Integration of palaeohydrological proxies into a peatland model: a new tool for palaeoecological studies

Anne Quillet,1* Michelle Garneau,1,2 Simon van Bellen,3 Steve Frolking4 and Eeva-Stiina Tuittila5

1 GEOTOP, Université du Québec à Montréal, Montréal QC, Canada
2 Département de Géographie, Université du Québec à Montréal, Montréal QC, Canada
3 School of Geosciences, University of Aberdeen, Aberdeen, UK
4 Institute for the Study of Earth, Oceans, and Space, University of New Hampshire, Durham, NH, USA
5 School of Forest Sciences, University of Eastern Finland, Joensuu, Finland

ABSTRACT

To assess the response of northern peatlands to hydrological changes, we analysed the response of a model designed to simulate peatland development at a millennial timescale, the Holocene Peat Model, to two hydrological drivers. The study is performed on two open ombrotrophic peatlands located in the James Bay region in North-eastern Canada. For both sites, two simulations were realized: one based on a precipitation reconstruction from pollen data, used as input in the model, and a second using a water-table depth reconstruction derived from testate amoebae to apply a forcing on the model. Simulated variations in carbon accumulation rates (CARs) and vegetation composition were analysed against palaeoecological datasets.

In both sites and for the two hydrological drivers, modelling results in CARs showed periods of net carbon loss that coincided with fluctuations in observed CARs, although net carbon loss cannot be traced in palaeoecological datasets per se. The comparison between plant macrofossil records and simulated vegetation distributions highlighted differences between precipitation and water-table depth-driven simulations. Thus, the methodology used was found useful to analyse the origin of vegetation shifts in macrofossil datasets. Copyright © 2014 John Wiley & Sons, Ltd.

KEY WORDS bog; carbon dynamics; Holocene; northern peatlands; model forcing; pollen; testate amoebae; transfer function

Received 19 April 2013; Revised 17 April 2014; Accepted 20 April 2014

INTRODUCTION

In northern peatlands, anoxic conditions limit decomposition and enable these ecosystems to store large amounts of organic carbon as peat. The total amount of carbon stored in northern peatlands is estimated at ca 500 Gt C (Yu, 2012) although they cover about 3% of the world’s terrestrial area (Charman, 2002). Peatlands have an impact on the climate radiative forcing at a millennial timescale (Frolking and Roulet, 2007) and are therefore of particular interest for global carbon cycle studies.

On the millennial timescale, studying carbon accumulation patterns of peatlands relies on the analysis of peat composition and stratigraphy. Peat is composed of more or less preserved plant assemblages recording past ecohydrological changes (e.g. Tuittila et al., 2007). Additionally, peatlands store fossils of testate amoeba assemblages that may be used in quantitative reconstructions of peatland water-table level and pH conditions (Mitchell et al., 2008) as well as other remnants that act as records of past local and regional conditions such as pollen and charcoal (Vääränta et al., 2007). The analysis of peatlands can support the understanding of variations in carbon dynamics throughout the Holocene (Garneau et al., in press).

Net carbon accumulation is the balance between production and decomposition. Both allogenic and autogenic processes can influence this balance. These complex processes have been the focus of numerous modelling efforts (Clymo, 1984; Hilbert et al., 2000; Frolking et al., 2001; Belyea and Baird, 2006; Ise et al., 2008; Frolking et al., 2010; Baird et al., 2012; Morris et al., 2012). Moreover, peatland ecohydrology, which is mainly influenced by regional climatic variations, local hydrological changes and autogenic successions in the peatland, involves different feedback processes that affect carbon accumulation. Over the last years, several modelling studies have aimed to take these processes into account (Eppinga et al., 2009; Morris et al., 2011; Baird et al., 2012; Morris et al., 2012).

The evaluation of the capacity of an ecosystem model to capture the mechanisms and reproduce their outcomes in realistic rates can be achieved by testing it against measured data. This approach is still rather rarely conducted in peat accumulation modelling because of the

*Correspondence to: Anne Quillet, GEOTOP, Université du Québec à Montréal, 201 avenue du Président-Kennedy, Montréal QC H2X 3Y7, Canada. E-mail: quillet.anne@courrier.uqam.ca
lack of complete datasets for the modelled period with adequate temporal resolution. Peatland development covers processes over a large variety of timescales that together leave a record on their net outcome in peat deposits. Recent development of quantitative palaeoecological methods and reconstruction of past environmental conditions (e.g. Seppä et al., 2008; Charman et al., 2009; Birks and Seppä, 2010; Väliranta et al., 2012) as well as the availability of multi-proxy data over a peatland history gives a novel opportunity for model evaluation.

The Holocene Peat Model (HPM) is a dynamic model simulating the transient evolution of a peatland since its early stages (Frolking et al., 2010). The aim of HPM is to capture northern peatland behaviour in order to quantify the amount of carbon sequestered in these ecosystems during the Holocene. HPM has so far been evaluated against site datasets (Mer Bleue Bog, Canada, Frolking et al., 2010) and a chronosequence formed by several sites in Finland (Tuittila et al., 2013). Moreover, sensitivity analyses have been performed on the model (Quillet et al., 2013a) highlighting its performance and limitations. These together identified water-balance calculation as a limitation in HPM because it relies on several parameters with large uncertainty, such as the peatland outflows and the watershed inflows influencing nutrient availability.

In this study, we aim to explore the manifold responses of peatland to hydrological changes by analysing the response of the HPM, namely carbon accumulation and vegetation dynamics, to different hydrological drivers. The settings are based on two palaeoecological proxies: precipitation reconstruction from pollen data (Viau and Gajewski, 2009) and water-table depth reconstruction derived from testate amoebae (van Bellen et al., 2011b). Simulation results are analysed against palaeoecological datasets of carbon accumulation rates (CARs) and plant macrofossils from two ombrotrophic peatlands located in North-eastern Canada. We hypothesize that the comparison between a simulation driven by reconstructed precipitation and a simulation forced with reconstructed water-table depths will allow the exploration of the model response variability in terms of carbon and vegetation dynamics during the whole development of the peatlands since their initiation. Moreover, this comparison is expected to help disentangle the origin of this variability because the chosen hydrological drivers respectively represent regional conditions and local conditions accounting for both allogenic regional signals and autogenic changes.

Former simulations with HPM were either performed with constant precipitation series (Quillet et al., 2013b; Quillet et al., 2013a) or with randomized precipitation series (Frolking et al., 2010; Tuittila et al., 2013). The use of a proxy as an input for precipitation in the model helps constrain some of the uncertainty in the simulation. Unlike reconstructed precipitation based on pollen records, the use of reconstructed water-table depths based on testate amoeba assemblages allows the integration of both allogenic and autogenic changes as they have been recorded at the study site during the development of the peatland. Comparing the two simulations is thus a great opportunity to explore further the dynamics and interactions occurring in the system at the millennial timescale.

Although forcing HPM with reconstructed water-table depths entails the elimination of the feedback processes between the peat and the water-table depth, the reconstructed water-table depth values that are used in the forcing are per se the result of the interactions between vegetation, peat properties and hydrological conditions that have varied over time. The results of the forcing experiment are thus based on the results of the ecohydrological interactions as they have been recorded in the peat.

**PALAEOECOLOGICAL ANALYSES**

**Sites**

The palaeoecological data needed to perform this analysis should be ideally taken from pristine peatlands showing typical development stages and analysed against bulk density, testate amoeba and plant macrofossil records. In order to capture the regional variability, we chose two peatlands located in the same region but showing two different although typical development patterns.

The two ombrotrophic peatland complexes are located in the Eastmain river watershed, boreal Québec, Canada. The region is characterized by post-glacial environments and comprises a gradient of ecosystems from closed-crown boreal forest in the south to open boreal forest in the north-east. The studied peatlands are located close to the recently created Eastmain Reservoir (Figure 1). In this watershed,
peatlands are estimated to cover about 8% of the area (Grenier et al. 2008).

The two sampled peatlands, Lac Le Caron (LLC) peatland (52°17′15″N/75°50′21″W) and Mosaik (MOS) peatland (51°58′55″N/75°24′06″W; Figure 1), are pristine open ombrotrophic raised bogs, dominated by Sphagnum and ericaceous shrubs. The development of these peatlands followed the retreat of the Laurentide Ice Sheet ca 7500 cal BP and took place through depression infilling and paludification at a later stage (van Bellen et al., 2011a). The current mean annual temperature for the region is −2 °C, and one third of the total annual precipitation (ca 0.74 m year−1) falls as snow (Hutchinson et al., 2009). LLC peatland developed in a depression edged by an escarpment, and peat thickness reaches 5 m in its deepest part. At its centre, LLC presents an open area including a few large pools and wet hollows and covers 2.24 km². MOS peatland developed on a relatively flat topographical basin. Its deepest point is found around 3 m. Overall, the peatland surface is much wetter than LLC and is characterized by a series of large pools and wet hollows in its central area. MOS covers 2.67 km². A more detailed description of both sites can be found in van Bellen et al. (2011a).

**Material collected and analyses**

Ecological reconstructions were obtained from central cores located near the thickest section of each peatland using a Jeglum (Box) corer for the first top metre and below that a Russian corer down to the mineral soil. Dry bulk density and organic carbon content were calculated after drying and loss-on-ignition (LOI) of 1-cm³ contiguous subsamples. Plant macrofossil analyses and testate amoeba analyses were performed at 4-cm resolution for each core. The cores were dated with radiocarbon (12 dates for LLC and 10 for MOS) and calibrated with the IntCal04 calibration curve (Reimer et al., 2004). The detailed techniques of analysis and a comprehensive description of the results are presented in van Bellen et al. (2011b).

**Water-table depth reconstruction**

We applied testate amoeba for water-table depth reconstruction. Testate amoebae are unicellular protists characterized by both their species-specific sensitivity to water-table depth and their resistance to decomposition (Mitchell et al., 2008). Identifying amoebae from a peat core allows quantitative reconstructions of the past water-table depths by use of a transfer function (Booth, 2008). The results of the transfer function provide a reconstruction of the peatland water-table depth since its early development. Water-table depths have been reconstructed for LLC and MOS (van Bellen et al., 2011b), with a mean squared error of ±0.11 and ±0.09 m respectively (Figure 3b and c).

**THE FORCING EXERCISE**

**The HPM**

The HPM includes feedbacks between vegetation, peat properties, water-table depth and climate (Figure 2). The model includes 12 plant functional types (PFTs, i.e. groups of species, refer also to Laine et al. (2012)) that together form assemblages. Each PFT has its own relative net primary productivity (NPP) and rate of decomposition and responds in its own way to water-table variations and nutrient status (Appendix Tables AI, AII and AIII). Further details on the physical processes behind the model can be found in Frolking et al. (2010).

**Methods**

To assess the response of the HPM to hydrological changes and to explore the influence of water-table depth on carbon accumulation and vegetation dynamics in the two boreal peatlands, studied by van Bellen et al. (2011a, 2011b), we took the following steps:

- HPM was calibrated to suit the local specificity of the sites using data from van Bellen et al. (2011a);
- HPM was provided with reconstructed precipitation from Viau and Gajewski (2009). One simulation per site was performed;
- HPM was forced with reconstructed water-table depths (van Bellen et al., 2011b); i.e. all components of the water-balance calculation (e.g. precipitation, run-off and evapotranspiration) are ignored, and reconstructed water-table depth values replace the water-balance calculation output in all other sections of the model. One simulation per site was performed.

**Calibration and initiation phase**

The purpose of the calibration is to adjust the model to the specificity of the site to be able to compare the simulation results with datasets from the peat cores. In order to minimize the impact of calibration on the dynamical processes of the model, the calibration parameters were limited to the site-specific parameters. These include region-specific parameters such as precipitation, potential evapotranspiration and potential NPP and site-specific parameters such as run-off, bulk density characteristics and relative NPP values. The calibration was performed with constant precipitation equal to contemporary mean annual precipitation. Once the calibration is chosen for each site, this setting was used to perform two simulations: one simulation with varying precipitation derived from the pollen reconstructions and one simulation with forced water-table depths derived from the testate amoeba reconstructions.
The calibration method chosen here focused on the reconstructed carbon accumulation and vegetation patterns. Therefore, we calibrated HPM against the shape of the bulk density curve of both peatlands that were obtained from LOI analyses. Thus, the parameters driving the shape of the bulk density curve, i.e. the parameters of the error function describing the anoxia, were adjusted. Because the factors driving the persistence of minerotrophic conditions are not yet well understood, parameters have to be estimated for each site. Nonetheless, there are several millions of possible combinations of calibration parameters because the model includes more than a hundred parameters, each potentially taking different values. The results of a sensitivity analysis performed on HPM helped constrain the number of parameters affecting carbon accumulation to a relatively small number (i.e. 26). In order to tally with the sensitivity analysis, each parameter value in this experiment lies within its range of plausible natural variations defined in Quillet et al. (2013a) and Quillet et al. (2013b). The site-specific parameters are in Table AIII of the Appendix.

Some model parameters are directly related to peatland location and hence were estimated from available data. Thus, several parameters were estimated for the region such as annual precipitation (current value ca 0.74 m year\(^{-1}\)) (Hutchinson et al., 2009), annual potential evapotranspiration (current value ca 0.4 m year\(^{-1}\); Canada Centre for Mapping and National Atlas Information Service, 1974) and maximum potential NPP estimated to ca 0.7 kg m\(^{-2}\) year\(^{-1}\) (Del Grosso et al., 2008). With the exception of precipitation, the site-specific parameter values are kept constant during the simulation. In this study, the relative NPP of some PFTs responds to some regional characteristics that differ from the original setting used to simulate the Mer Bleue bog located at a lower latitude (45.40°N) with a mean annual temperature of 6 °C (Frolking et al., 2010). Therefore, similarly to a Finnish experiment (Tuittila et al., 2013) and because the mean
annual temperature at our sites is $-2^\circ C$, the relative NPP of grasses, minerotrophic herbs and minerotrophic sedges has been lowered. Other parameters are ‘peatland specific’ and depend on both local peatland development and how the peatland is influenced by its adjacent environment (e.g. basin shape, nutrient input or hydrology). For the two bogs, we used different simulation lengths based on their basal ages (7562 years for LLC and 6984 years for MOS) and different parameter values for minimum bulk density and maximum bulk density increase (Appendix Table AIII). The two sites present differences in peat thickness at their centre and also different long-term carbon accumulation patterns influenced by both allogenic and autogenic processes (Figure 4). LLC has a concave accumulation curve; i.e. carbon accumulation is rapid during the early development stages and slows down thereafter, whereas carbon accumulation at MOS is nearly linear with time. Carbon accumulation patterns at both sites have been further analysed by van Bellen et al. (2011b). The parameter controlling the decomposition rate of the anoxic compartment, i.e. the length of the anoxia gradient, as well as parameters controlling the shape of the NPP curve (Appendix Table AIV) has a strong influence on carbon accumulation, and they have been adjusted for both sites (Quillet et al., 2013b; Quillet et al., 2013a).

In order to prevent the complete loss of the peat as a result of precipitation variation within the first few decades of a simulation and to develop sufficient peat thickness to keep the water table within the peat for the remainder of the simulation, each HPM simulation begins with an initialization phase, during which peat builds up until it reaches a certain thickness (Frolking et al., 2010). HPM does not simulate the specific details of peatland initiation but of peat accumulation subsequent to this initialization once the site has achieved ‘peatland’ status (in this study, a 10-cm organic layer). Once the ‘peatland status’ is reached, the water balance and the other feedbacks between the different processes are activated for the rest of the simulation. During the initialization phase, the water-table depth is kept constant (to insure that peat accumulates) at a level of 0.07 m below the surface (Frolking et al., 2010). In this study, 0.1 m of peat thickness was required to activate the dynamical processes and the water-balance calculation. This 0.1 m can be compared with the bottom section of the core, in which organic matter is mixed with other sediments and cannot be considered as peat. The peat produced during the initialization phase was thus not included in the final results.

**Addition of precipitation time series to the simulation setting.** For the purpose of representing past climatic variations, HPM offers the possibility to create a random series of mean annual precipitation derived from the current climatic precipitation average. This allows the simulation to be more realistic than constant precipitation but does not enhance the quality of the simulation in term of its historical reconstruction at sub-reconstruction resolution. Moreover, the different evaluations of HPM have shown that precipitation is, among all model parameters, one of the most influential (Frolking et al., 2010; Quillet et al., 2013b; Quillet et al., 2013a).

We thus used the Holocene precipitation reconstruction for the boreal and low arctic regions of Canada from Viau and Gajewski (2009). This reconstruction has been achieved using multiple pollen diagrams and the modern analogue technique. The obtained time series gives precipitation anomalies (i.e. deviations from the present average value) for northern Québec at centennial resolution for the last 9000 years BP. It was applied to both sites.

We built the reconstructed precipitation time series as input in the model by adding the present annual precipitation value (here 0.74 m year$^{-1}$) to these anomalies (Figure 3a). Because it has been shown in Frolking et al. (2010) that simulated accumulation rates were sensitive to persistence in precipitation variability at a centennial timescale rather than at an annual to decadal timescale, no randomization was applied to the annual precipitation series. The precipitation time series are thus based on a linear interpolation of the 100-year reconstruction values. The combination of this series with the calibration settings completes the baseline simulation frame of our two sites, which are hereafter named $P_{LLC}$ and $P_{MOS}$.

**Water-table depth forcing.** In order to highlight the role of the water balance in the simulation results, we also forced the model with water-table depth reconstructions from testate-amoeba assemblages (van Bellen et al., 2011b). The water-table depths have been interpolated according to the age–depth profiles so that the series have yearly resolution (Figure 3b and c). In these simulations, we deactivated the different components of HPM linked to the water-balance calculation so that neither precipitation, nor evapotranspiration, nor run-off and run-on influenced the results (Figure 2). Reconstructed water-table depths from testate amoebae thus replaced the water-table depth values calculated by the water-balance module in the original version of the model. These simulations are designated as $W_{LLC}$ and $W_{MOS}$ in the following sections.

**RESULTS**

**Precipitation and water-table depth**

Reconstructed precipitation based on the study from Viau and Gajewski (2009) and used as input in the simulations is presented in Figure 3a. This dataset does not present error
bars, although error might be important on reconstructed precipitation. However, for the purpose of this study, trends and variations in precipitation are needed, rather than actual precipitation amounts. We thus argue that this dataset can be used as an estimate for our study region during the Holocene. Figure 3b and c respectively present reconstructed water-table depths for LLC and MOS peatlands derived from testate-amoebe analyses (van Bellen et al., 2011b) along with simulated water-table depths. The error for these reconstructions varies depending on species composition and on the degree of decomposition of the peat. The water-table depth and precipitation time series are not expected to show similar trends because precipitation reconstruction from pollen data is a proxy for regional conditions, whereas water-table depth reconstruction from testate amoebe is a proxy for local conditions in peatlands, i.e. accounting for both allogenic climatic influences and autogenic ecohydrological feedbacks (Swindles et al., 2012). However, there were correspondences between them (e.g. around 7000 cal BP, where precipitation decreases and water-table depths in both records tend to increase). Other periods show dissimilar behaviour such as the period of high precipitation around 3750 cal BP (Figure 3a) that was not reflected in the water-table reconstructions (Figure 3b and c). Comparison between the simulated water-table depths in the $P_{LLC}$ and $P_{MOS}$ simulations and reconstructed water-table depths from testate amoebe (Figure 3b and c) showed comparable ranges, amplitudes and also general trends during the past 7000 years, suggesting that the water-balance calculation of the model gives reasonable results. Furthermore, these comparable trends point out the response of testate amoebe to precipitation on a millennial scale. On shorter timescales, however, some periods show clear discrepancies between the curves, for example, around 6000 cal BP at MOS and between ca 2000 and 1000 cal BP at both sites. During these periods, testate amoebe may be responding to other signals, perhaps linked to the fen–bog transition at MOS around 6000 cal BP and to some changes in the regional climatic conditions between 2000 and 1000 cal BP, as identified in other studies (Lamarre et al., 2012; van Bellen et al., 2013), or the model may be misrepresenting climate impacts on water-table dynamics.

**Carbon accumulation**

Accumulated carbon masses resulting from the simulation including reconstructed precipitation and from the water-table depth-forced simulation are presented in Figure 4. For comparison, this figure also presents the accumulated carbon obtained from the LOI analyses of peat cores. Overall, carbon accumulation at LLC (Figure 4a) showed a
concave shape with two periods of higher accumulation between 5500 and 4500 cal BP and during the last millennium, in the uppermost section of the core. Although the model was calibrated on carbon accumulation (i.e. total mass of carbon and basic shape of the carbon accumulation curve), these phases were not reproduced in the simulations, suggesting that they might be associated with other environmental variables or to autogenic processes not represented in HPM. Figure 5 allows the comparison of the annual CARs in more detail. For simplification, these results are identified as CARLLC and CARMOS in the next sections. CARLLC and CARMOS are compared with the carbon content of each cohort (i.e. simulated year) at the end of the simulation on panels a and b and with the net annual carbon balance on panels c and d. On all four panels, simulation results showed extremely high rates of accumulation at the beginning of the simulations. These values were probably artefacts of the initiation phase in HPM, which is less constrained. During the first development phase in LLC (Figure 5a and c), i.e. from ca 7500 to 5600 cal BP, both empirical data analyses and simulations showed similar trends. However, between 5600 and...
2500 cal BP, simulations showed rather constant CARs, and the carbon accumulation slowdown is only replicated in the \( W_{\text{LLC}} \) simulation in panel a. Indeed, \( \text{CAR}_{\text{LLC}} \) presented large fluctuations during this period. Only the water-table-forced simulation \( W_{\text{LLC}} \) showed similar fluctuations suggesting that the calculation of water balance in HPM could not induce these variations in the \( P_{\text{LLC}} \) simulation. For the last 1000 simulation years, accumulated carbon followed again a trend similar to the reconstructions (Figure 4a), and similar fluctuation patterns of the net annual carbon balance are observed for both \( P_{\text{LLC}} \) and \( W_{\text{LLC}} \) (Figure 5c). However, the simulated remaining carbon mass was much lower than the observation during this period (Figure 5a). This suggests that peat decomposition in the acrotelm might be overestimated in the model simulations.

The shape of the MOS cumulated carbon curve (Figure 4b) was very different from the LLC one because carbon accumulated almost linearly over time during the development of this peatland. Still, several periods of slight slowdown between 5500 and 4800 cal BP and between 1900 and 400 cal BP and a short period of faster carbon accumulation around 2000 cal BP were observed. The simulated accumulated carbon curves, on the contrary, presented many fluctuations between 7000 and 4000 cal BP indicating that the simulated initial phase of development was not representative of the original reconstructed conditions on the site. Indeed, CARs for MOS were low and relatively stable between 7000 cal BP and 5600 cal BP, whereas \( P_{\text{MOS}} \) and \( W_{\text{MOS}} \) net annual carbon-balance values varied much during the same period (Figure 5d). The short phase identified around 2000 cal BP and characterized by high CAR was poorly reproduced in the simulations. At the top of the MOS core (i.e. during the past 500 years AD), CAR fluctuated again. Similarly to the LLC results, these variations were reproduced in the net annual carbon balance from the \( W_{\text{MOS}} \) simulation (Figure 5d).

Periods during which decomposition exceeded production resulting in a net loss of carbon can only be identified in the simulation results; losses through decomposition leave no trace in the cores. However, long periods of net carbon loss result in lower CAR as quantified from peat cores. Unfortunately, if CARs fluctuate rapidly (interannual to decadal fluctuations), LOI analyses result in low apparent CARs rather than fluctuations because of the low time resolution of the analyses. \( P_{\text{LLC}} \) and \( P_{\text{MOS}} \) simulations presented large periods of carbon loss: e.g. between 2000 and 1000 cal BP for LLC and between 5800 and 5200 cal BP for MOS (Figure 4). CARs in Figure 5c and d suggested several shorter carbon loss periods. In LLC (Figure 5c), several severe decreases in \( \text{CAR}_{\text{LLC}} \) were characterized by a loss of carbon in the simulations. This was the case at \textit{ca} 7000 cal BP for both \( P_{\text{LLC}} \) and \( W_{\text{LLC}} \) and at \textit{ca} 5300, \textit{ca} 2800 and \textit{ca} 800 cal BP for \( W_{\text{LLC}} \). The \( P_{\text{LLC}} \) simulation generated other carbon loss events between 2000 and 500 cal BP, which coincided with fluctuations in \( \text{CAR}_{\text{LLC}} \). Interestingly, around 5400 cal BP, there was a drastic increase in \( \text{CAR}_{\text{LLC}} \), which was linked to high bulk density and translating into a drastic carbon loss in the \( W_{\text{LLC}} \) simulation. This suggests that the higher bulk density during this period could be associated with a carbon loss. A decrease appeared in \( \text{CAR}_{\text{MOS}} \) around the same period, and important carbon losses were simulated in both \( P_{\text{MOS}} \) and \( W_{\text{MOS}} \). HPM’s configuration for MOS might thus have been less resilient than for LLC simulations, even when the same precipitation reconstructions were used.

For MOS, simulated CARs showed a greater carbon loss frequency (Figure 5d). The \( W_{\text{MOS}} \) simulation showed carbon loss during periods where fluctuations were observed in \( \text{CAR}_{\text{MOS}} \) (e.g. at \textit{ca} 6400 and 100 cal BP). Nevertheless, \( P_{\text{MOS}} \) records important carbon losses at \textit{ca} 3600 and 3100 cal BP that match with \( \text{CAR}_{\text{MOS}} \) but are less severe in the \( W_{\text{MOS}} \) simulation. Around 2500 cal BP, the loss of carbon in the \( W_{\text{MOS}} \) simulation coincided with a large increase in \( \text{CAR}_{\text{MOS}} \): \( W_{\text{MOS}} \) followed here a water-table dropdown imposed by the water-table reconstruction. However, the processes that drove carbon accumulation at MOS during this period were obviously different from the ones included in the model. This could hypothetically be related to a strong and/or periodic influence of runoff and associated increase in nutrient input at the site that cannot be taken into account in the model because it considers that nutrient availability gradually vanishes with peat thickness.

### Vegetation distribution

Plant macrofossils offer another independent dataset that can enhance our system comprehension. A condensed version of the plant macrofossil diagrams is presented in Figures 6a and 7a for LLC and MOS respectively. Detailed plant macrofossil analyses can be found in van Bellen et al. (2011b). Here, the chosen vegetation classes aim at matching the different PFTs of the model for the sake of comparison. Therefore, when macrofossil identification was not sufficiently specific, PFTs were merged. Nevertheless, simulation results in Figures 6 and 7 highlight a strong resilience of PFTs relative to the macrofossil diagrams. For example, although feather mosses occur sporadically and with small percentages in the macrofossil diagrams, they are overrepresented in the simulations.

In LLC (Figure 6a), the fen phase was dominated by a combination of Cyperaceae and ligneous species that followed peatland initiation with an abundance of brown mosses. This fen phase lasted less than 400 years. At \textit{ca} 7200 cal BP, the very sharp fen to bog transition was completed, and \textit{Sphagnum} species (mainly section...
Acutifolia dominated the profile. In general, Sphagnum section Acutifolia remained dominant through time, although wetter Sphagnum species along with Cyperaceae occurred episodically.

In MOS (Figure 7a), the fen phase was largely dominated by Cyperaceae and lasted more than 1500 years. The fen to bog transition was gradual until Sphagnum section Acutifolia finally dominated the profile around 4700 cal BP. Contrasting
with the general stability of the LLC sequence, the MOS profile showed a periodic changeover of wet and dry plant assemblages, representative of the responsiveness to hydrological changes of this site.

The PLLC and WLLC simulation results (Figure 6b and c) start with a peatland initiation phase dominated by herbs and sedges rather than brown mosses. The simulated fen to bog transition was very gradual and not representative of the observed stepwise development at LLC. In the later phases, the vegetation was composed of both lawn and hummock Sphagnum species, which include Sphagnum section Sphagnum that are relatively less important in the LLC macrofossil record (Figure 6a). In general, the simulated vegetation was rather hydrophilous, and the xerophilous species (such as ligneous plants) were more resistant to changes than the macrofossil dataset would suggest. However, the general vegetation distribution pattern was well reproduced.

Looking in more detail at the vegetation sequence, some differences between PLLC and WLLC could be detected. In the WLLC simulation, hollow Sphagnum increased between 5200 and 4500 cal BP suggesting wetter conditions. However, no important change in vegetation occurred in the PLLC simulation or in the plant macrofossils. This suggests once again the important resilience of Sphagnum section Acutifolia species to changes in water-table depth, which is captured well in the model. On the other hand, at ca 5800, around 2500, and 1500 cal BP, the WLLC simulation captured the wet phases detected in the macrofossil assemblages, while PLLC only recorded a very wet phase between 2000 and 1000 cal BP. The wetter phases at ca 4000 and 500 cal BP were better represented in the PLLC simulation than in the WLLC simulation.

Similarly to the LLC results, the initiation phase in the PMOS and WMOS simulations showed a dominance of herbs and sedges. In the WMOS simulation, hydrophilous mosses occurred at levels where brown mosses were found in the macrofossil records. However, their abundance was exaggerated in the simulation, on the contrary to LLC results. During the bog phase (since ca 5500 cal BP), the alternation of wet and dry phases was represented by smooth variations in the Acutifolia versus Sphagnum sections in the plant assemblage. In both simulations, variations affected hollow Sphagnum and occasionally hydrophilous mosses. The simulated vegetation for the MOS site was strongly resilient to changes.

In the PMOS simulation, the appearance of hollow Sphagnum was in agreement with the macrofossil assemblages at 3300 and 2500 cal BP and matches also with several periods where Sphagnum section Sphagnum arise in the profile (e.g. around 3700 and between 1800 and 1300 cal BP). In the WMOS simulation, the small increases in the abundance of hollow Sphagnum and hydrophilous mosses also coincided with wetter periods in the macrofossil dataset (e.g. around 4700, between 3000 and 3500 and at ca 400 cal BP and at the top of the core). Here again, although some humid or wet phases were recorded simultaneously between 3900 and 2500 cal BP, PMOS and WMOS showed many asynchronous features along the profile.

**DISCUSSION**

Our results showed that, when calibration is carefully performed, peatland development is reasonably reproduced by HPM. The water-balance calculation of HPM delivered a water-table depth in agreement with the testate-amoeoba reconstructions, and CARs showed ranges comparable with those resulting from the LOI analyses. Variations in the macrofossil records were better represented in the PLLC and WLLC simulations than in the PMOS and WMOS simulations. The comparison between the results of the two sites presenting different geomorphic and ecohydrological conditions highlighted the capacity of the model to simulate different peatland development patterns. Differences in simulation representativeness, however, might be linked to the limitations of both the model and the experiment calibration.

**Model limitations**

Peatland initiation, as highlighted in the previous section, was not well reproduced in the simulations. Several factors limit its predictive power. The geomorphic characteristics of the sites and regions are not taken into account in HPM. Moreover, fen to bog transition in HPM is gradual, and minerotrophic species such as grasses or herbs remain present in the assemblage for several thousand years after the Sphagnum establishment. This behaviour is not recorded in the macrofossil assemblages. In HPM, the transition is driven by peat accumulation solely and thus cannot be abrupt. We observed this inability of HPM to produce abrupt transitions also in a chronosequence of several mires (Tuittila et al., 2013).

When looking at the carbon accumulation results, the variability of the PLLC and WLLC simulations was reduced in comparison with the simulations for the MOS site, which showed large variability (Figure 5d). The opposite was observed in the simulated vegetation distributions, where the PLLC and WLLC simulations showed a much greater variability than the PMOS and WMOS simulations (Figures 6 and 7). These behaviours are probably related to the differences in anoxia gradient parameterization in both sites (Appendix Table III). In the current version of HPM, the representation of the anoxia gradient highly depends on the decision of the user; i.e. parameter
values have to be chosen, and no comparable site data are so far available to estimate these values. This creates an important source of uncertainty in the simulations.

Additionally, differences in the parameter estimating the minimum profile relative transmissivity probably affected the results (Appendix Table III). At MOS, this value was high, and hence, water-table depth fluctuated rapidly in comparison with LLC (Figure 3b and c). Rapid changes in the water-table depth of the Pmos simulation also affected CARs, which therefore showed rapid shifts in MOS (Figure 5b). Unfortunately, the minimum profile relative transmissivity value had to be kept high in order to limit the total carbon mass and to insure that the simulation remained representative of the MOS site. This parameter was already identified as a cause of uncertainty in the results from a sensitivity analysis of HPM (Quillet et al., 2013b; Quillet et al., 2013a).

The limitations presented here collectively suggest that ecohydrological processes are the weak area in our understanding of peatland dynamics and its representation on process-based models. Knowledge of the anoxia gradient, the relative transmissivity and the fen to bog transition needs to be enhanced in order to improve calibration and most probably also the representativeness of the model results.

The role of water-table depth forcing in the simulation results

In the case of carbon accumulation, simulations with reconstructed precipitation tended to be smooth or to show isolated peaks that lasted only a couple of years (Figure 5). The comparison between reconstructed precipitation and reconstructed water-table depths from testate amoebae (Figure 3) highlights both the independence of the two records and the complexity of their response. The relationship between water-table depth and precipitation at this timescale appeared to be nonlinear. Indeed, changes in water-table depth in a peatland can occur for several reasons independently from precipitation: other climatic changes (e.g. temperature and evapotranspiration), disturbances (e.g. fire), autogenic changes (e.g. fen–bog transition, lateral expansion, etc.) and hydrological changes.

Accumulated carbon in P LLC diverges during 3000–1000 BP, which is when the water-table depth reconstruction is in poorest agreement with pollen reconstruction (Figures 3b and 4a). On the other hand, accumulated carbon in P MOS does not diverge much from the core data, while W MOS diverges during 6500–5500 BP, when the simulated water-table depth is in poorest agreement with testate-amoeba reconstruction (Figures 3c and 4b). It can thus not be argued that water-table depth forcing provided, overall, better results in terms of carbon accumulation than the simulation driven by reconstructed precipitation.

Contrary to our expectations, the forcing experiment did not indubitably improve the representation of the vegetation distribution. While W LLC results seem to be in greater agreement than P LLC with macrofossil data, W MOS clearly failed to represent the major variations in macrofossils. In fact, MOS peatland presents a great variability in macrofossil records but also presents a flatter topographical basin than LLC and is thus subject to less effective drainage (van Bellen et al., 2011a). Plant macrofossils showed that the MOS site has been very sensitive to hydrological variations.

Moreover, prescribed water-table depths have a strong influence on HPM plant assemblages. In the W MOS simulation, there is little variability in the simulated plant community composition after the fen stage, while in the W LLC simulation, vegetation variability is mostly between Sphagnum species (Figures 6c and 7c). In the cores from these sites, however, there is much more variability, particularly in the woody vegetation fraction (Figures 6a and 7a). This indicates that PFT composition in HPM may be too stable; the smooth functional dependence on water table and peat depths (Frolking et al., 2010) misses some important control on plant community dynamics, e.g. species interactions.

Additionally, the lack of representation of the variability in the model results might be related to the poor resolution of the testate-amoeba dataset. Indeed, 4-cm resolution is coarse and cannot capture rapid (i.e. decadal to centennial) changes in testate-amoeba assemblages, which are known to respond very rapidly to water-table fluctuations (Warner et al., 2007; Mitchell et al., 2008). Water-table reconstructions based on testate-amoeba analyses at higher resolution would be helpful to assess the role of the water-table forcing on the model results. Moreover, the resilience to changes varies between proxies; e.g. plant assemblages respond with a lag of decades and appear generally buffered to changes in water table via self-regulation of moisture content and the competition between species (Viliranta et al., 2012). Nonetheless, HPM will not simulate rapid and large shifts in vegetation composition without equivalently rapid and large shifts in water-table depth. The causes of variability in the simulation results should be further investigated in order to assess the role of calibration and of site specificity in these processes.

Long-term net carbon loss

One major finding of this study, the loss of carbon during the peatlands’ history was emphasized by the several periods of long-term carbon loss occurring in the simulation results. Some of these periods occurred in the simulation runs with precipitation reconstructions, others in the simulations forced with water-table reconstructions, and they appeared in the simulations of both sites. Several studies focusing on the contemporary net carbon balance of peatlands highlight the great interannual variability of the carbon balance that can result into a change from a net sink to a net source (e.g. Alm et al., 1999; Roulet et al., 2007; Nilsson et al., 2008; Koehler et al., 2011). For example, Roulet...
et al. (2007) measured the carbon balance at Mer Bleue Bog in Canada during 6 years and estimated that values can vary between a carbon gain of 105 g m$^{-2}$ year$^{-1}$ and a carbon loss of 50 g m$^{-2}$ year$^{-1}$. Although these values are only available for relatively short time periods (less than a decade), these results are in the same range of amplitudes as our simulation results (Figure 5c and d). This gives us confidence that the representation of carbon loss phases in the HPM simulation, although they cannot be validated against field data, was plausible. Other processes may have an impact on the net carbon balance on a millennial timescale such as vegetation shifts, but lacking data make it difficult to evaluate this behaviour in the model. Yu (2011) interpreted carbon fluxes of peatlands from different regions all over the globe using the available basal dates and carbon accumulation profiles. He found that the net carbon balance in the northern peatlands showed large fluctuations during the Holocene and periods of long-term net carbon loss occurring in tropical peatlands.

**Tracing vegetation history in relation to climate and other forcing**

Considering that the HPM simulations have limitations and that the model is designed to reproduce large-scale patterns of peatland development, we argue that the proper reproduction of a vegetation shift in a simulation implies that the processes responsible for this shift are included in the model. As a corollary, simulation results can be helpful at identifying the causes of shifts and variations in the macrofossil dataset. However, caution is advised in the historical interpretation of the results because the chronology of our sites is coarse and because the results are also compared with the pollen reconstruction from Viau and Gajewski (2009) based on a different chronology and including some error.

For example, between 4100 and 3900 cal BP, both macrofossil records (Figures 6a and 7a) indicated a change in vegetation towards more hydrophilous plant associations. Both present a decline in Sphagnum section Acutifolia in LLC with an increase in Cyperaceae, ligneous fragments and hydrophilous Sphagnum species. During this period, both LLC and MOS recorded decreasing trends in CAR (Figure 5), associated with decreases in bulk density, and a high amount of unidentified organic matter (Figures 6a and 7a). Moreover, during this period, the carbon accumulation showed a slowdown for P$_{MOS}$ and high carbon loss for W$_{MOS}$ (Figure 5d). In agreement with our results, the synthesis from Garneau et al. (in press) reports a general decrease in peat accumulation rates from 4000 cal BP in different boreal peatlands located on the Québec province territory.

At that time, around 4000 cal BP, reconstructed water-table depths were ~0.15 m at both sites, although the MOS water table was declining (Figure 3b and c). Additionally, a period of increased precipitation occurred slightly earlier (i.e. ca 4200 cal BP) and reached its maximum around 3800 cal BP (Figure 3a). The results of the water-table depth forcing (Figures 6c and 7c) did not record any major variation in the vegetation during this period. However, the P$_{LLC}$ and P$_{MOS}$ simulations showed a clear decline of hummock Sphagnum to the favour of more hydrophilous PFTs (and of ombrotrophic herbs in the case of P$_{LLC}$). The increase in precipitation might thus be involved in the sudden vegetation change towards wetter associations in both LLC and MOS around 4000 cal BP. HPM was unable to capture these dynamics.

Between ca 6000 and 5700 cal BP, MOS presented a shift in vegetation with increasing Cyperaceae to the detriment of ligneous species (Figure 7a). This wet shift coincides with the observed slight decrease in CARs reconstructed from the LOI analyses (Figure 5b). Simulated vegetation distributions showed a large presence of hydrophilous mosses and hollow Sphagnum in the W$_{MOS}$ simulation (Figure 7c), but no drastic vegetation change is observed in the P$_{MOS}$ simulation (Figure 7b). Because only water-table-forced simulations could reproduce this vegetation shift, we argue that precipitation was probably not a major control on vegetation dynamics during this period. Moreover, a fire-induced change resulting in a wet shift (Sillasoo et al., 2011; Morris et al.,) can probably be dismissed because no fire has been recorded at MOS during this period, and fire frequencies were low in the region (van Bellen et al., 2012). This event could thus be related to autogenic changes in the MOS peatland such as a local change in hydrology.

**Multiple proxies**

Regarding both carbon accumulation and vegetation distribution results, we observe that certain events (i.e. periods of carbon loss and dry or wet periods in the plant assemblages) are replicated in the simulations with reconstructed precipitation, and others are rather replicated when HPM’s water-table depth is forced. This suggests that the two simulation experiments supplement each other. As usually highlighted in palaeoecological studies, we observe that the use of multiple proxies, each of them characterized by a specific sensitivity to allogenic and autogenic changes, can be useful in modelling studies to reproduce the historical changes in a peatland. Moreover, using multiple proxies from the same peat core (and thus following the same age–depth model) as input in the model eliminates errors associated with tuning (Blaauw, 2012). This exercise facilitates comparison between results from different proxies.

**CONCLUSION**

The dynamic response of peatlands to ecohydrological changes has been assessed by the comparison of two simulation experiments on the development of two peat bogs located in the James Bay region in North-eastern Canada, with the help of a reconstructed precipitation time series and with a
forcing of the water-table depth reconstructed from testate-amoebo analyses. These simulations allowed the comparison between regional signals and local conditions taking both allogenic and autogenic signals into account.

In this study, HPM simulated phases of carbon loss corresponding to periods of low or sharp decrease in CARs that are comparable with contemporary carbon gas flux measurements. Moreover, the results highlight the capacity of HPM to reproduce general patterns in two peatlands presenting different geomorphic and hydrological conditions influencing the ecological response while pointing out the weakness in the knowledge on peatland ecohydrological processes.

The differences in the model responses that we found between sites stress the important heterogeneity between peatlands located in the same region; this heterogeneity makes large-scale modelling challenging. The successful simulation of variations observed in the paleorecords indicates that the model comprehends the representation of processes driving these variations. Thus, we conclude that the methodology applied here can be used to help distinguish the various causes of carbon accumulation shifts in paleoecological studies.

ACKNOWLEDGEMENTS

The authors acknowledge Dr Alain Tremblay (Environment Production, Hydro-Québec) for logistic and financial support within the Eastmain-I project, Dr Zicheng Yu, Dr Lisa Belyea, Dr Marie Larocque and Dr Andy Baird for their helpful comments on the manuscript. AQ was supported by funds from the Canadian Foundation for Climate and Atmospheric Sciences, by funds supporting the Chaire Déclique at GEOTOP – Université du Québec à Montréal (MG, SvB). SF was supported by a National Science Foundation grant ATM-0628399, EST by the Academy of Finland (218101).

APPENDIX HPM PARAMETERS: DESCRIPTION AND VALUES.

Differences between sites are in bold type.

Table A1. PFT-specific parameter description.

<table>
<thead>
<tr>
<th>PFT-specific parameter description</th>
<th>Units</th>
<th>Symbol</th>
</tr>
</thead>
<tbody>
<tr>
<td>Peat depth for optimum productivity</td>
<td>m</td>
<td>$h_{\text{opt}}^{\text{PDi}}$</td>
</tr>
<tr>
<td>Productivity range around the optimum</td>
<td>m</td>
<td>$\sigma_{\text{PDi}}^{\text{PDi}}$</td>
</tr>
<tr>
<td>WTD for optimum productivity</td>
<td>m</td>
<td>$Z_{\text{opt}}^{\text{WTI}}$</td>
</tr>
<tr>
<td>Productivity range around the optimum</td>
<td>m</td>
<td>$\sigma_{\text{WTI}}^{\text{WTI}}$</td>
</tr>
<tr>
<td>Relative net primary productivity (NPP)</td>
<td>–</td>
<td>NPP$^{\text{rel}}$</td>
</tr>
<tr>
<td>Above-ground NPP</td>
<td>–</td>
<td>AG$^{\text{frac}}$</td>
</tr>
<tr>
<td>Decomposition rates</td>
<td>year$^{-1}$</td>
<td>$k_0$</td>
</tr>
</tbody>
</table>

Table AII. PFT-specific parameter values for LLC.

<table>
<thead>
<tr>
<th>PFT ID</th>
<th>$Z_{\text{opt}}^{\text{WTI}}$</th>
<th>$\sigma_{\text{WTI}}^{\text{WTI}}$</th>
<th>$\sigma_{\text{opt}}^{\text{WTI}}$</th>
<th>$h_{\text{opt}}^{\text{PDi}}$</th>
<th>$\sigma_{\text{PDi}}^{\text{PDi}}$</th>
<th>$\sigma_{\text{opt}}^{\text{PDi}}$</th>
<th>NPP$^{\text{rel}}$</th>
<th>AG$^{\text{frac}}$</th>
<th>$k_0$ (year$^{-1}$)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Grass</td>
<td>1</td>
<td>0.40</td>
<td>0.40</td>
<td>0.40</td>
<td>0.01</td>
<td>1.00</td>
<td>0.90</td>
<td>0.55</td>
<td>0.50</td>
</tr>
<tr>
<td>Minerotrophic herb</td>
<td>2</td>
<td>0.10</td>
<td>0.30</td>
<td>0.30</td>
<td>0.30</td>
<td>1.00</td>
<td>0.90</td>
<td>0.55</td>
<td>0.50</td>
</tr>
<tr>
<td>Minerotrophic sedge</td>
<td>3</td>
<td>0.10</td>
<td>0.40</td>
<td>0.40</td>
<td>0.10</td>
<td>2.00</td>
<td>1.50</td>
<td>0.75</td>
<td>0.20</td>
</tr>
<tr>
<td>Minerotrophic shrub</td>
<td>4</td>
<td>0.20</td>
<td>0.20</td>
<td>1.00</td>
<td>1.00</td>
<td>2.00</td>
<td>1.50</td>
<td>0.50</td>
<td>0.50</td>
</tr>
<tr>
<td>Brown moss</td>
<td>5</td>
<td>0.01</td>
<td>0.20</td>
<td>0.05</td>
<td>0.10</td>
<td>1.50</td>
<td>1.50</td>
<td>0.50</td>
<td>1.00</td>
</tr>
<tr>
<td>Hollow Sphagnum</td>
<td>6</td>
<td>0.01</td>
<td>0.20</td>
<td>0.15</td>
<td>2.00</td>
<td>1.50</td>
<td>19.00</td>
<td>0.50</td>
<td>1.00</td>
</tr>
<tr>
<td>Lawn Sphagnum</td>
<td>7</td>
<td>0.10</td>
<td>0.06</td>
<td>0.40</td>
<td>2.00</td>
<td>1.50</td>
<td>19.00</td>
<td>0.50</td>
<td>1.00</td>
</tr>
<tr>
<td>Hummock Sphagnum</td>
<td>8</td>
<td>0.20</td>
<td>0.10</td>
<td>0.50</td>
<td>2.00</td>
<td>1.50</td>
<td>19.00</td>
<td>0.50</td>
<td>1.00</td>
</tr>
<tr>
<td>Feather moss</td>
<td>9</td>
<td>0.40</td>
<td>0.40</td>
<td>0.60</td>
<td>4.00</td>
<td>6.00</td>
<td>19.00</td>
<td>0.25</td>
<td>1.00</td>
</tr>
<tr>
<td>Ombrotrophic herb</td>
<td>10</td>
<td>0.20</td>
<td>0.20</td>
<td>0.20</td>
<td>4.00</td>
<td>2.00</td>
<td>19.00</td>
<td>0.25</td>
<td>0.50</td>
</tr>
<tr>
<td>Ombrotrophic sedge</td>
<td>11</td>
<td>0.20</td>
<td>0.30</td>
<td>0.30</td>
<td>4.00</td>
<td>2.00</td>
<td>19.00</td>
<td>0.50</td>
<td>0.20</td>
</tr>
<tr>
<td>Ombrotrophic shrub</td>
<td>12</td>
<td>0.30</td>
<td>0.30</td>
<td>1.00</td>
<td>4.00</td>
<td>2.00</td>
<td>19.00</td>
<td>0.50</td>
<td>0.50</td>
</tr>
</tbody>
</table>
REFERENCES


