate, we provide the uncalibrated dates in Table 1 for comparison with previous work.

Finally, it is important to note that while we conducted a new study of the macrofossil content of the peat in one palsa and in one FTP in Field 4, we also cross-referenced other studies of closely related palsas and FTPs (Arlen-Pouliot and Bhiry, 2005; Roy, 2007) for comparison and discussion.

TOPOGRAPHIC MAPPING

The GPS 900 was used to map the topography of Fields 3 and 4 to a precision of 10 mm (horizontal measure) and 20 mm (vertical measure). The data points track the relief of the study field: There are very few data points on flat areas and many more points concentrated



FIGURE 1. Location map of the study site along the eastern coast of Hudson Bay. The study site consists of two fields: (a) Palsa Field 3 and (b) Field 4 within the same permafrost peatland, near Whapmagoostui-Kuujjuarapik (northern Québec). Both fields contain palsas and filled thermokarst ponds (FTP).

TABLE 1
Radiocarbon and calibrated ages.

Site (See Fig. 1)	Depth (cm)	Laboratory number	Date ¹⁴ C (yr BP)	Interval (cal yr BP)	Calibrated date (cal yr BP)
Palsa	0–1	ULA-1644	640 ± 15	655–625	580
Palsa	23–24	ULA-1645	1665 ± 15	1680–1650	1550
Palsa	35–36	ULA-1646	2135 ± 15	2150-2120	2130
Palsa	90–91	ULA-1647	3820 ± 15	3835-3805	4180
Palsa	140–141	ULA-1648	4505 ± 15	4520-4490	5120
Palsa	162–153	ULA-1649	4760 ± 15	4775–4745	5530
FTP	50-51	ULA-1669	280 ± 20	300–260	310

in areas where the surface is irregular in shape. The distance between the points varies between 0.5 and 5 m and covers a surface area of 0.3 km². Analysis of the data using ArcGIS 9.3 software made it possible to generate several measurements of the terrain (e.g., elevation and slope), topographic profiles, and statistics concerning the height of the palsas. The digital elevation model was created using a natural neighbor interpolation method with a resolution of 2 m.

Results and Interpretation

PEAT ACCUMULATION RATE

In the palsa located in Field 4, peat began to accumulate over the silty sediments at 5530 cal yr BP (Fig. 2). Between 5530 and 5120 cal yr BP, the rate of accumulation was low, as little as 0.29 mm yr⁻¹. This rate increased significantly to 0.53 mm yr⁻¹ between 5120 and 4180 cal yr BP. From this date, the rate decreased to 0.27 mm yr⁻¹ (between 4180 and 2130 cal yr BP) and then to 0.22 mm yr⁻¹ (between 2130 and 580 cal yr BP). The decline of peat accumulation at around 580 cal yr BP would likely have been due to the inception of permafrost, because the peat drainage would have significantly improved.

MACROFOSSIL DATA OF THE PALSA

Four macrofossil zones (MP-1 to MP-4) were distinguished based on the macrofossil assemblages (Fig. 3). The remains in MP-2 are particularly well preserved.

Macrofossil Zone MP-1: 153–142 cm (5530–5120 cal yr BP)

The macrofossil zone MP-1 contains the remains of Triglochin maritima and Carex paleacea/salina, two species that are typically found in halophytic or brackish environments (Rousseau, 1974; Marie-Victorain, 1995). Species from hydrophilic or hygrophilic environments such as Carex aquatilis, Luzula sp., and Potentilla palustris (Rousseau, 1974; Marie-Victorain, 1995) were also found (Fig. 3, part b). Some seeds resembling those from Deschampsia cespitosa were also identified, which is a species that colonizes the estuary zones (Marie-Victorain, 1995). A small number of shrub macro-remains such as those of Betula glandulosa (which can establish itself in many different environments) and Salix sp. was also identified. Salix sp. typically grows on the water's edge (Marie-Victorain, 1995). Some leaves from brown mosses were also identified, primarily Calliergon giganteum (Fig. 3, part c), which grows in rich or intermediate minerotrophic conditions and in shallow waters (Ireland, 1982).

Macrofossil Zone MP-2: 142–122 cm (5120–4750 cal yr BP)

Carex magellanica ssp. irrigua/limosa and Carex disperma were well established in this zone. The latter is typically associated with intermediate fen conditions (Vitt and Chee, 1990; Muller, 2002), while C. magellannica and C. limosa indicate rich fen conditions (Wheeler et al., 1983) rather than poor fen conditions (Lavoie, 1984; Deshaye and Morisset, 1985; Anderson et al., 1996). As a result of this overlap, it is difficult to say with certainty what the trophic conditions were like during this phase based on these plant remains alone.

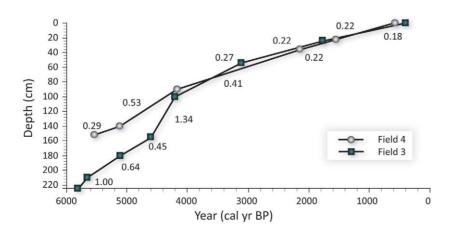
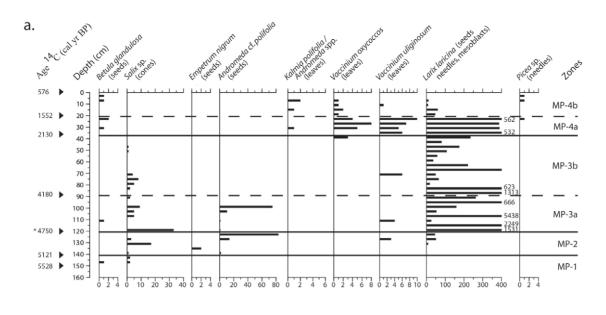
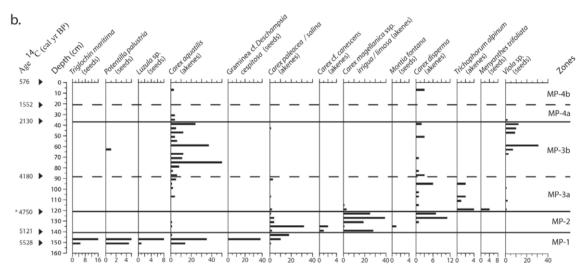


FIGURE 2. Peat accumulation rate of the studied palsa located in Field 4 and peat accumulation rate of the palsa located in Field 3, as studied by Arlen-Pouliot and Bhiry (2005).





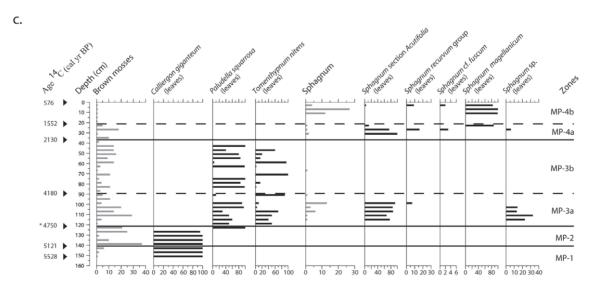


FIGURE 3. Macrofossil diagram of the studied palsa. (a) Shrub and tree macrofossil diagram of the palsa (number of macrofossils per 50 cm³); (b) herb macrofossil diagram of the palsa (number of macrofossils per 50 cm³); and (c) brown mosses and sphagnum macrofossil diagram of the palsa (macrofossil percentages). Zones are distinguished based on the macrofossil assemblages.

Nevertheless, the abundance of macro-remains of brown mosses such as *Calliergon giganteum* supports the hypothesis that the local conditions were rich to intermediately minerotrophic (Vitt and Chee, 1990). The continued presence of *Carex paleaceal salina* in the site is indicative of the incursion of seawater. Several seeds of *Andromeda* spp. were also found. Given its stratigraphic position at the bottom of the monolith, it is reasonable to infer that it is *Andromeda polifolia* rather than *Andromeda glaucophylla*, because the latter species thrives in ombrotrophic conditions (Pellerin et al., 2009). Several remains of *Vaccinium uliginosum* were also found. The first needles of *Larix laricina* were identified at a depth of 130 cm, dating from approximately 5000 cal yr BP (Fig. 3, part a).

Macrofossil Zone MP-3: 122-38 cm (4750-2130 cal yr BP)

Macrofossil zone MP-3 was subdivided into two subzones: MP-3a and MP-3b.

Macrofossil subzone MP-3a is 32 cm thick (122-90 cm) and accumulated between 4750 and 4180 cal yr BP. It contains Trichophorum alpinum remains, which are indicative of intermediate fen or rich fen conditions (Anderson et al., 1996). Carex magellanic/limosa disappeared at this time, while Carex disperma persisted in the site, as is evident from the fact that its macro-remains were found in almost every level. The moss remains were more frequent in this subzone and in some cases composed 25% of the sample. The mosses were represented by Paludella squarrosa and Tomethypnum nitens, species that colonize rich to intermediate fen or calcicolous fen (Crum and Anderson, 1981; Ireland, 1982). These species were subsequently replaced by Calliergon giganteum. This subzone is also characterized by the appearance of Sphagnum represented by S. acutifolia, a hummock species (Wallén et al., 1988). Finally, starting from the first level of this subzone, there is a significant increase in the number of needles from Larix laricina.

In subzone MP-3b (90–38 cm; 4180–2130 cal yr BP), the abundance of *Carex aquatilis* and *Viola* sp. remains, in addition to the reappearance of *Potentilla palustris*, are indicative of an increase in moisture in the peatland at the study site (Rousseau, 1974; Lavoie, 1984; Deshaye and Morisset, 1985; Deshaye and Cayouette, 1988). This interpretation is supported by the decline (in many different levels) of *Larix laricina*. *Sphagnum* disappeared completely from the site, while the brown mosses *Tomenthypnum nitens* and *Paludella squarrosa* were still present.

Macrofossil Subzone MP-4: 38-0 cm (2130-576 cal yr BP)

This subzone reflects ombrotrophic conditions. Two subzones were identified: subzone MP-4a, marked by a very dense forest cover, followed by a phase dominated by *Sphagnum* (subzone MP-4b).

In subzone MP-4a (38–22 cm), which lasted between 2130 and 1552 cal yr BP, all of the cyperaceous species disappeared and were replaced by species that live in relatively well drained conditions. These species include *Vaccinium uliginosum*, *V. oxycoccos*, and *Betula glandulosa*. *V. oxycoccos* is another species that grows in poor minerotrophic environments in addition to ombrotrophic environments (Payette, 1978). *Larix laricina* remains are abundant in this zone, while only one needle of *Picea* sp. was identified in the last level. The mosses still occupy the site, although the high degree of decomposition has made it hard to identify their remains. *Sphagnum* reappeared on the site during this phase and was represented by species such as *S. acutifolia*,

S. cf. fuscum, S. magellanicum, and S. recurvum. Generally, these species are indicative of acidic dry conditions (Ireland, 1982).

The proportion of trees to shrubs in subzone MP-4b (22–0 cm; 1552–576 cal yr BP) decreased significantly. The decline of *Larix laricina* is particularly conspicuous. The site was dominated by *Sphagnum*, in particular *S. magellanicum*, which is an ombrotrophic species that grows in open environments (i.e., in areas that lack forest cover) (Bastien and Garneau, 1997). Several *S. recurvum sphagnum* macrofossils were also found. The only herbaceous species that were identified were *Carex aquatilis* and *C. disperma*, although these were only present on one level.

MACROFOSSIL DATA FROM THE FILLED THERMOKARST POND (FTP)

Macrofossil data from the FTP may be grouped into three zones (Fig. 4). Zone MT-1 is distinct from the others because of the high degree of peat humification.

Macrofossil Zone MT-1 (62-54 cm)

The peat that accumulated in this zone is dark brown and highly decomposed. Several species of ericaceous plants were identified, including *Vaccinium uliginosum*, *V. oxycoccos*, *Kalmia polifolia/Andromeda* spp., and *Chamaedaphne calyculata*. Several remains from *Larix laricina* and *Picea* sp. were also recovered. The majority of these species grow in poor minerotrophic to ombrotrophic conditions (Vitt and Chee, 1990). Some *Sphagnum* leaves from the *recurvum* group, from *S. lindbergii*, and from *S. ripariu* were present in the three levels that we analyzed. Leaves and stems from the mosses *Calliergon stramineum* and *Drepanocladus exannulatus/fluitans* were also identified. *Sphagnum lindbergii*, *S. riparium*, as well as the two mosses are all species that colonize fen, moist depressions, thermokarst ponds, or the edges of ponds (Crum and Anderson, 1981; Gauthier, 2001).

Macrofossil Zone MT-2 (54-2 cm)

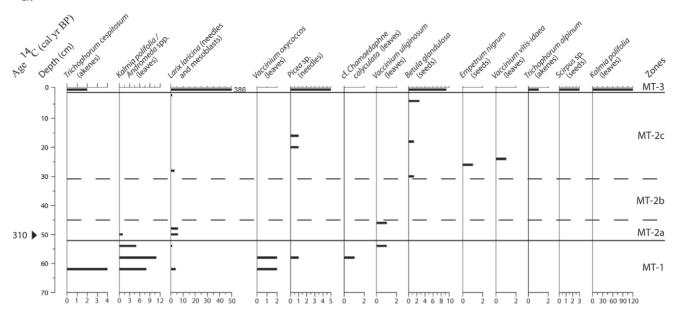
Macrofossil zone MT-2 is characterized by moist and poor trophic conditions. However, based on plant macrofossil data, three subzones were identified: MT-2a, MT-2b and MT-2c.

In MT-2a (54-46 cm), there are very few tree, shrub, and herbaceous remains. However, there is an abundance of bryophyte remains, and some Larix laricina needles were also found. Subzone MT-2b is characterized by the absolute dominance of bryophytes. Sphagnum in particular is present in great numbers, composing up to 85% of the macrofossil assemblage. Sphagnum is represented by S. riparium and S. lindbergii. The primary type of brown moss is C. stramineum, and only a few traces of D. exannulatus/fluitans were present. Macrofossil subzone MT-2C is also dominated by Sphagnum, which was represented by S. riparium and S. lindbergii. The moss C. stramineum is also abundant here, constituting up to 30% of the sample. D. exannulatus/fluitans is also present in five levels. Moreover, some needles of Picea sp. and of Larix laricina were also identified, as well as seeds from Betula glandulosa, some leaves from Empetrum nigrum and Vaccinium vitis-idaea. These latter species grow in soils that are better drained (Blondeau, 1989).

Macrofossil Zone MT-3 (2-0 cm)

In this very thin zone, several needle fragments from *Larix* laricina and *Picea* sp. were identified, while the proportion

a.



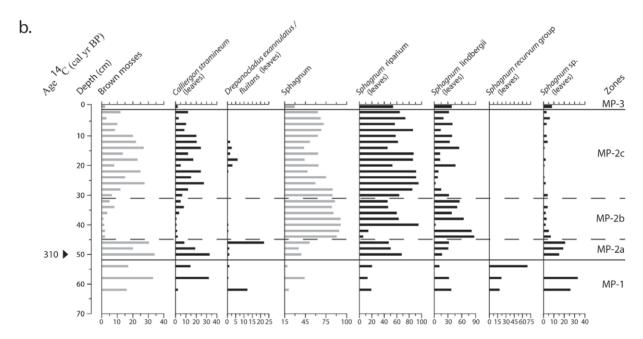


FIGURE 4. Macrofossil diagram of the filled thermokarst pond (FTP). (a) Herb, shrub, and tree macrofossil diagram of the FTP (number of macrofossils per 15 cm³); and (b) brown mosses and sphagnum macrofossil diagram of the FTP (macrofossils percentages). Zones are distinguished based on the macrofossil assemblages.

of bryophytes declined significantly. Some seeds from *Betula glandulosa* and some very well preserved leaves from *Kalmia polifolia* were found. Seeds from *Scirpus* sp., which generally grows in an aquatic milieu, were also found (Rousseau, 1974).

GEOMORPHOLOGIC ANALYSIS AND MAPPING

Topographic data were collected every 0.5 to 5 m in Field 3 and Field 4. The data were used to generate a comprehensive topographic

profile of the various components of the peat (i.e., ground level, the summit of the palsa, the sides of the palsa, etc.). The height of the palsas in Field 3 and Field 4 was calculated using a digital elevation model based on this topographical profile. This implies generating a three-dimensional model from topographic data collected in the study area.

General Topographic Profile of the Peatland (Fields 3 and 4)

Field 4 is bounded to the southwest by a hill, while Field 3 is located 100 m south of another hill. The two fields lie 200 m apart and

are separated by a stream. In Field 4, the elevation is 107 to 107.5 m in the east and 105 to 105.5 m in the northwest. There is thus a slight downward slope toward the northwest, leaving a height difference of between 2 and 2.5 m (Fig. 5). Field 3, whose average elevation is 106 m, is characterized by a more irregular surface elevation, and its palsas reach a height of between 110 and 111 m (Fig. 5).

Average Height of Palsas

Given the relatively flat surface of Field 3, it was possible to calculate the height of each palsa by subtracting the height of the ground level (which was determined to be 106 m in Field 3) from the highest point of each palsa. The height of the palsas varied between 1.93 and 5.22 m, with an average of 3.66 m. Since the ground in Field 4 was not flat (with a decline from the southeast to the northwest), the height of the palsas was calculated with reference to where they were located in the field. The average height varied between 2 and 3 m.

Slope Analysis

The degree of slope of the palsas in Fields 3 and 4 was estimated using the digital elevation model. The change in color,

from pale green to red, represents the contour of the palsas (Fig. 6). It is evident that the sides of the palsas in Field 3 are steeper than those in Field 4.

Discussion

COMPARISON BETWEEN THE EVOLUTION OF TWO PALSA FIELDS IN THE SASAPIMAKWANANISTIKW PEATLANDS

Based on a comparison of paleoecological data between two palsa fields located in the same peatland and compared against data obtained at the regional scale, it was possible to identify several allogenic and autogenic factors that influenced the development of both sites.

The Synchronic Evolution of the Two Palsa Fields

The evolution of the two fields was largely synchronous in terms of the respective trophic conditions (Fig. 7). The subtle differences in the development history of the two palsas may be attributable to dating uncertainty. Each field underwent the same succession of phases: an initial marsh, then a minerotrophic phase (comprising rich, intermediate, and poor stages), followed by an

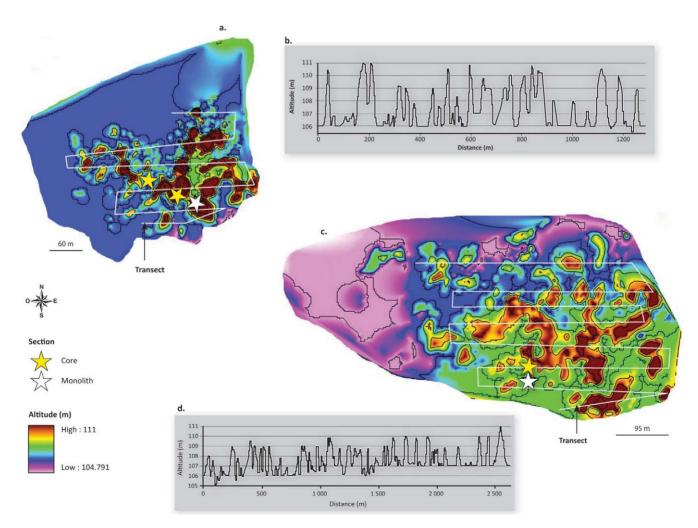


FIGURE 5. (a) Topographic map of Field 3; (b) elevation of palsas in Field 3; (c) topographic map of Field 4; and (d) elevation of palsas in Field 4. Note that in Field 4 the average elevation decreases to the east and palsas are lower than in Field 3.

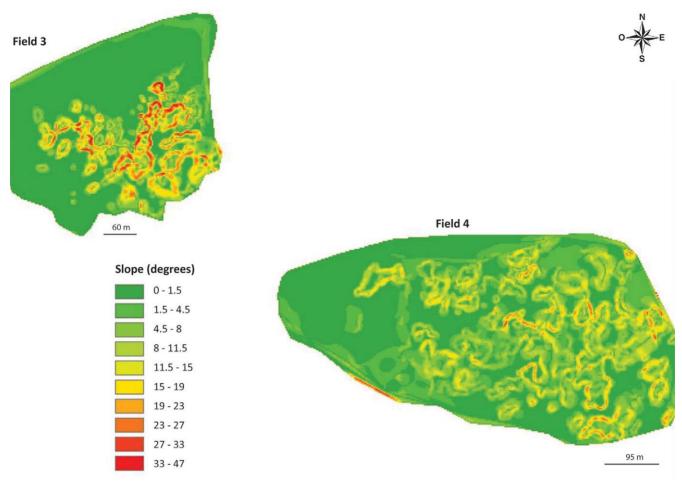


FIGURE 6. The degree of slope of the palsas in Field 3 and Field 4. Note that the sides of the palsas in Field 3 are steeper than in Field 4.

ombrotrophic phase. Subsequently, palsas formed on each site but began to decline at the end of the Little Ice Age. This decline was followed by the creation of thermokarst ponds.

Marsh Phase

Peat began to accumulate in the site very soon after the retreat of the Tyrrell Sea, which flooded the region sometime between approximately 7900 and 7800 yr BP (Hillaire-Marcel, 1976). In Field 3, the first plant remains were dated to 5800 cal yr BP, while in Field 4 the date is approximately 5530 cal yr BP. Thus, peat formation may initially have started in Field 3 and would have extended into the peripheral zones via centrifugal expansion. In fact, the topographic data gathered from the two sites corroborate this interpretation, especially the presence of a flat area on Field 3 and an upward western slope on Field 4. The rapid replacement of species that live in brackish water with species that thrive in freshwater marshes could be explained by a rapid lowering of sea level caused by the isostatic uplift. It has been noted elsewhere that peatland formation began in northern Québec during this period (i.e., between 7000 to 5000 cal yr BP) (Payette, 1988; Lavoie and Payette, 1995; Lavoie et al., 1997; Bhiry et al., 2007; Beaulieu-Audy et al., 2009). By contrast, in Europe and Asia the formation of northern peatlands occurred much earlier, between approximately 9000 and 8000 cal yr BP (Foster and Fritz, 1987; Almquist-Jacobson and Foster, 1995; Oksanen et al., 2001, 2003; Yu et al., 2003). This significant difference in onset is the result of an earlier deglaciation event.

Minerotrophic Phase

The water level became progressively lower, causing the site to transform into a poor fen. This phase was very brief in Field 4, lasting no more than 300 years (from 5100 to 4800 cal yr BP). In Field 3, by contrast, this phase lasted approximately 1000 years (from 5600 to 4600 cal yr BP). Nevertheless, the rate of accumulation in both palsa fields was the same: 0.51 mm yr⁻¹ and 0.55 mm yr⁻¹, respectively. This phase was completed in a virtually synchronous manner in each field: 4750 cal yr BP in Field 4 and 4620 cal yr BP in Field 3. The intermediate fen phase lasted approximately 500 years and ended in a synchronous manner in both fields at around 4200 cal yr BP. While the duration of this phase was the same in both fields, the rate of peat accumulation was very different. In fact, within Field 4, the rate of accumulation essentially remained the same at 0.54 mm yr⁻¹, but in Field 3 the rate increased significantly to a rate of 1.34 mm yr⁻¹.

The evolution of the peatland during the rich and intermediate fen phases occurred during the Hypsithermal period, during which time the climate was warm and dry and caused water evaporation from the ecosystems (e.g., Payette and Filion, 1993; Lavoie et al.,

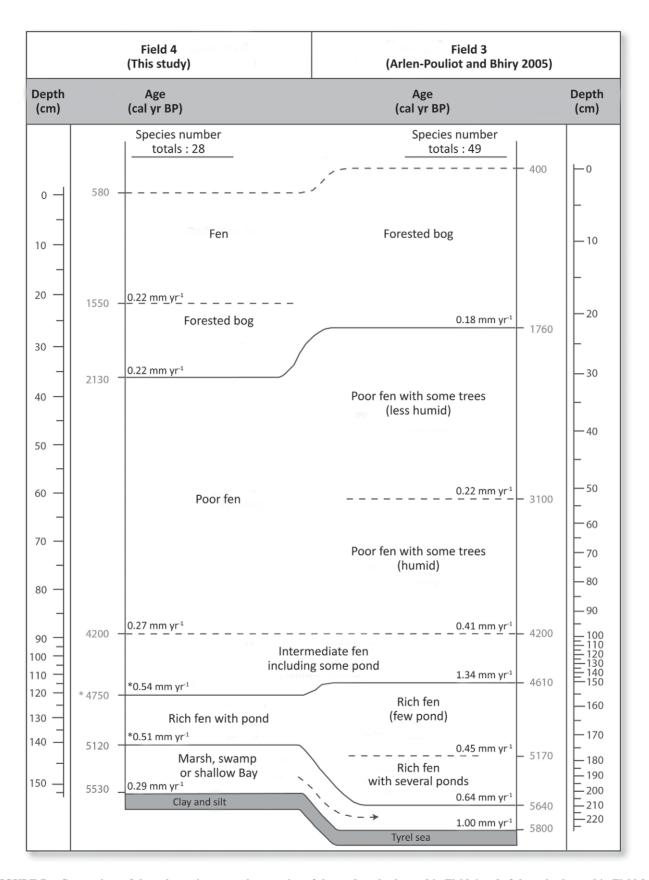


FIGURE 7. Comparison of the paleoenvironmental succession of the study palsa located in Field 4 and of the palsa located in Field 3, as studied by Arlen-Pouliot and Bhiry (2005). The two fields are within the same peatland.

1997; Cayer, 2002). A decrease in the water table was especially notable between 5300 and 4600 cal yr BP in subarctic Québec (e.g., Payette and Filion, 1993). Some studies have shown that the temperature was between 1 and 3 °C warmer during that period than it is in the present day (Lavoie et al., 1997; Oksanen et al., 2001). These climate conditions could have accelerated the transition to poor conditions by causing the water-table level to decrease. Nevertheless, thick peat accumulation would have also contributed to this transition.

The poor minerotrophic phase lasted between 4200 and 2130 cal yr BP in Field 4 and between 4200 and 1760 cal yr BP in Field 3. This phase was marked by a slight increase in the ground-water level in each field. Several studies noted an increase in lake levels after 3500 yr BP (Payette and Filion, 1993; Cayer, 2002; Miousse et al., 2003). The increase in humidity occurred in the Kwakwatanikapistikw peatland (located only a few kilometers from the study site) at approximately 3400 cal yr BP (Bhiry and Robert, 2006). The synchronous nature of these changes in northern Québec as well as in the south (Lavoie and Richard, 2000; Almquist-Jacobson et al., 2001) indicates that the increase in humidity was linked to a cooling of the climate during the Neoglacial period, which started at about 3500 cal yr BP. In the two sectors of the peatland, the poor minerotrophic phase was also marked by a decrease in the rate of peat accumulation. In Field 4, the rate decreased from 0.54 mm yr⁻¹ to 0.27 mm yr⁻¹, while in Field 3 it declined from 1.34 mm yr⁻¹ to 0.41 mm yr⁻¹ between 4200 and 3100 cal yr BP, and then it further declined to 0.22 mm yr⁻¹ between 3100 and 1760 cal yr BP.

Ombrotrophic Phase

The ombrotrophication of the site began slightly earlier in Field 4 relative to Field 3 (2100 and 1750 cal yr BP). The rates of accumulation within the two fields were very low, 0.22 and 0.17 mm yr⁻¹, respectively. The ombrotrophic phase in Field 4 may be divided into two distinct periods: one is marked by a dense forest cover (prior to 1550 cal yr BP), while the other consists of a thick moss layer and the absence of forest cover (after 1550 cal yr BP). Even if climate cooling in the late Holocene may have favored the ombrotrophication of the site, the main cause of this process was the thickness of the peat deposit and the associated nutrient impoverishment and pH decrease.

Establishment of Permafrost and the Formation of Palsas

The palsa and the collapsed palsa that transformed into the FTP were elevated after 400 cal yr BP. Several other palsas and FTPs located in the same peatland yielded similar ages (Arlen-Pouliot and Bhiry, 2005). The climate cooling associated with the Little Ice Age (500 to 200 yr BP) caused permafrost establishment in the peatland. Ice lenses formed in the underlying sediment that in turn caused the palsas to rise. The moss cover helped to insulate the ground in the summer and conducted the cold in the winter (Zoltai and Tarnocai, 1975; Zoltai et al., 1988; Couillard and Payette, 1985; Kuhry, 2008).

Formation of Thermokarst Ponds

The permafrost began to melt at the end of the Little Ice Age (Dionne, 1984; Allard and Séguin, 1987a; Laprise and Payette, 1988; Laberge and Payette, 1995). According to several studies,

the collapse of palsas was likely the result of several factors: namely, the increase of temperatures, more humid summers, and an increase in snow precipitation (Seppälä, 1982; Payette and Delwaide, 2000; Arlen-Pouliot and Bhiry, 2005). The melting of the permafrost induced thermokarst pond formation, both in the studied peatland as well as elsewhere in the subarctic. Moreover, according to Arlen-Pouliot and Bhiry (2005) and Roy (2007), and as was found in this study, these ponds were likely to have been very rapidly filled in by peat.

Three thermokarst ponds were compared: two of these are in Field 3 and were studied by Arlen-Pouliot and Bhiry (2005) and Roy (2007), while one is in Field 4 (and is studied here for the first time). This comparison demonstrates that the conditions of the new thermokarst ponds are minerotrophic (Fig. 8). For two of the three ponds, this phase lasted an average of 300–400 years, and the change to ombrotrophic conditions was recent. This change would have been linked to a progressive drying generated by the accumulation of peat in addition to evaporation and evapotranspiration.

DIFFERENTIAL DEVELOPMENT OF TWO PALSA FIELDS

Despite the synchronous changes within the two fields, significant differences were noted. These include the rate of peat accumulation, the number of species found in the peat monoliths, and the presence or absence of forest cover during the ombrotrophic phase.

Rate of Accumulation

Before 4200 cal yr BP, the rate of peat accumulation in Field 3 was approximately double that in Field 4 (Fig. 2). This phenomenon appears to indicate a higher level of saturation of the soil within Field 3, which permitted a greater diversity of vegetation and a lower rate of peat decomposition. Numerous species that grow in very humid environments were identified in Field 3, which also supports this interpretation. Moreover, it is very probable that the rapid development of the peat was encouraged by the abundance of cyperaceaes within Field 3. This interpretation is supported by studies such as those of Thormann et al. (1998), which demonstrate that the productivity of grasses would be positively correlated with the water-table level. Moreover, Bauer et al. (2003) and Muller (2002) have correlated the dominance of the herbaceous strata with higher rates of peat accumulation.

The slope of the underlying substrate likely also affected the distribution of nutrients, which would have had a direct influence on vegetation growth. In effect, according to Malmer et al. (1992), the nutrients in the minerotrophic peat initially came from water flowing on the surface (i.e., water filled with erosion sediments) and from precipitation. A stagnant water peatland accumulates nutrients from two sources (surface water and precipitation), whereas a peatland on a slope tends to lack these nutrients. The quantity of available nutrients was thus likely the cause of more significant plant productivity at the center of Field 3.

Ecological Diversity

The number of species found in each field is a key differentiating factor: 49 species were found in the palsa in Field 3, compared to 28 in the palsa in Field 4. It has already been recognized that the availability of nutrients from streams encourages ecological

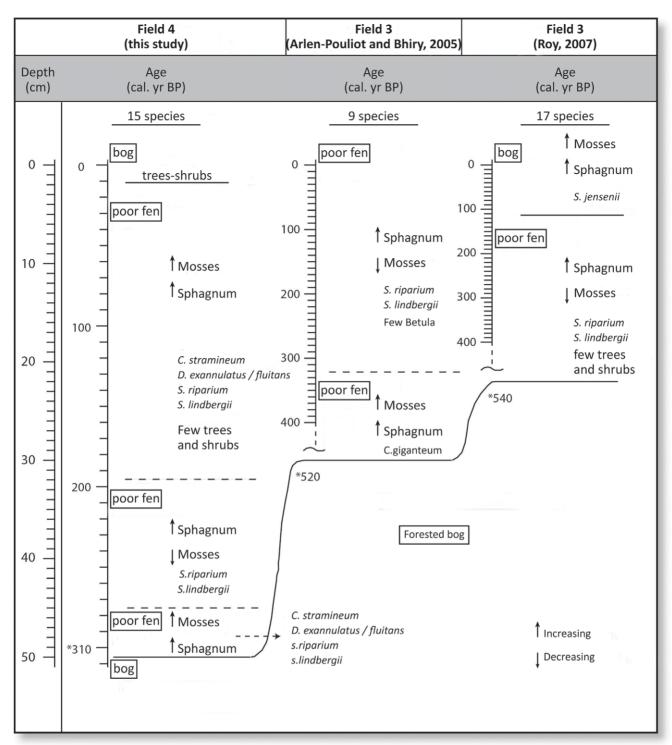


FIGURE 8. Comparison of the paleoenvironmental succession of three FTPs located within the same peatland. In Field 3, one FTP was studied in Arlen-Pouliot and Bhiry (2005) and one in Roy (2007). In Field 4, the FTP has been studied here for the first time.

diversity. According to the study by Vitt and Chee (1990), vascular plants are significantly affected by the quantity of nutrients such as calcium, magnesium, potassium, iron, salt, and so on, in the water. The bryophytes are more likely correlated with changes in alkalinity—that is, the acidity of the milieu (Vitt and Chee, 1990). Taking the findings of Malmer et al. (1992) into account, it is possible that the topography of the slope on Field 4 contributed to the low species diversity within this sector.

The total number of recorded species was 9, 15, and 17 in the FTPs (Fig. 8), which could be explained by the location of ponds within the palsa fields. In particular, the two ponds that have the greatest diversity are located on the periphery of the palsa fields, which would have exposed them to rich circulating water. The FTP in Field 3 (as studied by Arlen-Pouliot and Bhiry, 2005) demonstrates very limited ecological diversity (9 species). The reasons for this are linked to the position of the

pond at the center of the field surrounded by palsas that block access to the stream.

Beginning at around 4800 cal yr BP, Field 4 was colonized by *Larix larcina*, which persisted through 1500 cal yr BP, when it almost disappeared. In Field 3, by contrast, this species persisted up until the formation of palsas around 400 cal yr BP. It is also possible that the topography of the peatland encouraged this difference by contributing to the persistence of the rich and humid conditions that would have been necessary to the survival of *Larix larcina* in Field 3.

LINK BETWEEN PALSA HEIGHT AND THE TOPOGRAPHY OF THE SITES

The high water level in Field 3 would have facilitated the formation of a number of ice lenses in the silt-clay sediments under the peat during the Little Ice Age. This would form part of the explanation as to why the height of the palsas is greater in this field as compared to Field 4. This interpretation is corroborated by Kujala et al. (2008), who noted that the volume of water in the peat is closely linked to its thermal conductivity. That is to say, the more humid the peat is, the more likely it is to conduct the cold. Within Field 3, the palsa surface was free of snow during the winter, which permitted the cold to penetrate to the permafrost and helped to maintain it. By contrast, the palsas of Field 4 were lower and possibly covered by snow in the winter. Snow cover would have insulated the peat, thereby promoting palsa degradation.

Conclusion

The comparative study of two palsa fields located in the same peatland (Sasapimakwananistikw, Whapmagoostui-Kuujjuarapik), with a further comparison to data at the regional scale, has brought into view the respective contributions of allogenic and autogenic factors to the evolution of the two sites.

The climate certainly played a significant role in the evolution of the peatland. In particular, the cold conditions of the Neoglacial period would have brought about a transition to ombrotrophic conditions. Moreover, the effect of climate is evident in the formation of permafrost in the two sites during the cold climate of the Little Ice Age. The recent climate warming has also contributed to the degradation of palsas and the formation of FTPs.

In addition to climate, geologic factors such as the slope of the underlying substrate had a considerable impact on the evolution of the peatland. Peat formation began within a basin that corresponds to the location of Field 3, which then extended toward Field 4 up a slight slope. The water table may be perched within the peatland, but it is possible that a depression of approximately 2 m between the two fields caused drainage of the subterranean groundwater toward the northwest. By contrast, the topography of the basin is flat at the center of Field 3. Starting in 6000 cal yr BP, high levels of water would have saturated the field, and nutrients would have been readily available. These conditions would have facilitated the increase in species diversity and the accumulation of peat as well as (and more importantly) the formation of higher palsas. The wetter conditions would also have delayed the onset of poor trophic conditions in Field 3 as compared to Field 4. Tree species flourished longer in Field 3 up until the point that palsas began to form, while within Field 4 trees disappeared soon after the ombrotrophication of the site (at 1550 cal yr BP).

A hydrological study of the Sasapimakwananistikw peatland should be conducted in order to determine the relationships between the topography under the peatland, drainage, humidity, and the quantity of nutrients in the two sectors of the peat. It would also be worthwhile to do further research on the newly formed thermokarst ponds, taking into account their evolution and their role as a source of greenhouse gas.

Acknowledgments

This project has been supported by grants to N. Bhiry from the Natural Sciences and Engineering Research Council of Canada (NSERC) and the Department of Indian Affairs and North Canada. Thanks are extended to M. Bélanger, C. Rousseau, C. Lacroix, and S. Aubé-Michaud for field assistance; É. Robert and L. Marcoux for laboratory help; and L. Burns and the anonymous reviewers for their insightful comments on this manuscript. We are also grateful to Claude Tremblay and the Centre d'études nordiques for the logistic support, to the communities of Whapmagoostui and Kuujjuarapik for their precious collaboration, and to Bill Keller for the follow-up and encouragement.

References Cited

- Allard, M., and Séguin, M. K., 1987a: The Holocene evolution of permafrost near tree line, on the eastern coast of Hudson Bay (northern Québec). *Canadian Journal of Earth Sciences*, 24: 2206–2222.
- Allard, M., and Séguin, M. K., 1987b: Le pergélisol au Québec nordique: bilan et perspectives. Géographie physique et Quaternaire, 41: 141–152.
- Allard, M., and Tremblay, G., 1983: La dynamique littorale des îles Manitounuk durant l'Holocène. Zeitschrift für geomorphologie, 47: 61–95
- Almquist-Jacobson, H., and Foster, D. R., 1995: Toward an integrated model for raised-bog development: theory and field evidence. *Ecology*, 76: 2503–2516.
- Almquist-Jacobson, H., Dieffenbacher-Krall, A. C., Flanagan-Brown, R., and Sanger, D., 2001: The Holocene record of lake levels of Mansell Pond, central Maine, USA. *The Holocene*, 11: 189–201.
- An, W., and Allard, M., 1995: A mathematical approach to modelling palsa formation: insights on processes and growth conditions. *Cold Regions Science and Technology*, 23: 231–244.
- Anderson, D. S., Davis, B. D., Rooney, S. C., and Campbell, C. S., 1996: The ecology of sedges (Cyperaceae) in Maine peatlands. Bulletin of the Torrey Botanical Club, 1232: 100–110.
- Arlen-Pouliot, Y., and Bhiry, N., 2005: Palaeoecology of a palsa and a filled thermokarst pond in a permafrost peatland, subarctic Québec, Canada. *The Holocene*, 15: 408–419.
- Bastien, D. F., and Garneau, M., 1997: Clé d'identification macroscopique de 36 espèces de sphaignes de l'Est du Canada. Ottawa, Ontario: Commission géologique du Canada, Rapport divers no 61.
- Bauer, I. E., Gignac, L. D., and Vitt, D. H., 2003: Development of a peatland complex in boreal western Canada: lateral site expansion and local variability in vegetation succession and long-term peat accumulation. *Canadian Journal of Botany*, 81: 833–847.
- Beaulieu-Audy, V., Garneau, M., Richard, P. J. H, and Asnong, H., 2009: Holocene palaeoecological reconstruction of three boreal peatlands in the La Grande Rivière region, Québec, Canada. *The Holocene*, 19: 459–476.
- Bhiry, N., 2008: Dynamique écologique et hydrologique des mares thermokarstiques entourbées d'une tourbière pergélisolée subarctique. XIième congrès quadriannuel de l'Association québécoise pour l'étude du Quaternaire. Baie-Comeau, Québec, 19 à 22 août 2008, 8–9.

- Bhiry, N., and Filion, L., 2001: Analyse des macrorestes végétaux. *In* Payette, S., and Rochefort, L. (eds.), *Écologie des tourbières du Québec-Labrador*. Québec, Canada: Presse de l'Université Laval, 259–273.
- Bhiry, N., and Robert, E. C., 2006: Reconstruction of changes in vegetation and trophic conditions of palsa in a permafrost peatland, subarctic Québec, Canada. *Écoscience*, 13: 56–65.
- Bhiry, N., Payette, S., and Robert, E. C., 2007: Peatland development at the arctic tree line (Québec, Canada) influenced by flooding and permafrost. *Quaternary Research*, 67: 426–437.
- Bhiry, N., Delwaide, A., Allard, M., Bégin, Y., Filion, L., Lavoie, M.,
 Nozais, C., Payette, S., Pienitz, R., Saulnier-Talbot, E., and Vincent,
 W., 2011: Environmental change in the Great Whale River region,
 Hudson Bay: five decades of multi-disciplinary research by Centre
 d'études nordiques (CEN). Écoscience, 18: 182–203.
- Blondeau, M., 1989: La flore vasculaire des environs d'Akulivik, Nouveau-Québec. Provancheria, 23: 1–80.
- Camill, P., 2005: Permafrost thaw accelerates in boreal peatlands during late-20th century climate warming. *Climatic Change*, 68: 135–152.
- Cayer, D., 2002: Histoire post-marine et holocène d'un lac subarctique, sédimentologie, minéralogie et géochimie isotopique. M.Sc. thesis, Université Laval, Québec, Québec, Canada, 136 pp.
- Couillard, L., and Payette, S., 1985: Évolution holocène d'une tourbière à pergélisol (Québec nordique). *Canadian Journal of Botany*, 63: 1104–1121.
- Crum, H. A., and Anderson, L. E., 1981: Mosses of Eastern North America. 2 vols., New York: Columbia University Press.
- Deshaye, J., and Cayouette, J., 1988: La flore vasculaire des îles et de la presqu'île de Manitounuk, baie d'Hudson: structure phytogéographique et interprétation bioclimatique. *Provancheria*, 2: 1–74.
- Deshaye, J., and Morisset, P., 1985: La flore vasculaire du Lac à l'Eau Claire, Nouveau-Québec. *Provancheria*, 18: 1–52.
- Dionne, J.-C., 1984: Palses et limite méridionale du pergélisol dans l'hémisphère nord: le cas de Blanc-Sablon, Québec. Géographie physique et Quaternaire, 38: 165–184.
- Environment Canada, 2010: National Climate Data and Information Archive. Accessed online on 17 November 2010 at http://www.climate.weatheroffice.gc.ca.
- Foster, D. R, and Fritz, S. C., 1987: Mire development, pool formation and landscape processes on patterned fens in Dalarna, central Sweden. *Journal of Ecology*, 75: 409–437.
- Gauthier, R., 2001: Les sphaignes. *In* Payette, S., and Rochefort, L. (eds.), *Écologie des tourbières du Québec-Labrador*. Québec, Canada: Presse de l'Université Laval, 91–128.
- Hillaire-Marcel, C., 1976: La déglaciation et le relèvement isostatique sur la côte est de la baie d'Hudson. Cahier de géographie du Québec, 20: 185–220.
- Ireland, R. R., 1982: Moss Flora of the Maritime Provinces. Ottawa, Canada: National Museums of Canada, Museum of Natural Sciences.
- Jones, M. C., Booth, R. K., Yu, Z., and Ferry, F., 2013: A 2200-year record of permafrost dynamics and carbon cycling in a collapse-scar bog, interior Alaska. *Ecosystems*, 16: 1–19.
- Juggins, S., 2002: *Paleo Data Plotter, Beta test version 1.0.* Newcastle upon Tyne, U.K.: University of Newcastle.
- Kuhry, P., 2008: Palsa and peat plateau development in the Hudson Bay Lowlands, Canada: timing, pathways and causes. *Boreas*, 37: 316–327.
- Kujala, K., Seppälä, M., and Holappa, T., 2008: Physical properties of peat and palsa formation. *Cold Regions Science and Technology*, 52: 408–414
- Laberge, M.-J., and Payette, S., 1995: Long-term monitoring of permafrost change in a palsa peatland in northern Québec, Canada. Arctic and Alpine Research, 27: 167–171.
- Laprise, D., and Payette, S., 1988: Évolution récente d'une tourbière à palses (Québec subarctique: analyse cartographique et dendrochronologique. Canadian Journal of Botany, 66: 2217–2227.

- Lavoie, C., and Payette, S., 1995: Analyse macrofossile d'une palse subarctique (Québec nordique). Canadian Journal of Botany, 73: 527–537.
- Lavoie, C., Elias, S. A., and Payette, S., 1997: Holocene fossil beetles from a treeline peatland in subarctic Québec. *Canadian Journal of Zoology*, 75: 227–236.
- Lavoie, G., 1984: Contribution à la connaissance de la flore vasculaire et invasculaire de la Moyenne-et-Basse-Côte-Nord, Québec/Labrador. *Provancheria*, 17: 1–149.
- Lavoie, M., and Richard, P. J. H., 2000: Postglacial water-level changes of a small lake in southern Québec, Canada. *The Holocene*, 10: 621–634.
- Malmer, N., Horton, D. G., and Vitt, D. H., 1992: Element concentrations in mosses and surface waters of western Canadian mires relative to precipitation chemistry and hydrology. *Ecography*, 15: 114–128.
- Marie-Victorain, F., 1995: La flore laurentienne. 3º édition. Montréal, Québec: Presses de l'université de Montréal.
- Matthews, J. A., Dahl, S.-O., Berrisford, M. S., and Nesje, A., 1997: Cyclic development and thermokarstic degradation of palsas in the mid-alpine zone at Leirpullan, Dovrefjell, southern Norway. *Permafrost and Periglacial Processes*, 8: 107–122.
- Miousse, L., Bhiry, N., and Lavoie, M., 2003: Isolation and water-level fluctuations of Lake Kachishayoot, northern Québec, Canada. *Quaternary Research*, 60: 149–161.
- Muller, S. D., 2002: Influence de la végétation sur l'accumulation de la tourbe au Québec méridional. *Comptes Rendus Biologies*, 325: 629–640.
- Oksanen, P. O., Kuhry, P., and Alekseeva, R. N., 2001: Holocene development of the Rogovaya River peat plateau, European Russian Arctic. *The Holocene*, 11: 25–40.
- Oksanen, P. O., Kuhry, P., and Alekseeva, R. N., 2003: Holocene development and permafrost history of the Usinsk Mire, northeast European Russia. *Géographie physique et Quaternaire*, 57: 169–187.
- Parsekian, A. D., Jones, B. M., Jones, M., Grosse, G., Walter Anthony, K. A., and Slater, L., 2011: Expansion rate and geometry of floating vegetation mats on the margins of thermokarst lakes, northern Seward Peninsula, Alaska, USA. *Earth Surface Processes and Landforms*, 36: 1889–1897.
- Payette, S., 1978: La flore vasculaire du golfe de Richmond, Baie d'Hudson, Nouveau-Québec. *Provancheria*, 7: 1–68.
- Payette, S., 1988: Late-Holocene development of subarctic ombrotrophic peatlands: allogenic and autogenic succession. *Ecology*, 69: 516–531.
- Payette, S., 2001: La stratigraphie. In Payette, S., and Rochefort, L. (eds.), Écologie des tourbières du Québec-Labrador. Québec, Canada: Presse de l'Université Laval, 345–369.
- Payette, S., and Delwaide, A., 2000: Recent permafrost dynamics in a subarctic floodplain associated with changing water levels, Québec, Canada. *Arctic, Antarctic, and Alpine Research*, 32: 316–323.
- Payette, S., and Filion, L., 1993: Holocene water-level fluctuations of a subarctic lake at the tree-line in northern Québec. *Boreas*, 22: 7–14
- Payette, S., Delwaide, A., Caccianiga, M., and Beauchemin, M., 2004: Accelerated thawing of subarctic peatland permafrost over the last 50 years. *Geophysical Research Letters*, 31: L18208, doi: http:// dx.doi.org/10.1029/2004GL020358.
- Pellerin, S., Lagneau, L.-A., Lavoie, M., and Laroque, M., 2009: Environmental factors explaining the vegetation patterns in a temperate peatland. *Comptes Rendus Biologies*, 332: 720–731.
- Porsild, A. E., and Cody, W. J., 1980: *Vascular Plants of Continental Northwest Territories*. Ottawa, Canada: National Museum of Natural Sciences.
- Rousseau, C., 1974: Géographie floristique du Québec/Labrador. Québec, Canada: Les presses de l'Université Laval.
- Roy, N., 2007: Paléoécologie d'une mare thermokarstique comblée, Whapmagoostui-Kuujjuarapik, Québec nordique. Mémoire de baccalauréat, l'Université Laval, Québec, Québec, Canada, 31 pp.

- Seppälä, M., 1982: An experimental study of the formation of palsas. *In* Proceedings of the Fourth Canadian Permafrost Conference. Ottawa, Canada: National Research Council of Canada, 36–42.
- Seppälä, M., 1990: Depth of snow and frost on a palsa mire, Finnish Lapland. *Geografiska Annaler*, 72A: 191–201.
- Sollid, J. L., and Sørbel, L., 1998: Palsa bogs as a climate indicator: examples from Dovrefjell, southern Norway. *Ambio*, 27: 287–291.
- Stuiver, M., Reimer, P. J., and Braziunas, T. F., 1998: High-precision radiocarbon age calibration for terrestrial and marine samples. *Radiocarbon*, 40: 1127–1151.
- Thormann, M. N., Bayley, S. E., and Szumigalski, A. R., 1998: Effects of hydrologic changes on aboveground production and surface water chemistry in two boreal peatlands in Alberta: implications for global warming. *Hydrobiologia*, 362: 171–183.
- Vincent, J. S., 1989: Le Quaternaire du sud-est du Bouclier canadien. In Fulton, R. J. (ed.), Le Quaternaire du Canada et du Groenland. Ottawa, Canada: Commission géologique du Canada, 266–295.
- Vitt, D. H., and Chee, W. L., 1990: The relationships of vegetation to surface water chemistry and peat chemistry in fens of Alberta, Canada. *Plant Ecology*, 89: 87–106.
- Wallén, B., Falkengren-Grerup, U., and Malmer, N., 1988: Biomass, productivity and relative rate of photosynthesis of *Sphagnum* at different water levels on a south Swedish peat bog. *Ecography*, 11: 70–76.

- Wheeler, G., Glaser, P. H., Gorham, E., Wetmore, C. M., Bowers, F. D., and Janssens, J. A., 1983: Contributions to the flora of the Red Lake peatland, northern Minnesota, with special attention to *Carex. The American Midland Naturalist*, 110: 62–96.
- Yu, Z., Vitt, D. H., Campbell, I. D., and Apps, M. J., 2003: Understanding Holocene peat accumulation pattern of continental fens in western Canada. *Canadian Journal of Botany*, 81: 267–282.
- Zoltai, S. C., 1971: Southern limit of permafrost features in peat landforms, Manitoba and Saskatchewan. Geological Association of Canada, Special Paper 9: 305–310.
- Zoltai, S. C., 1993: Cyclic development of permafrost in the peatlands of northwestern Alberta, Canada. Arctic and Alpine Research, 25: 240–246.
- Zoltai, S. C., and Tarnocai, C., 1975: Perennially frozen peatlands in the western Arctic and Subarctic of Canada. *Canadian Journal of Earth Sciences*, 12: 28–43.
- Zoltai, S. C., Tarnocai, C., Mills, G. F., and Veldhuis, H., 1988: Wetlands of subarctic Canada. *In National Wetlands Working Group* (ed.), *Wetlands of Canada*. Ecological Land Classification Series, No. 24: 55–96.

MS accepted May 2013