

**Holocene carbon accumulation rates from three ombrotrophic peatlands in boreal Quebec,
Canada: impact of climate-driven ecohydrological change**

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Abstract

Understanding the processes controlling peatland carbon (C) sequestration is critical to anticipate potential changes in the global C cycle in response to climate change. Although identification of these factors may be relatively straightforward on seasonal timescales, at centennial to millennial

timescales complexities arise due to interactions between climate, vegetation, hydrology and long-term ecological processes. To better understand the factors controlling long-term C accumulation, Holocene rates of C sequestration were quantified from three pristine ombrotrophic peatlands in boreal Quebec, northeastern Canada (52°N, 75-76°W). Bulk density and loss-on-ignition analyses, combined with radiocarbon dating and age-depth modelling, were used to estimate long-term apparent rates of carbon accumulation. Past changes in vegetation and water table depth were obtained from plant macrofossil and testate amoeba analysis. Earliest regional peat accumulation started ~7520 cal BP, with long-term rates of C sequestration varying between 14.9 and 22.6 g m⁻² yr⁻¹. High C sequestration rates occurred during the mid-Holocene when relatively stable *Sphagnum* section *Acutifolia* communities were present, while low rates were found during the cooler late-Holocene when Cyperaceae and ligneous vegetation were more dominant. However, C sequestration was highly variable among cores, implying that local topography, geomorphology and hydrology, or disturbance factors such as fire, mediate the influence of climate on C accumulation. Reconstructed water-table depths reveal several dry shifts since 3000 cal BP, suggesting that episodic cold and dry conditions during the late-Holocene may have contributed to lower C sequestration rates. Given the intensity of the water table shifts at these times, we hypothesize that recurrent episodes of frozen subsurface peat might have intensified surface drying. As projected by climate scenarios, anticipated warmer and wetter conditions may lead to greater stability of hummock *Sphagna* cover and increased C sequestration potential in boreal peatlands.

A Introduction

Peatlands are environments where anaerobic conditions restrict decomposition, leading to the accumulation of organic matter through time. Over millennia, a small net imbalance between net primary production (NPP) and decomposition of northern peatland biomass has resulted in a global stock of organic carbon (C) attaining ~547 Pg (Yu et al., 2010). Peatland C dynamics have affected climate change during the past millennia, by providing long-term positive and negative feedbacks on atmospheric greenhouse gas concentrations (Frolking and Roulet, 2007).

Besides important long-term C sinks, ombrotrophic peatlands constitute high-resolution archives of climatic change due to their sensitivity to variations in atmospheric moisture balance (Charman, 2002). Consequently, stratigraphic surveys of both past C sequestration and reconstructions of past hydroclimate from these systems may provide insight into future projections of C dynamics in response to climatic change. In this study, we quantified long-term C accumulation rates and investigated past variations in hydroclimatic conditions and plant assemblages at three peatlands in boreal Quebec, northeastern Canada.

Factors regulating the strength of the peatland C sink vary at different timescales (Yu, 2006b). Short-term relative rates of NPP and decomposition, quantified by net ecosystem productivity (NEP), are primarily linked to shifts in water table depth (WTD) and peat surface temperature (e.g. Bubier et al., 2003; Pelletier et al., in review; Silvola et al., 1996). However, on millennial timescales, changes in peatland vegetation and WTD, and thus C sequestration, are driven by a combination of allogenic and autogenic factors. Globally, climate regime may be the principal allogenic factor having a concomitant effect on both vegetation and hydrology (Barber et al., 1994), although fire, permafrost or geological processes (e.g. isostatic uplift) may be as important in certain regions (Glaser et al., 2004; Pitkänen et al., 1999; Turetsky et al., 2007). Autogenic factors affecting C sequestration may include surface microtopography dynamics

(Eppinga et al., 2009; Swanson, 2007) and hydrology-induced limits to vertical peat growth (Belyea and Clymo, 2001; Yu et al., 2003).

Holocene variations in C sequestration have been reconstructed in various peatland types and climatic regimes. Most studies in northern peatlands show a slowdown of net vertical C accumulation towards the late-Holocene (e.g. Turunen and Turunen, 2003; Turunen et al., 2001; Yu, 2006a), although one would expect an apparent net acceleration, as the duration of decay processes is higher in older peat (Clymo, 1984). Late-Holocene climatic cooling, affecting peatland ecohydrology and probably NPP, may have been responsible for declining rates of C sequestration. Nevertheless, long-term surface drying driven by autogenic factors associated with peatland development may have also contributed to late Holocene declines in C sequestration. In this study, we quantified variations in Holocene C accumulation from three pristine boreal peatlands located in the Eastmain region, northeastern Canada. In addition, by directly quantifying past peatland vegetation and water table fluctuations, linkages among C accumulation, dominant vegetation and hydrological conditions were investigated. Finally, we also used our data to infer patterns of regional climate change based on replicate variations within cores.

A Study region

Peat cores were recovered from the deepest parts of the pristine ombrotrophic peatlands Lac Le Caron (LLC; 52°17'15"N / 75°50'21"W), Mosaik (MOS; 51°58'55"N / 75°24'06"W) and Sterne (STE; 52°02'37"N / 75°10'23"W), located in the Eastmain river watershed in the boreal region of the James Bay lowlands, Quebec, Canada (Fig. 1). Regional mean annual temperature is -2.1

$\pm 0.2^{\circ}\text{C}$ (January: $-22.0 \pm 0.5^{\circ}\text{C}$; July: $14.6 \pm 0.2^{\circ}\text{C}$), mean precipitation is 735 ± 12 mm, of which about one third falls as snow, and the mean value for growing degree days above 0°C is 1763 (interpolated means and standard errors of 1971-2003 NLWIS data; Hutchinson et al., 2009). Further details on the study region and peatlands can be found in van Bellen et al. (accepted).

A **Material and methods**

B *The use of multiple proxies*

Palaeoenvironmental reconstructions are preferentially based on multiple proxies, as independent records may prevent spurious reconstructions from a single proxy (Blaauw et al., 2010; Charman et al., 1999). Multiple proxies are particularly valuable in retrospective studies of peatland C dynamics, because rates of C accumulation are a product of multiple interacting factors (e.g., climate, vegetation, hydrology). Shifts in peat-forming vegetation are often related to changes in C sequestration, and plant macrofossils allow the identification of these past plant communities. In addition, plant macrofossils constitute an archive of moisture balance conditions, as changes in vegetation are primarily driven by hydroclimatic shifts if disturbance is absent. Likewise, assemblages of testate amoebae are recognized as good indicators of water table depth (WTD) in *Sphagnum*-dominated peatlands, especially when transfer functions are applied (e.g. Booth, 2008; Charman et al., 2007; Mitchell et al., 2008). Testate amoebae are highly sensitive to short-term (seasonal) and long-term (decadal) variations in WTD (Booth, 2010; Warner et al., 2007).

B *Fieldwork*

One core was recovered from the deepest part of each peatland (van Bellen et al., accepted), using a Box corer (10×10 cm width) to sample the upper 1 m and Russian peat samplers (4.5- to 7.5-cm diameter) for deeper peat. Sampled monoliths were wrapped in plastic, transferred to polyvinyl chloride tubes and stored at 4°C until analysis.

B *Laboratory work*

Prior to specific treatment, cores were sliced into contiguous 1 cm subsamples. Long-term apparent carbon accumulation rates (LORCA) were calculated from bulk density and loss-on-ignition (LOI) analyses. The amount of organic matter (OM) was defined as the product of bulk density and LOI (Dean, 1974). Bulk density was determined from contiguous 1 cm³ subsamples after drying for 16 hours at 105°C. Subsequently, LOI analysis was performed at 550 C for 3.5 hours (Heiri et al., 2001). The amount of organic C was calculated assuming a mean of 0.5 g C g⁻¹ OM (Turunen et al., 2002).

Plant macrofossil analysis was performed at 4 cm resolution. Subsamples (4 cm³) were gently heated in distilled water with addition of 5% KOH and carefully rinsed through a 125-µm sieve. A binocular microscope (×10-×40) was used to identify peat-forming vegetation. Vegetation types were estimated as volume percentages of the 4-cm³ subsample; seeds, charcoal fragments and *Cenococcum* sclerotia were counted and acarid mite/insect fragments were scaled 1 to 10

(1=rare, 10=abundant). *Sphagnum* sections were determined using a microscope ($\times 40$ - $\times 100$) based on branch leaf characteristics because stem leaves, which are often essential for the identification to species level, were rarely found. A plant macrofossil reference collection (Garneau, 1995) was used for identification; vegetation terminology is from Marie-Victorin (1995) and *Sphagnum* taxonomy follows Ayotte and Rochefort (2006).

Testate amoeba assemblages were analyzed at the same resolution as plant macrofossils.

Subsamples (1 cm³) were gently boiled in distilled water according to the protocol described by Hendon and Charman (1997) and *Lycopodium* (or to some samples *Eucalyptus*) was added as an exotic marker to permit the calculation of test concentrations. The material between 355 and 15 μm was retained after sieving. A total of 150 specimens was counted in most samples, although for a few samples this count total could not be achieved. Samples containing less than 75 tests were considered unreliable, which is broadly consistent with the recommendation of Payne and Mitchell (2008) that counts of 50 may be adequate for some sites and counts of 100 are likely to be sufficient for most sites. Abundance of species was expressed as a percentage of the total tests counted. The common rotifer *Habrotrocha angusticollis* was included in the percentage calculations. Taxonomy follows Charman et al. (2000) except as modified by Booth (2008). Plant macrofossil and testate amoeba diagrams were created using C2 and plotted against depth (Juggins, 2007). Zones were identified on a visual basis, according to patterns in vegetation, testate amoebae and C accumulation.

A total of 34 samples were submitted to Keck-CCAMS facility (Irvine, USA) and Beta Analytic Inc. (Miami, USA) for dating by ¹⁴C accelerator mass spectrometry (AMS). Sample material was preferentially *Sphagnum* stems (Nilsson et al., 2001), although in some cases *Picea* or Ericaceae leaf fragments were dated (Table I).

B *Data analysis*

Radiocarbon ages were calibrated using the IntCal04 calibration curve (Reimer et al., 2004) within the *Bchron* software package in *R* (Haslett and Parnell, 2008; <http://www.r-project.org>; R Development Core Team, 2009). One radiocarbon date on the STE core was identified as an outlier and was therefore omitted when developing the age-depth model. *Bchron* was further used for age-depth modelling, considering vertical accumulation as a continuous monotonic process applying piecewise linear interpolation. This approach includes creation of the 95% ‘highest density region’ of any level in the sediment record, thereby allowing estimations of the age uncertainty of any horizon within the cores. All ages were expressed as calendar years before present (BP = before AD 1950). Age-depth models were based on these calibrated ages and the age of the peatland surface, established at -56 cal BP (i.e. AD 2006). Age estimates were rounded to the nearest decade.

A transfer function based on 650 modern assemblages from peatlands in eastern and mid-continental USA was used to infer quantitative WTD from fossil testate amoeba assemblages (Booth, 2008). The widespread distribution of many testate amoeba taxa, and the similarity in the ecology of taxa among regions, suggests that the calibration dataset of Booth (2008) should provide reliable water-table depth estimates in boreal Quebec, particularly along a relative water-table depth gradient (e.g. Booth, 2008; Booth et al., 2008; Charman and Warner, 1997). A weighted average-partial least squares model was used, as it showed optimal r^2 and RMSEP values although application of other models resulted in similar reconstructions (Booth 2008). Water-table depth reconstructions were expressed as raw values and were also detrended by a

LOWESS filter with a 50% smoothing factor. Smoothing was performed to remove long-term trends caused by autogenic factors (i.e. lateral expansion and consequential drainage; Charman et al., 2006) to highlight hydrological changes most likely linked to hydroclimate variability.

Records from different cores were standardized by calculating the difference from the mean of all observations, divided by its standard deviation (i.e. z-scores). Important events of extremely high or low water table levels were visually linked, taking account of the uncertainty associated with each chronology.

Apparent C accumulation rates were defined as the product of sample C density and vertical accumulation rate (Tolonen and Turunen, 1996) and plotted as a function of age to facilitate inter-site comparisons. However, short-term shifts in C accumulation rates should be interpreted with caution, as our age-depth models were not highly resolved and thus generally failed to detect decadal to centennial shifts in vertical accumulation rates. Generally, episodes of slow vertical accumulation coincided with the presence of denser peat. As a result, decadal to centennial episodes of slow vertical accumulation not detected by age-depth models may be displayed as unrealistic peaks in C accumulation rate (i.e. post-fire; Kuhry, 1994). To account for these flaws in the age-depth models, C accumulation rates were additionally quantified by the mean rate between subsequent radiocarbon-dated levels.

(Table I)

A Results

B *LLC bog*

C *Ecohydrological reconstructions*

Peat accumulation started around 7520 cal BP under minerotrophic conditions followed by an early shift to ombrotrophy around 7210 cal BP (Fig. 2, Table II). Stratigraphic analyses show an important stable presence of *Sphagna* and high concentrations of testate amoebae throughout the deeper parts of the profile (zones LLC2, LLC3 and LLC4; Fig. 2). From 4170 cal BP vegetation assemblages alternate between *Sphagnum*, Cyperaceae and Ericaceae dominance (zone LLC5). This trend is accentuated between 2960 and 330 cal BP, when repeated high-magnitude fluctuations in WTD (2-30 cm below surface) are registered through shifting testate amoeba assemblages of *Diffflugia pulex*, *Amphitrema flavum*, *Amphitrema wrightianum*, *H. angusticollis*, *Heleopera sphagni* and *Hyalosphenia subflava* (zones LLC6 and LLC7; Fig. 2 and Table II). In addition, large charcoal fragments (>2 mm) indicate repeated fires on the coring site or in its vicinity, concentrated between 2520 and 390 cal BP. Well-preserved *Sphagnum* section *Acutifolia* peat accumulated since 330 cal BP, while a shift to more humid conditions is apparent in the uppermost section of the stratigraphy (zone LLC8).

(Fig. 2)

(Fig. 3)

C Carbon accumulation and bihydrological proxies

The LLC age-depth model shows a convex shape, indicating that vertical peat accumulation slowed down during the late-Holocene, except for the uppermost part that is partially represented by the acrotelm (Fig. 3a). The reconstruction of C accumulation in LLC shows that rates have varied considerably during the Holocene (Fig. 4) with a mean of $22.6 \text{ g m}^{-2} \text{ yr}^{-1}$. Despite high decomposition, C accumulation rates were high during the fen phase (zone LLC1; Table II). Besides this period, rapid C accumulation occurred at the upper part of zone LLC2 (~5700-5040 cal BP), characterized by moderate water tables and *Sphagnum* section *Acutifolia*. C accumulation slowed down during zones LLC4 and LLC5 (4420-2960 cal BP), attaining minima of $9\text{-}11 \text{ g m}^{-2} \text{ yr}^{-1}$ in zone LLC6 (2960-1250 cal BP). This period of limited C sequestration was characterized by high mean water tables interspersed with episodic dry surfaces (Fig. 4). The corresponding tendencies of dry-indicating macrofossils and the inferred WTD show that extreme fluctuations in surface hydrology have occurred during the period of slow accumulation, although low temporal sample resolution between 4000 and 1000 cal BP somewhat complicates the interpretation. A large increase in C sequestration rates started at the onset of zone LLC7 at 1250 cal BP. The acceleration in C accumulation may well be related to the establishment of *Sphagnum* section *Acutifolia*, mediated by a climatic warming enhancing primary production. During the last millenium, C sequestration rates varied only slightly between $25 \text{ and } 30 \text{ g m}^{-2} \text{ yr}^{-1}$ and, except for diminishing *Sphagnum* presence around 400 cal BP, vegetation remained relatively stable.

(Fig. 4)

B *MOS bog*

C *Ecohydrological reconstructions*

Plant macrofossil analyses suggest that *Sphagna* were less important in MOS than LLC (Fig. 5). *Sphagnum* section *Acutifolia*, implying relatively dry local conditions, has been present during the Holocene, yet collapsed frequently at the expense of other *Sphagnum* sections, Cyperaceae or Ericaceae (Fig. 5, Table III). Following peat inception at 7070 cal BP, fen conditions persisted until 5450 cal BP with water tables at the surface as indicated by high amounts of *A. wrightianum*, *D. pulex* and *A. flavum* (zone MOS1). Nevertheless, WTD reconstructions should be interpreted with caution as less than 75 specimens were counted in some samples. The mid-Holocene (zones MOS2 and MOS3) is characterized by *Sphagnum*-Cyperaceae and *Sphagnum*-Ericaceae peat with *D. pulex* and *A. flavum*. Zone MOS4, starting around 1940 cal BP, shows a general increase in Ericaceae, less dominant *Sphagnum* presence and sporadic *Pleurozium schreberi* around 1890 and 1000 cal BP. Episodic low water tables are encountered during this period, identified by *H. subflava*. Testate amoeba assemblages at these times are unusual, with large amounts of species associated to both rather wet (*A. discoides* and *A. flavum*) and dry optima (*D. pulex*, and *H. subflava*). Finally, a steady increase in *Sphagnum* section *Cuspidata* started ~240 cal BP continuing until present-day, although a dry shift was marked by *H. subflava* presence around 150 cal BP (zone MOS5, Table III).

(Fig. 5)

C *Carbon accumulation and biohydrological proxies*

The MOS age-depth relationship is close to linear, lacking the slowdown of vertical accumulation that was evident at LLC (Fig. 3b). Nevertheless, mean apparent C accumulation rate for MOS is substantially lower at $15.4 \text{ g m}^{-2} \text{ yr}^{-1}$. Although MOS shows long-term variations in accumulation rates throughout the Holocene, trends are less clear than in LLC (Fig. 6). In accordance, the vegetation record shows no clear long-term tendencies. C accumulation rates remained relatively stable between 10 and $20 \text{ g m}^{-2} \text{ yr}^{-1}$ from the start of local peat accumulation until the first half of zone MOS3 (~ 2700 cal BP), followed by highest accumulation rates (17 - $32 \text{ g m}^{-2} \text{ yr}^{-1}$) until the start of zone MOS4 at 1940 cal BP. This peak is associated with an important presence of *Sphagnum* section *Acutifolia* and WTD averaging 9 - 14 cm, while decomposition, indicated by the amounts of UOM, was low. The lowest C accumulation rates of $12 \text{ g m}^{-2} \text{ yr}^{-1}$ and considerably fluctuating water table levels are reconstructed for the period 1920 - 1180 cal BP.

(Fig. 6)

B *STE bog*

C *Ecohydrological reconstructions*

The entire sequence of STE has high amounts of Ericaceae/wood peat and, except for the upper 60 cm, low presence of *Sphagna* (Fig. 7). As in LLC and MOS, *A. flavum*, *D. pulex* and *H. subflava* are the most frequent testate amoebae (Fig. 7). In accordance with the dominance of ligneous vegetation, reconstructed water-table depths were generally lower than LLC and MOS and hydrological fluctuations showed high amplitudes. Peat accumulation started from 7010 cal BP under minerotrophic conditions. High decomposition has resulted in very low countable quantities of testate amoebae for zone STE1 (Table IV). Of the three peatlands, STE shows the latest transition to ombrotrophy around 4410 cal BP. *Sphagnum* section *Acutifolia* established during ombrotrophication and remained relatively important throughout zone STE2 until 3230 cal BP. At the onset of STE3, *Sphagnum* section *Acutifolia* decreased, while Cyperaceae and *H. subflava* became more abundant. Extremely dry surface conditions, starting 1090 cal BP, distinguish zone STE4 from adjacent zones, while water tables remained between 25 and 37 cm below the surface from 990 to 450 cal BP. During this period, *H. subflava* and *D. pulex* dominate the assemblages, and the vegetation cover was characterized by Ericaceae and *Picea*. A consecutive hydrological shift centered around 220 cal BP allowed an accumulation of well-preserved *Sphagnum* peat (zone STE5).

(Fig. 7)

C *Carbon accumulation and biohydrological proxies*

Peat accumulation in STE shows highly variable rates, with rapid accumulation during the mid-Holocene (Fig. 3c). With the exception of high rates during the mid-Holocene, C has been sequestered continuously at 10-20 g m⁻² yr⁻¹, resulting in a Holocene LORCA of 14.9 g m⁻² yr⁻¹ (Fig. 8). The fen phase is associated with low sequestration rates (zone STE1). The subsequent mid-Holocene period of enhanced C accumulation shows abundance of *Sphagnum* section *Acutifolia* (Fig. 8; zone STE2). The two peaks observed around 4410 and 3650 cal BP are principally the result of reconstructed phases of rapid vertical accumulation of peat formed under dry conditions. Improbable sharp increases in C accumulation rates, associated with this highly decomposed peat, is likely the result of flaws in the age-depth model. Nevertheless, C sequestration rates were relatively constant during the major part of the Holocene. The 1110-620 cal BP period of slow accumulation coincides with declining water table levels and a persistent extremely dry peatland surface (WTD attaining 37 cm; zone STE4), while *Sphagnum* presence generally diminished and ligneous vegetation increased.

(Fig. 8)

B *Regional palaeohydrological variability: climatic influence*

The compiled palaeohydrological reconstructions from the ombrotrophic portion of the three sites cover the last 4300 years. Although the uncertainty of our age-depth models complicates precise correlations among the sites, numerous hydrological shifts are observed since 3000 cal BP at all sites. Within the uncertainty of our chronologies, at least seven dry and four wet events were probably registered regionally (Fig. 9). Dry conditions were centered around

2790, 2500, 1910, 1290, 770, 400 and 140 cal BP, with the dry events at 770 and 400 BP particularly well recorded by the three sites. Regional wet shifts appear to have occurred around 2330, 1390 and 930 cal BP, and all sites indicate wetter conditions after ~150 cal BP (Fig. 9). In addition, MOS and STE records show increasing *Sphagnum* section *Cuspidata* during the last century, strengthening the interpretation of the testate amoeba record.

(Fig. 9)

A Discussion

B Linkages among long-term C sequestration, vegetation and hydrology

Although we may assume a uniform climatic history for the Eastmain region, the apparent rates and the timing of shifts in C accumulation are highly variable between peatlands. Mean Holocene LORCA has been higher in LLC with $22.6 \text{ g m}^{-2} \text{ yr}^{-1}$ compared to MOS and STE, with 15.4 and $14.9 \text{ g m}^{-2} \text{ yr}^{-1}$ respectively. To be able to estimate causes for differential C sequestration patterns, the entire accumulation history and environmental context of each core should be taken into account. C accumulation rates have been higher during the early bog phases of LLC (zone LLC2, 7210-5040 cal BP), when a combination of a persistent *Sphagnum* section *Acutifolia* cover and probably favorable mid-Holocene climatic conditions (Kaufman et al., 2004; Viau et al., 2006) allowed a rapid vertical accumulation. High rates of accumulation may have resulted of a limited decomposition due to the decay-resistant nature of *Sphagnum* section

Acutifolia. Although climatic conditions would have been equally favorable for MOS and STE, *Sphagnum* could not yet become dominant in the local vegetation during this period as minerotrophic conditions persisted until 5450 cal BP in MOS and 4410 cal BP in STE. Globally, fens may be less efficient C sinks than bogs (Turunen et al., 2002), although C accumulation under minerotrophic conditions was high in LLC ($>30 \text{ g m}^{-2} \text{ yr}^{-1}$) and low in STE ($7\text{-}14 \text{ g m}^{-2} \text{ yr}^{-1}$). The lack of *Sphagna* during minerotrophic conditions likely contributed to the slow C sequestration in MOS and STE.

Of all the peatlands in this study, the most important temporal variations in C sequestration are observed in LLC (Fig. 4), with a mid-Holocene (5790-4170 cal BP) period of rapid accumulation and a late-Holocene (4170-1250 cal BP) period of slow accumulation. The vegetation record shows a similar subdivision with a relatively stable *Sphagnum* cover that collapsed repeatedly between 4000-1300 cal BP. The compilation of all stratigraphic data shows that C accumulation rates declined simultaneously with a rise in mean water table of ~ 10 cm at the onset of LLC3 (5040 cal BP), although vegetation composition remained stable until 4170 cal BP (Fig. 6). This may indicate that diminishing C sequestration was driven primarily by a shift in WTD, that was exacerbated when *Sphagna* finally collapsed after 4170 cal BP. An initial persistence of relatively high water tables may have exerted a stress on *Sphagnum* section *Acutifolia*, followed by a replacement by other *Sphagnum* sections and Cyperaceae and a continued slowdown of C accumulation.

Furthermore, slowest C sequestration in LLC between 2960 and 1250 cal BP was characterized by fluctuating water tables (zone LLC6). Extremely low water tables cause a slow passage of organic matter through the acrotelm, resulting in a high decay potential. Moreover, hummock *Sphagna* NPP may decrease due to shading as Ericaceae cover increases (Heijmans et al., 2001).

On the other hand, extremely high water tables may enhance microtopographical gradients by expanding wet hollows and increasing hummock height (Swanson, 2007). In addition, wet bog surfaces are associated with bryophytes that are sensitive to decomposition. Fluctuating water tables may have caused testate amoebae assemblages consisting of *H. subflava* and *A. discoides* as observed in MOS4. *A. discoides* is typically most abundant in wet habitats whereas *H. subflava* is characteristic of drier habitats (Booth, 2008), but the co-dominance of the two has been observed in several studies and may be the result of high seasonal-to-interannual variability in moisture (Booth et al., 2008; Charman et al., 2007; Sullivan and Booth, in review). Indeed, maximum C accumulation has been associated with an acrotelm thickness of 10-15 cm, typical for lawns or low hummocks (Belyea and Clymo, 2001).

Different vegetation and fluctuating water tables may partially explain the differences in C sequestration during the bog stages within LLC as well as differences between the sites. Previous research showed that LLC bog has a strong surface topography gradient at $\sim 5 \text{ m km}^{-1}$ that may have supported efficient general drainage (van Bellen et al., accepted), which may have contributed to more stable ombrotrophic conditions and hummock *Sphagna* cover.

Neoglacial cold conditions could have further limited accumulation in LLC by lowering primary production and limiting the duration of the growing season (Mauquoy et al., 2002a). Cooling conditions leading to decreased NPP have been reported from tree stands close to the Eastmain region after 4650 cal BP (Arseneault and Sirois, 2004). Although decreasing C accumulation rates are perceptible between 1430 and 1180 cal BP in MOS and 1070 and 660 cal BP in STE, climate-driven depressed primary production may have been less important in these peatlands, as C sequestration was already limited due to the absence of an important *Sphagnum* cover.

The long-term effect of climate on NEP may be illustrated by large spatial patterns of peatland C storage (Yu et al., 2009). C accumulation rates have an optimum in the ‘temperature-precipitation space’ at 0-2.5°C mean annual temperature (Yu et al., 2009) and generally diminish following nordic and oceanic gradients in Quebec, i.e. from a cool and moist to a cold and dry regime. Thus, it is likely that Neoglacial conditions have limited C sequestration in peatlands within the northern Quebec climatic context. Studies on boreal and subarctic Quebec peatland C accumulation indeed show a general slowdown of accumulation during the Neoglacial cooling. Beaulieu-Audy et al. (2009) showed declining rates of peat accumulation starting around 4000 cal BP in northern Quebec. Providing late-Holocene records, Loisel and Garneau (2010) obtained minimum C accumulation of $<10 \text{ g m}^{-2} \text{ yr}^{-1}$ from two cores in MOS peatland during the 2500-1000 cal BP period.

Corresponding dry and wet shifts registered in Eastmain region peatlands may imply a climatic forcing that limited C sequestration. However, inconsistencies between the studied sites show that internal factors are likely to have mediated external forcing of C sequestration at varying intensities. Reconstructions of Eastmain peatland C accumulation at the ecosystem scale have already shown that long-term peatland development is affected by site-specific factors such as basin topography (van Bellen et al., accepted).

B *Late-Holocene climate change in the Eastmain region*

The replicated shifts in peatland WTD may indicate an enhanced climatic influence on ecosystem functioning since 3000 cal BP. Ombrotrophic peatland hydrology is directly linked to the balance between precipitation and evapotranspiration, although the respective importance of

precipitation and temperature to this balance may vary between regions and climatic regimes and even in the course of peatland development (Booth, 2010; Charman et al., 2009). The combined records of water table fluctuations show that during the late-Holocene (3000 cal BP-present) hydroclimatic conditions may have been less stable than during the mid-Holocene (7000-4000 cal BP) (Fig. 9). However, comparison of the two periods is complicated for several reasons. First, we do not have a combined record that covers the entire mid-Holocene. In addition, different stages in long-term peatland development may have differential sensitivities to external factors. Finally, the comparison of the frequency, duration and timing of hydrological shifts between mid- and late-Holocene is complicated by lower temporal resolution of the late-Holocene record and the larger age uncertainty for mid-Holocene shifts. Relatively low-resolution analyses, with one sample each 4 cm, may imply that some dry shifts may have been missed. In an eastern Newfoundland peatland, Hughes et al. (2006) found high-frequency hydrological variability during the mid-Holocene, possibly related to global climatic instability. However, regional differences in hydroclimatic context and concomitant differential sensitivity to climatic driving factors likely hamper direct comparisons of Newfoundland and James Bay region records.

In northeastern Canada, cooling climatic conditions are associated with the intrusion of dry Arctic air masses (Carcaillet and Richard, 2000; Girardin et al., 2004). Hence, past cooling events may have been concomitant with a decrease in both annual precipitation and potential evaporation, resulting in contrasting effects on peatland water tables. Eastern Canadian climate history can be summarized by a mid-Holocene thermal maximum (Kaufman et al., 2004; Viau et al., 2006) and a gradual cooling trend that started between 5000 and 4000 cal BP (Arseneault and Sirois, 2004; Filion, 1984; Kerwin et al., 2004). This Neoglacial period affected the distribution

of boreal ecozones with more severe fire events (Ali et al., 2008; Ali et al., 2009; Arseneault and Sirois, 2004; Asselin and Payette, 2005; Payette and Gagnon, 1985), whereas permafrost gradually developed in subarctic Quebec peatlands (Bhiry et al., 2007; Bhiry and Robert, 2006; Lamarre, 2010). This period may have been characterized by humid climatic conditions as shown by regional increases in lake levels (Miousse et al., 2003; Payette and Filion, 1993). In addition to Neoglacial cooling, the Medieval Warm Period (MWP), centered around 1000 cal BP (Filion, 1984) and subsequent LIA cooling have been registered in northern Quebec ecosystems (Bhiry and Robert, 2006; Viau and Gajewski, 2009). Recurrent LIA cold/wet shifts have been observed in peatlands in northern Europe (De Vleeschouwer et al., 2009; Mauquoy et al., 2002b), coinciding with solar activity minima centered around AD 1300, 1500, 1700 and 1850. In Quebec, minimum temperatures and permafrost aggradation have been reported around 800 and 400-450 cal BP (Asselin and Payette, 2006; Bhiry and Robert, 2006; Payette et al., 1985; Viau and Gajewski, 2009) yet the minimum around AD 1800-1850 and the subsequent trend towards warmer and wetter conditions are better documented (Bergeron and Archambault, 1993; Bergeron et al., 2001; Denneler et al., 2008; Girardin et al., 2004; Jacoby and D'Arrigo, 1989). Based on the number of standard deviations, our inferred dry shifts were more intense than wet shifts (Fig. 9), in spite of the apparent underestimation of WTD at the dry end of the gradient that is evident in cross validation of the transfer function (Booth, 2008).

Given the solid indications for long-term regional late-Holocene cooling and assuming that summer precipitation is more important to bog surface moisture than winter precipitation, the replicated dry surface events may be interpreted as forced by cold-dry climatic shifts. Indeed, the reconstructed dry shifts 8, 9 and 10, dated around 770, 400 and 140 cal BP, correspond to reported northern Quebec LIA cooling episodes. Previous research in LLC showed similar dry

shifts between 1370-1070, 870-560 and 530-350 cal BP (Loisel and Garneau, 2010), while cooling-associated wet shifts were reconstructed in a peatland in Newfoundland around 600 and 200 cal BP (Hughes et al., 2006). The 1370-1070 cal BP shift from Loisel and Garneau (2010) corresponds to dry shift 6 (Fig. 9), whereas the subsequent events coincide with shifts 8 and 9. Given the replicability and the extent of drying, we hypothesize that dry events have been amplified by a decadal persistence of frozen peat horizons. Some of the rapid shifts to near-surface water tables that followed these dry episodes (e.g. observed around 2400 cal BP in STE, 360 cal BP in LLC, as well as the ongoing rising water table in MOS), might thus be triggered by a collapse of frozen horizons. Melting effects may have been amplified by an autogenic effect: an anterior dry bog surface caused enhanced decomposition that concomitantly decreased hydraulic conductivity of the acrotelm peat, resulting in a potential for rapidly rising water tables and an extremely wet peatland surface. For instance, this autogenic effect may have amplified the effect of wetter climatic conditions causing high water tables (wet shift 11) since the end of the last LIA episode (Girardin et al., 2006; Payette et al., 2004).

Peatland thermokarst features are presently close to the Eastmain region, whereas the actual southern limit of sporadic peatland palsas is located ~140 km northward (Thibault and Payette, 2009). Although these residual palsas are not in equilibrium with present-day climate, past climatic variability might have been large enough to have caused episodic frozen peatland surfaces in the Eastmain region. Nevertheless, except for testate amoeba-inferred extremes in WTD, associated dry-indicating vegetation assemblages and horizons of highly decomposed peat, we have no evidence for the past occurrence of persisting frozen peat in the Eastmain region. It is likely that LIA cooling resulted in declining C sequestration rates (Mauquoy et al., 2002a), although high-resolution dating control is essential for confirmation.

A Conclusion

Holocene peat C accumulation rates in three peatlands of the Eastmain region have been spatially and temporally highly variable, with Holocene averages between 14.9 and 22.6 g m⁻² yr⁻¹. Rapid sequestration is associated with phases of important *Sphagnum* section *Acutifolia* presence during the warmer mid-Holocene, whereas low rates occur during the late-Holocene, when Cyperaceae and ligneous vegetation were abundant and water table levels showed high-amplitude fluctuations. However, high variability in C accumulation patterns implies a complex ecosystem response to driving factors and thus understanding of the interaction between climate, water table levels and vegetation mediated by local factors is essential in explaining differential tendencies. Varying patterns of C sequestration within the climatically uniform Eastmain region show that differential timing in ombrotrophication between coring sites may have been critical for patterns of long-term C sequestration.

Coinciding extremes in WTD may indicate the presence of seven cold/dry events in the region since 3000 cal BP. Possibly due to a more accurate chronology towards the present, three LIA cooling events may be best represented in the stratigraphy as indicated by (extremely) dry peatland surfaces. Given the past proximity of peatland palsas, episodes of persisting frozen peat might have contributed to the important water level drawdown in the studied peatlands.

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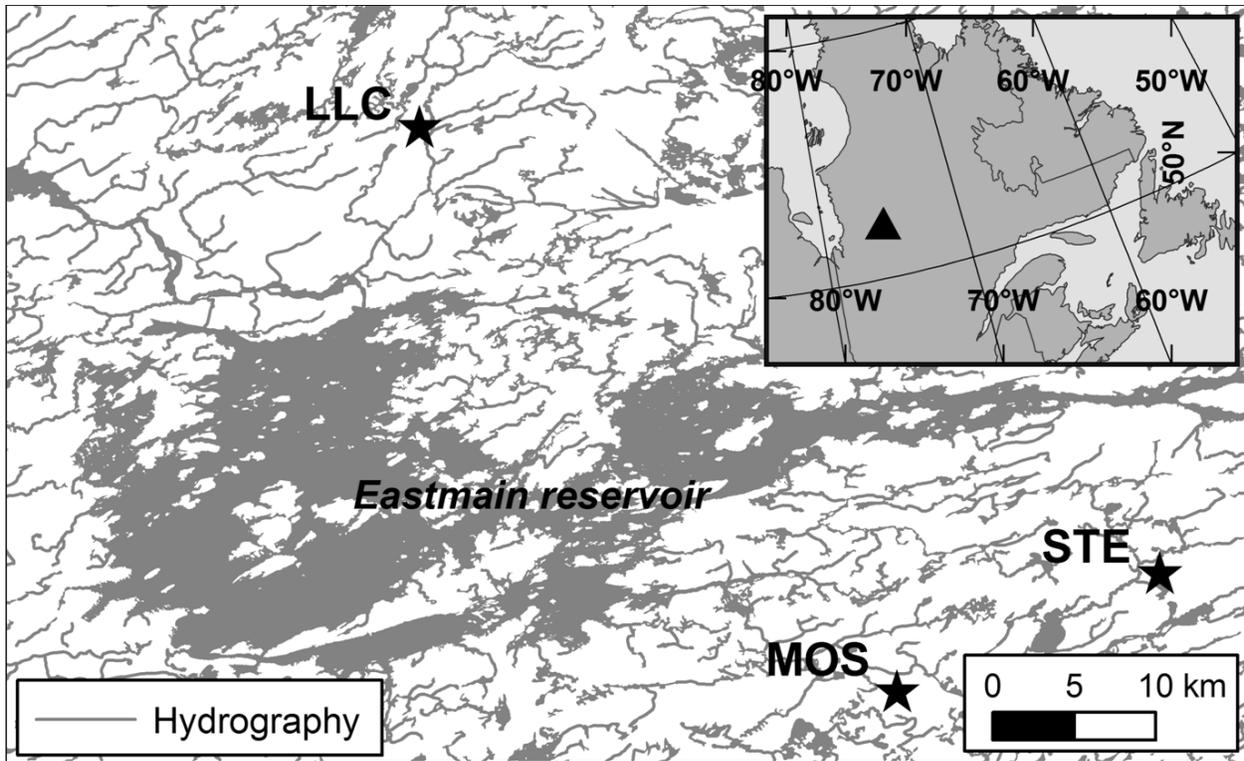


Fig. 1. Study region.

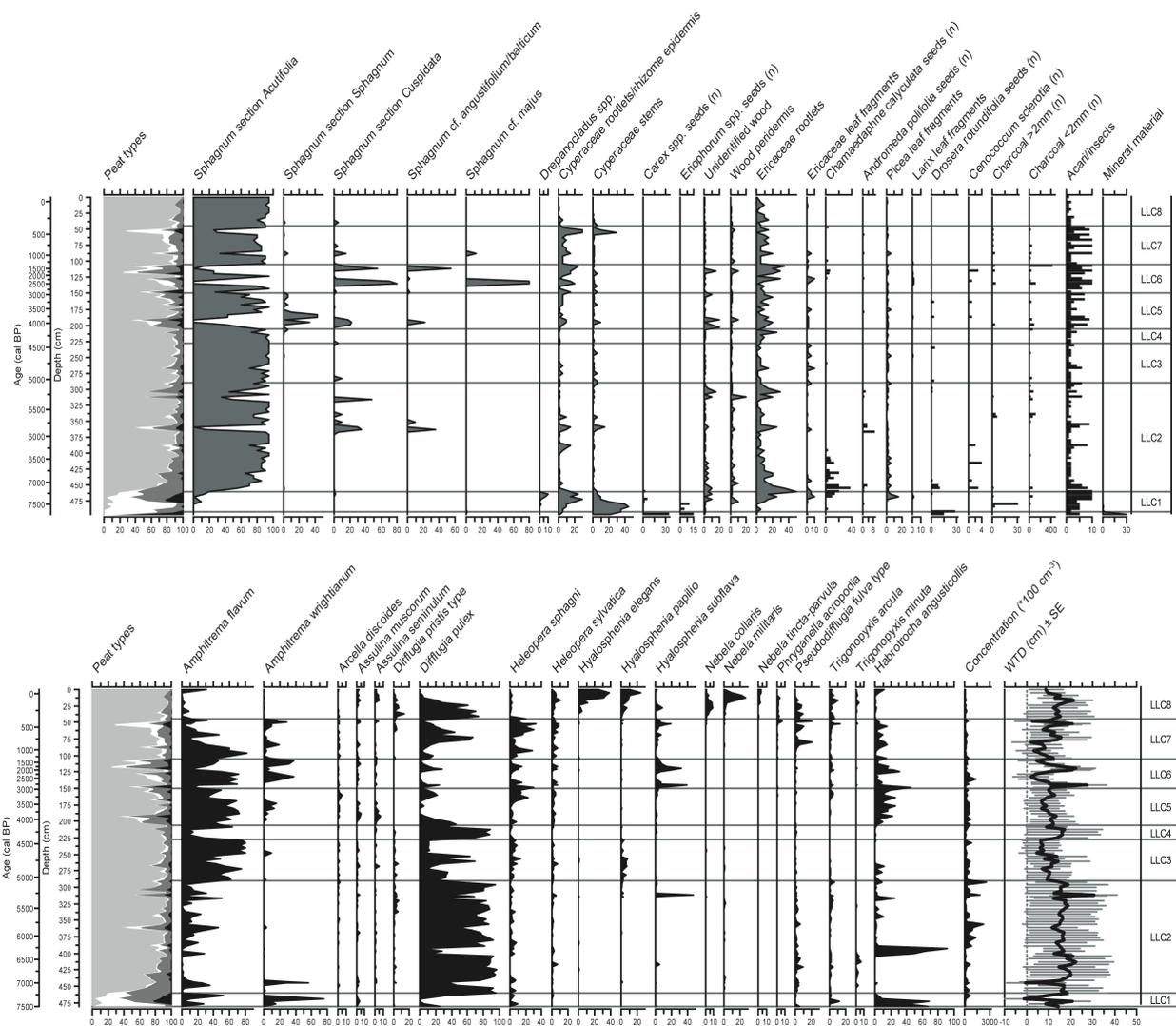


Fig. 2. Plant macrofossil (upper) and testate amoeba diagram for LLC. Peat types are subdivided into *Sphagnum* peat (light grey), sedge peat (white), ligneous peat (dark grey) and unidentified organic matter (black). Amoeba quantities are expressed as percentages.

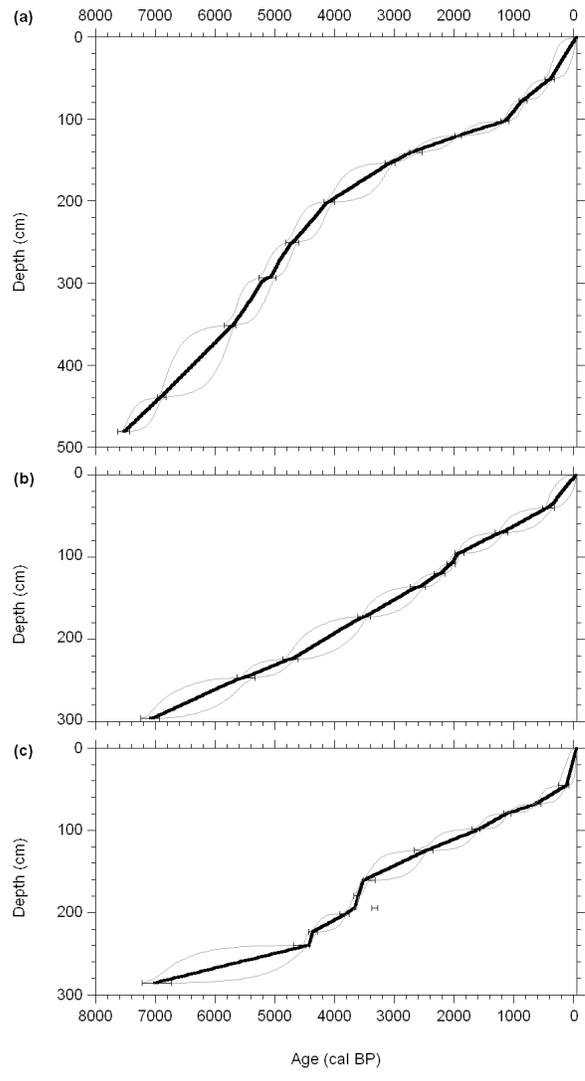


Fig. 3. Age-depth models (solid black line). Grey lines mark the 95% confidence interval. a) LLC; b) MOS; c) STE.

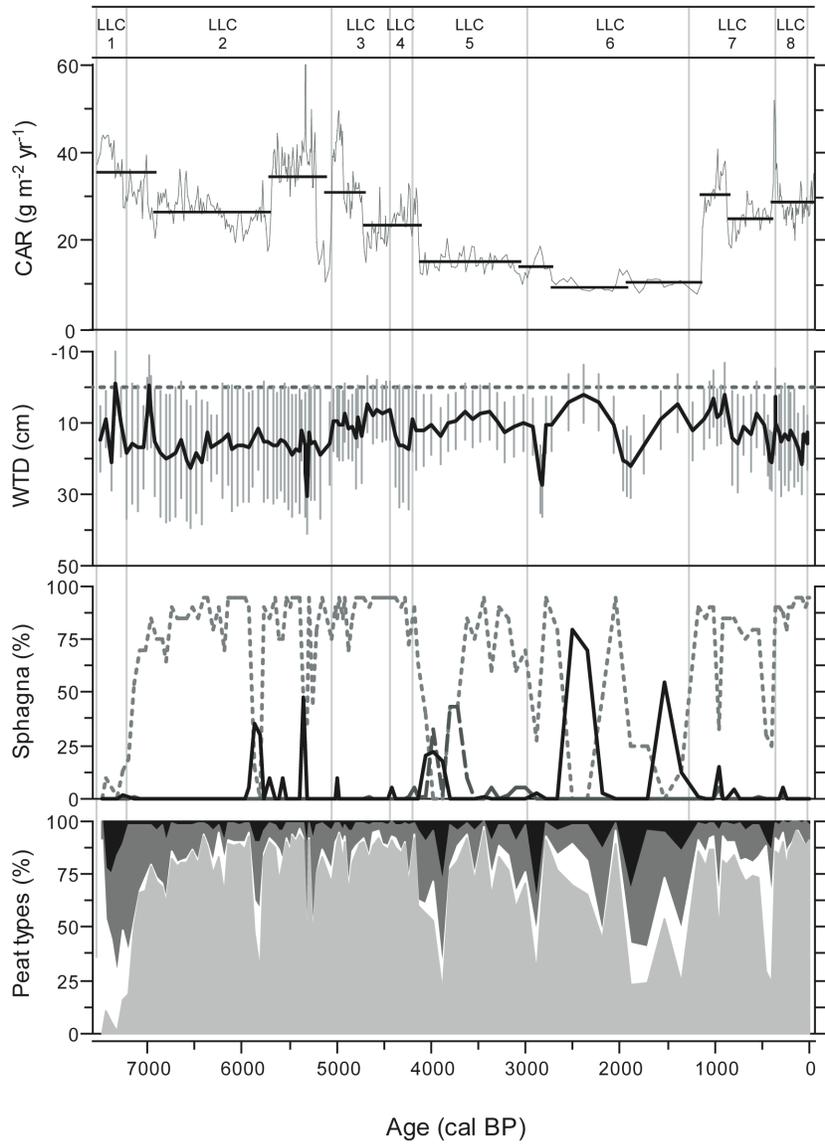


Fig. 4. LLC C accumulation rate, WTD, *Sphagna* presence and peat types. *Sphagna* shows *Sphagnum* sections *Acutifolia* (dotted line), *Sphagnum* (dashed line) and *Cuspidata* (solid line). Peat types are subdivided into *Sphagnum* peat (light grey), sedge peat (white), ligneous peat (dark grey) and unidentified organic matter (black).

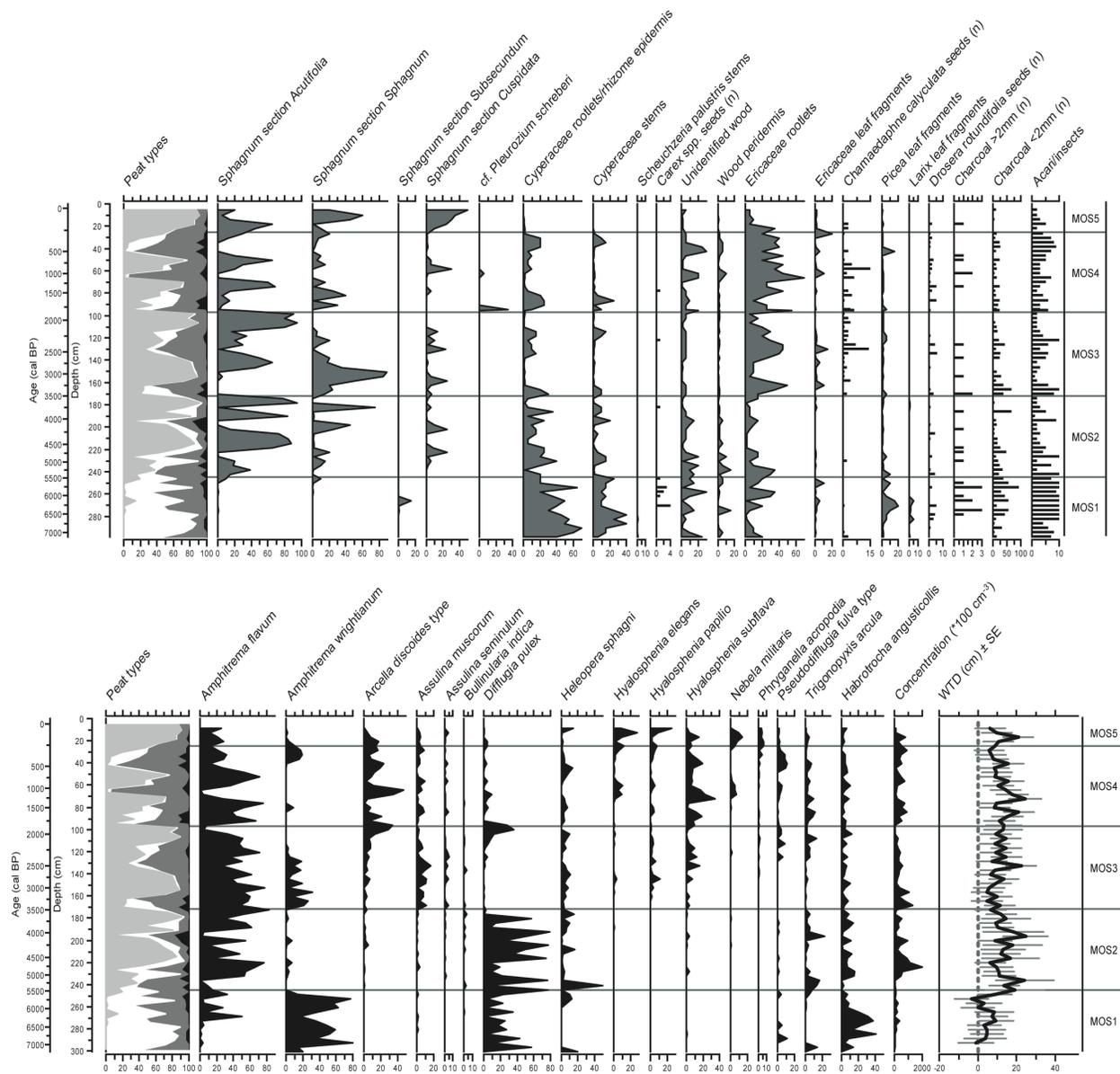


Fig. 5. Plant macrofossil (upper) and testate amoeba diagram for MOS. Peat types are subdivided into *Sphagnum* peat (light grey), sedge peat (white), ligneous peat (dark grey) and unidentified organic matter (black). Amoeba quantities are expressed as percentages.

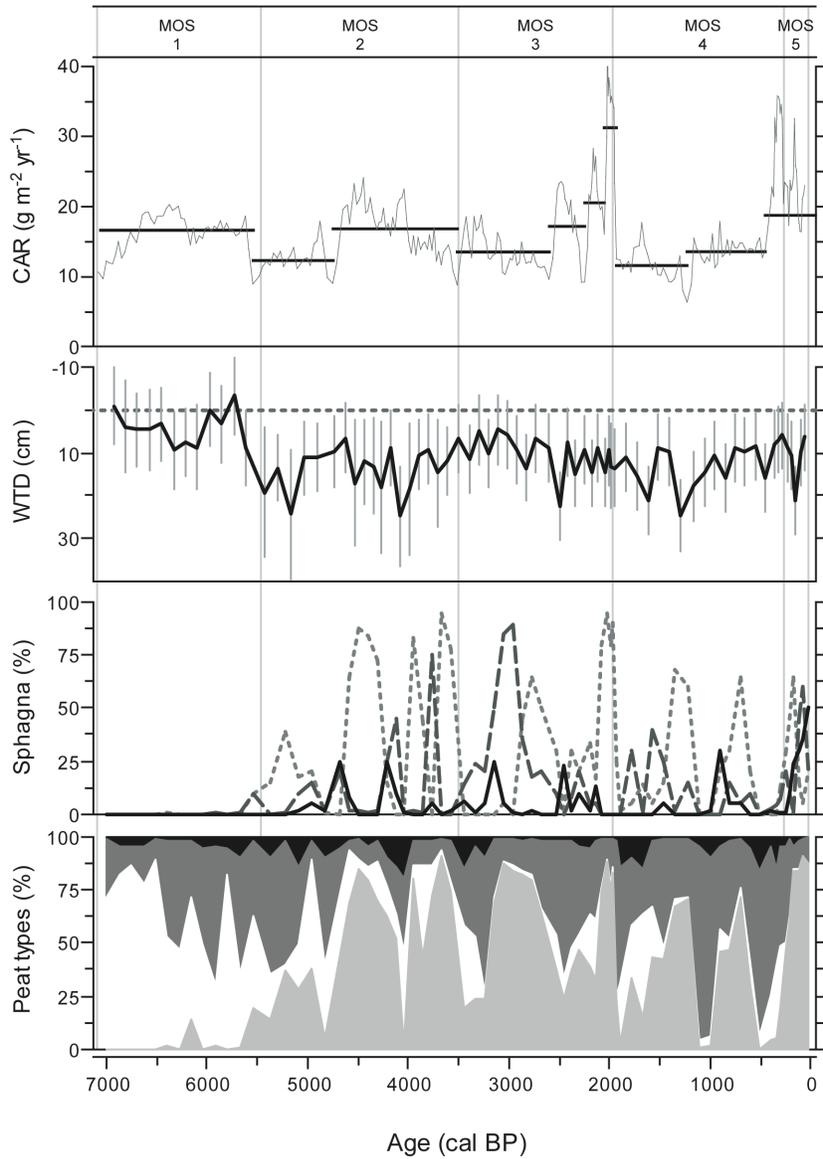


Fig. 6. MOS C accumulation rate, WTD, *Sphagna* presence and peat types. *Sphagna* shows *Sphagnum* sections *Acutifolia* (dotted line), *Sphagnum* (dashed line) and *Cuspidata* (solid line). Peat types are subdivided into *Sphagnum* peat (light grey), sedge peat (white), ligneous peat (dark grey) and unidentified organic matter (black).

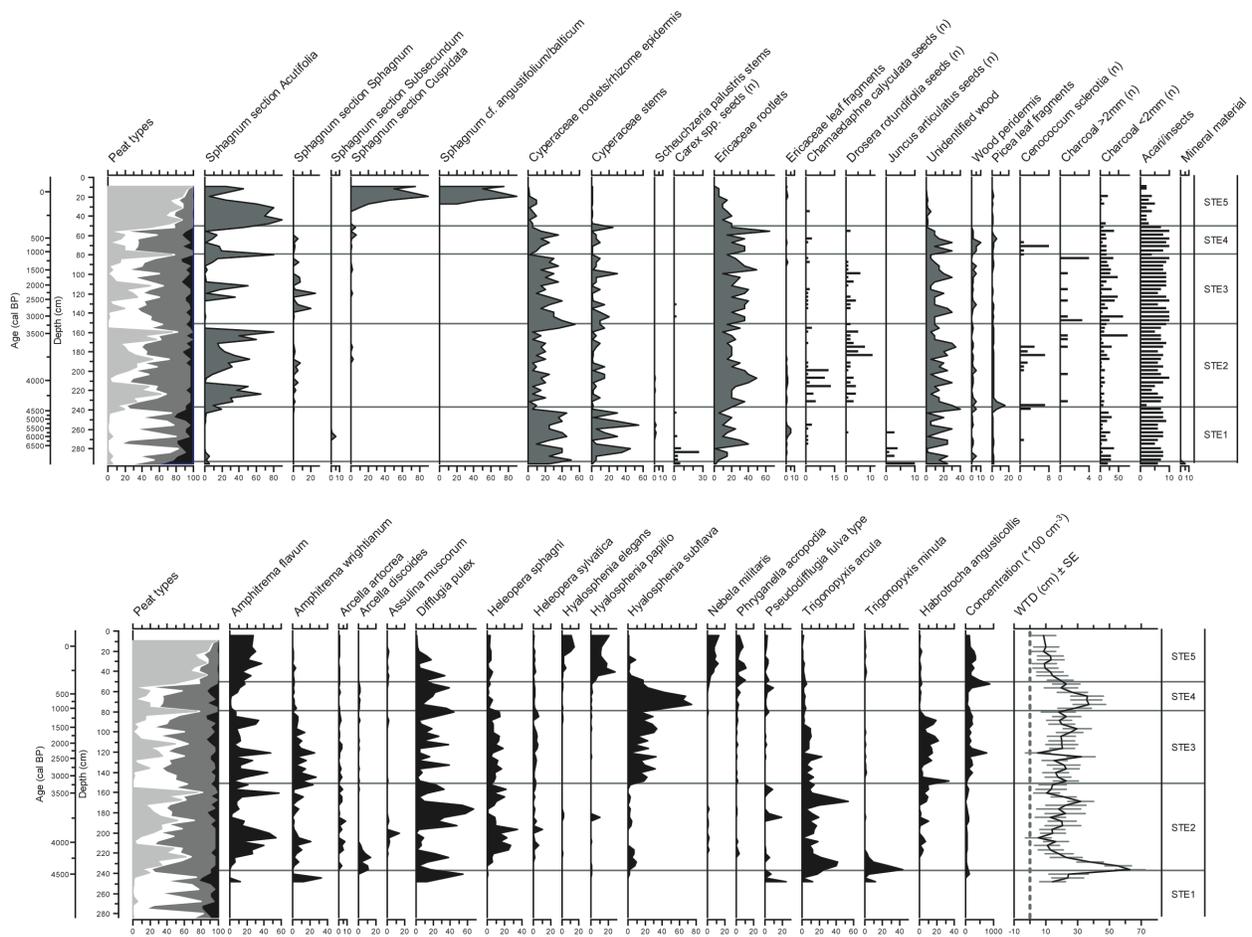


Fig. 7. Plant macrofossil (upper) and testate amoeba diagram for STE. Peat types are subdivided into *Sphagnum* peat (light grey), sedge peat (white), ligneous peat (dark grey) and unidentified organic matter (black). Amoeba quantities are expressed as percentages.

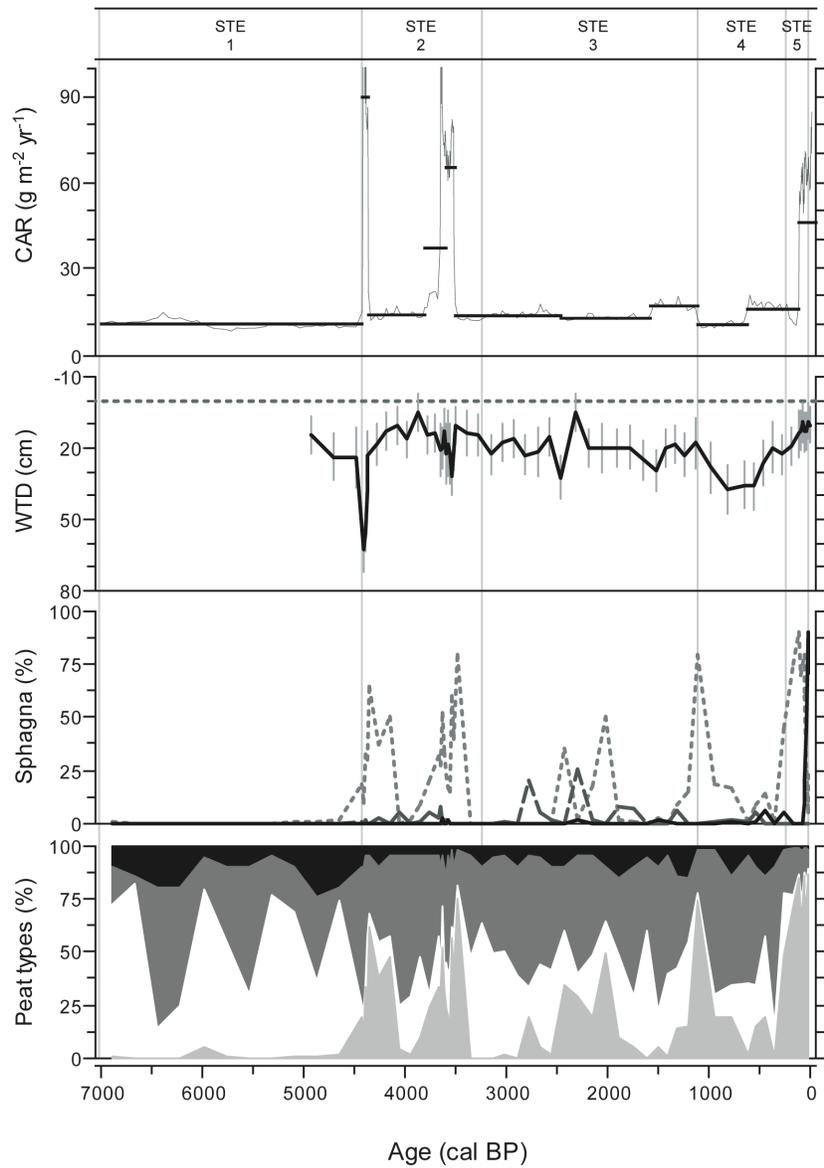


Fig. 8. STE C accumulation rate, WTD, *Sphagna* presence and peat types. *Sphagna* shows *Sphagnum* sections *Acutifolia* (dotted line), *Sphagnum* (dashed line) and *Cuspidata* (solid line). Peat types are subdivided into *Sphagnum* peat (light grey), sedge peat (white), ligneous peat (dark grey) and unidentified organic matter (black).

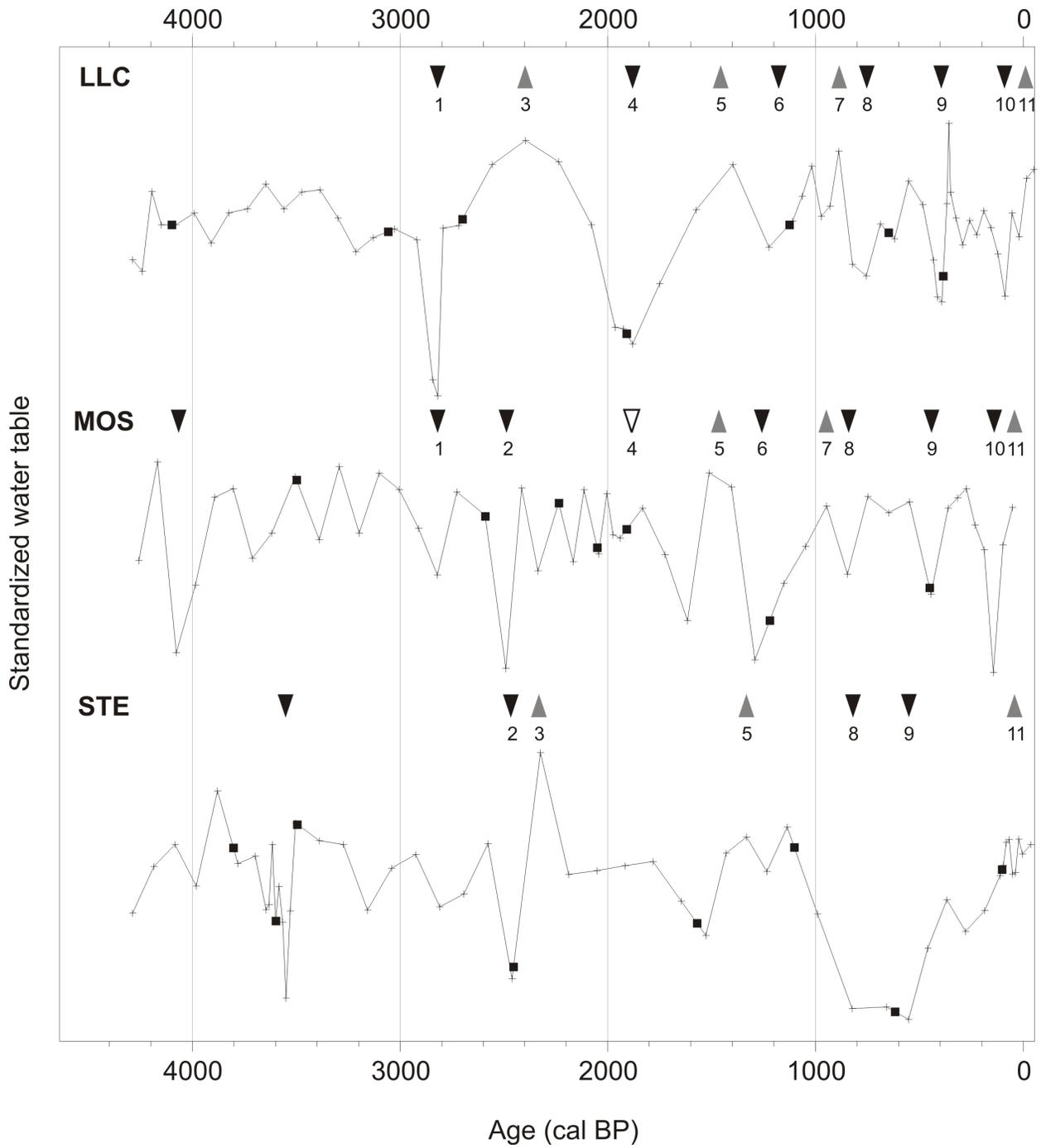


Fig. 9. Detrended and normalized late-Holocene WTD reconstructions. Black triangles indicate dry shifts, grey triangles indicate wet shifts and open triangle indicates a dry shift that was observed from plant macrofossils only. Black squares show dated levels. Equally numbered

shifts may be corresponding taking into account the 95% confidence interval for the level considered.

Table I. Radiocarbon datings sorted by core. Age is defined by the median of the 2σ -range.

Site	Core	Sample depth (cm)	Laboratory number	Material dated	^{14}C age (BP)	2σ range (cal BP)	Age (cal BP)
LLC	C	51-52	UCIAMS43480	Sph stems	340±20	317-480	391
	C	77-78	UCIAMS58634	Sph stems	915±15	777-906	846
	C	102-103	UCIAMS50203	Sph stems	1205±15	1072-1225	1140
	C	120-121	UCIAMS57419	Sph stems	1980±15	1872-1991	1924
	C	140-141	UCIAMS57421	Sph stems	2550±15	2531-2748	2716
	C	153-154	UCIAMS50204	Sph stems	2915±15	2984-3155	3057
	C	201-202	UCIAMS43479	Sph stems	3745±20	3996-4171	4107
	C	250-251	UCIAMS58636	Sph stems	4165±20	4596-4819	4701
	C	293-294	UCIAMS50205	Sph stems	4450±15	4980-5265	5110
	C	351-352	UCIAMS43478	Sph stems	4985±20	5653-5844	5701
	C	439-440	UCIAMS50206	Sph stems	6055±15	6821-6968	6912
	C	480-483	Beta223743	Eric leaf frs	6640±40	7431-7627	7520
	MOS	C	40-41	UCIAMS57424	Sph stems	355±15	325-522
C		70-71	UCIAMS54958	Sph stems	1270±25	1095-1313	1223
C		95-96	UCIAMS64586	Sph stems	1990±20	1837-1985	1924
C		108-109	UCIAMS67515	Sph stems	2065±25	1976-2119	2043
C		120-121	UCIAMS54959	Sph stems	2225±25	2157-2335	2237
C		136-137	UCIAMS64588	Sph stems	2490±20	2478-2728	2591
C		172-173	UCIAMS54960	Sph stems	3275±25	3405-3604	3506
C		224-225	UCIAMS54961	Sph stems	4185±25	4609-4863	4739
C		246-247	UCIAMS57426	Sph stems	4740±15	5333-5634	5534
C		296-297	Beta223744	Sph stems	6200±40	6936-7237	7072
STE	C	45-46	UCIAMS54962	Sph stems	105±30	75-260	116
	C	67-68	UCIAMS58645	Picea leaf frs	600±20	548-646	620
	C	79-80	UCIAMS64589	Sph stems	1175±20	1039-1166	1112
	C	98-99	UCIAMS54963	Sph stems	1715±25	1568-1697	1578
	C	124-125	UCIAMS65381	Sph stems	2445±20	2351-2663	2461
	C	160-161	UCIAMS54964	Sph stems	3255±30	3316-3521	3505
	C	179-180	UCIAMS67514	Sph stems	3415±25	3588-3671	3597
	C	201-202	UCIAMS65382	Sph stems	3485±20	3757-3912	3805
	C	223-224	UCIAMS54965	Sph stems	3960±30	4283-4431	4362
	C	239-240	UCIAMS58643	Sph stems/Picea leaf frs	3975±15	4422-4685	4424
	C	285-286	UCIAMS40360	Sph stems	6225±20	6731-7219	7007

Table II. Stratigraphic zonation for LLC.

Zone	Depth (cm)	Age (cal BP)	Main features
LLC8	45-0	330-present	Well- preserved <i>Sphagnum</i> section <i>Acutifolia</i> peat with <i>Diffugia pulex</i> and water tables between 9-21 cm below the surface with an important dry shift around 100 cal BP.
LLC7	105-45	1250-330	<i>Sphagnum</i> peat with both <i>Amphitrema flavum</i> and <i>Diffugia pulex</i> . Fluctuating water tables with persisting lowest water tables around 410 cal BP, associated with episodic highly decomposed peat
LLC6	150-105	2960-1250	Decomposed <i>Sphagnum</i> peat with Ericaceae and Cyperaceae. Highly fluctuating water tables (2-30 cm below surface) with rapid alternation of wet- and dry-indicating amoebae. Deep water tables (~22-27 cm below the surface) centered ~1920 and ~2830 cal BP
LLC5	206-150	4170-2960	Decomposed <i>Sphagnum</i> peat with occasional Ericaceae and Cyperaceae. Stable water tables (7-13 cm below surface) with <i>Amphitrema flavum</i> and <i>Habrotrocha angusticollis</i>
LLC4	228-206	4420-4170	Well-preserved <i>Sphagnum</i> section <i>Acutifolia</i> peat with <i>Diffugia pulex</i> and stable water tables (15-20 cm below surface)
LLC3	290-228	5040-4420	Well preserved <i>Sphagnum</i> section <i>Acutifolia</i> peat with <i>Amphitrema flavum</i> and high water tables (5-15 cm below surface)
LLC2	460-290	7210-5040	Well-preserved <i>Sphagnum</i> section <i>Acutifolia</i> peat with <i>Diffugia pulex</i> and stable water tables (15-20 cm below surface)
LLC1	482-460	7520-7210	Wet fen conditions: decomposed Cyperaceae and <i>Drepanocladus</i> peat with <i>Habrotrocha angusticollis</i> and <i>Amphitrema wrightianum</i>

Table III. Stratigraphic zonation for MOS.

Zone	Depth (cm)	Age (cal BP)	Main features
MOS5	25-0	240-present	Well-preserved <i>Sphagnum</i> peat with a single dry shift at 17 cm/150 cal BP
MOS4	97-25	1940-240	Ericaceae- <i>Sphagnum</i> peat with <i>Amphitrema flavum</i> , <i>Arcella discoides</i> and <i>Hyalosphenia subflava</i> . Fluctuating water tables (6-25 cm below surface) with important dry shifts centered around 1890 cal BP (presence of <i>Pleurozium schreberi</i>) and 1290 cal BP (presence of <i>Hyalosphenia subflava</i> and <i>Trigonopyxis arcula</i>).
MOS3	172-97	3480-1940	<i>Sphagnum</i> -Ericaceae peat with <i>Amphitrema flavum</i> . Relatively stable water tables and accelerating accumulation toward the end of the period
MOS2	245-172	5450-3480	<i>Sphagnum</i> -Cyperaceae peat with <i>Diffugia pulex</i> and <i>Amphitrema flavum</i> . Fluctuating water tables (6-25 cm below surface)
MOS1	297-245	7070-5450	Wet fen conditions. Cyperaceae and Ericaceae peat with <i>Amphitrema wrightianum</i> , <i>Diffugia pulex</i> and <i>Habrotrocha angusticollis</i>

Table IV. Stratigraphic zonation for STE.

Zone	Depth (cm)	Age (cal BP)	Main features
STE5	50-0	220-present	Well-preserved <i>Sphagnum</i> peat with <i>Amphitrema flavum</i> and <i>Hyalosphenia papilio</i> , shifting toward <i>Cuspidata</i> section dominance
STE4	79-50	1090-220	Highly decomposed Ericaceae/wood-Cyperaceae peat with <i>Hyalosphenia subflava</i> and extremely low water tables (20-37 cm below surface)
STE3	151-79	3230-1090	Decomposed Ericaceae/wood-Cyperaceae peat with <i>Sphagnum</i> and <i>Hyalosphenia subflava</i> . Unstable water tables.
STE2	237-151	4410-3230	Ericaceae/wood- <i>Sphagnum</i> peat with <i>Amphitrema flavum</i> , <i>Diffugia pulex</i> and <i>Trigonopyxis arcula</i> . Highly fluctuating water tables (5-31 cm below surface)
STE1	286-237	7010-4410	Fen conditions. Highly decomposed Cyperaceae and Ericaceae peat