

# Modeling Northern Peatland Decomposition and Peat Accumulation

Steve Frolking,<sup>1\*</sup> Nigel T. Roulet,<sup>2,3</sup> Tim R. Moore,<sup>2,3</sup>  
Pierre J. H. Richard,<sup>3,4</sup> Martin Lavoie,<sup>4</sup> and Serge D. Muller<sup>3,4</sup>

<sup>1</sup>*Institute for the Study of Earth, Oceans, and Space, University of New Hampshire, Durham, New Hampshire 03824, USA;*

<sup>2</sup>*Department of Geography, McGill University, 805 Sherbrooke Street West, Montreal, Quebec, H3A 2K6, Canada;* <sup>3</sup>*Centre for Climate and Global Change Research, McGill University, 805 Sherbrooke Street West, Montreal, Quebec, H3A 2K6, Canada;*

<sup>4</sup>*Département de Géographie, Université de Montréal, C.P. 6128, Montréal, Quebec, H3C 3J7, Canada*

## ABSTRACT

To test the hypothesis that long-term peat accumulation is related to contemporary carbon flux dynamics, we present the Peat Decomposition Model (PDM), a new model of long-term peat accumulation. Decomposition rates of the deeper peat are directly related to observable decomposition rates of fresh vegetation litter. Plant root effects (subsurface oxygenation and fresh litter inputs) are included. PDM considers two vegetation types, vascular and nonvascular, with different decomposition rates and aboveground and belowground litter input rates. We used PDM to investigate the sensitivities of peat accumulation in bogs and fens to productivity, root:shoot ratio, tissue decomposability, root and water table depths, and climate. Warmer and wetter conditions are more conducive to peat accumulation. Bogs are more sensitive than fens to climate conditions. Cooler and drier conditions lead to the lowest peat accumulation when productivity is more temperature sensitive than decomposition rates. We also compare peat age–depth profiles to field data. With a very general parameter-

ization, PDM fen and bog age–depth profiles were similar to data from the the most recent 5000 years at three bog cores and a fen core in eastern Canada, but they overestimated accumulation at three other bog cores in that region. The model cannot reliably predict the amount of fen peat remaining from the first few millennia of a peatland's development. This discrepancy may relate to nonanalogue, early postglacial climatic and nutrient conditions for rich-fen peat accumulation and to the fate of this fen peat material, which is overlain by a bog as the peatland evolves, a common hydrosere succession in northern peatlands. Because PDM sensitivity tests point to these possible factors, we conclude that the static model represents a framework that shows a consistent relationship between contemporary productivity and fresh-tissue decomposition rates and observed long-term peat accumulation.

**Key words:** peatland; decomposition; carbon accumulation; model; peat.

## INTRODUCTION

Peatland ecosystems accumulate carbon because annual net primary productivity (NPP) of the peatland vegetation generally exceeds the annual de-

composition of litter and peat. Relative to other ecosystems, northern peatlands have low rates of NPP (Thormann and Bayley 1997), decomposition (Brinson and others 1981; Bartsch and Moore 1985; Johnson and Damman 1993; Belyea 1996; T. R. Moore unpublished), and net carbon dioxide (CO<sub>2</sub>) exchange (Frolking and others 1998), but over millennia NPP has been greater than decomposition. Hence, northern peatlands have been a

Received 19 June 2000; accepted 24 January 2001.

*Current address for M. Lavoie:* Centre d'Etudes Nordiques, Université Laval, Pavillon Abitibi-Price, Sainte-Foy, Quebec, G1K 7P4, Canada

\*Corresponding author; e-mail: steve.frolking@unh.edu

persistent sink for CO<sub>2</sub>, averaging 0.02 to 0.03 kg CO<sub>2</sub>-C m<sup>-2</sup> y<sup>-1</sup> over the past 5000–10,000 years (Gorham 1995; Tolonen and others 1992). This has resulted in 200–450 Pg C being sequestered in about 3.5 million km<sup>2</sup> of northern peatlands (Gorham 1991). Slow decomposition rates in northern peatlands result from the combined effects of limited oxygen diffusion into saturated peat leading to anoxic conditions for a large portion of the peat profile (Clymo 1992); the inherent resistance to decomposition of some peatland vegetation tissues, particularly *Sphagnum* (see, for example, Johnson and Damman 1993; Hogg 1993); and generally cool temperatures of peat (Puranen and others 1999). Clymo (1984) hypothesized that the accumulation of peat has a theoretical limit because even very low decomposition rates applied to an ever-increasing mass of peat will eventually approach and equal NPP. The rate of decomposition in the anoxic zone of the peatland and the long-term NPP ultimately control the time it takes for a peatland to grow and the final mass of carbon stored in a peatland.

In Clymo's peat models (Clymo 1984, 1992), a constant water table depth divides the peat profile into a surface oxic zone (or acrotelm), where faster aerobic decomposition pathways dominate, and a deeper anoxic zone (or catotelm), where slower, anaerobic decomposition occurs. These peat accumulation models do not explicitly simulate the mass balance of the surface, oxic peat; instead they are models of catotelm peat accumulation and assume that the acrotelm is a constant mass that "floats" on top of the accumulating catotelm. Litter mass loss during passage through the oxic zone is typically 80%–90% (Clymo 1992); therefore, the input of mass to the anoxic zone would be 10%–20% of total vegetation litter production. The anoxic zone or catotelm peat decomposes very slowly, at roughly 0.1% of the oxic zone rate (Belyea and Clymo 1999). In one formulation (Clymo 1984), the input and decomposition rates are assumed to be constant, and the accumulation of peat in the anoxic zone is modeled as

$$\frac{dM}{dt} = P^* - kM \quad (1)$$

where  $M$  is the peat mass,  $P^*$  is the input to the anoxic zone, and  $k$  is the anoxic zone decomposition rate. Peat continues to accumulate at an ever-declining rate until, barring major disturbances, it eventually reaches steady state:

$$M(t) = \frac{P^*}{k} (1 - e^{-kt}) \xrightarrow[t \rightarrow \infty]{} \frac{P^*}{k} \quad (2)$$

The mass,  $M$ , is the catotelm mass, which is usually a large majority of the total peat. Values for the two parameters  $P^*$  and  $k$  are not directly derived from nor comparable to any measurements of peatland vegetation productivity or fresh-tissue decomposition. Instead they are empirically determined by fitting this equation to age–depth profile data of catotelm peat (Clymo 1984, 1992; Clymo and others 1998).

The Peat Decomposition Model (PDM) was developed with the primary objective of testing the hypothesis that long-term peat accumulation is consistent with observed rates of vegetation productivity and fresh-tissue decomposition. Like the model of Clymo (1984), PDM is a static model simulating long-term peat accumulation and age–depth profiles under constant conditions (NPP and water table depth). We extend the work of Clymo by modeling the complete acrotelm/catotelm peat profile. Decomposition rates down the peat profile are directly linked to observable initial mass-loss rates of fresh peat litter tissue, which have been measured for numerous peatland plant tissues (for example, see Belyea 1996; Johnson and Damman 1993; Hogg 1993; Bartsch and Moore 1985). Mass input rates for the model are equal to observable litter production of peatland vegetation. We also directly simulate the effects of plant roots, which deliver both fresh litter and oxygen some distance down the peat profile. Finally, PDM considers two vegetation types, vascular and nonvascular, with different initial decomposition rates and different aboveground and belowground litter input rates that can thus be used to explore the influence of vegetation type on peat accumulation. The inclusion of both roots and two vegetation types allows the model to simulate both bogs (with fewer root inputs generally above the mean water table and, typically, a higher fraction of moss inputs) and fens (with more root litter inputs going deeper than the mean water table and, typically, a lower fraction of moss inputs). Our objective in this initial model development is to explore how well such a simple static model can produce reasonable peat age–depth profiles without curve fitting, using parameters representing mean peatland characteristics, based on field and laboratory measurements. We use sensitivity analyses and comparisons with a selection of field-based age–depth profiles with known individual paleoecological histories.

## MODEL

Most models of soil organic matter dynamics aggregate the accumulated organic matter into one or several pools. The pools can have characteristic and constant decay rates, or they can have a time-varying decay rate that is a function either of time or some characteristic of the organic matter pool, such as its lignin–nitrogen ratio (for example, see review by Paustian and others 1997). Ågren and Bosatta (1996b) have developed a theoretical approach in which the dynamics of litter quality (related to its susceptibility to decomposition) and soil carbon are linked by coupled differential equations through the activity of the decomposer community. Under certain simplifying assumptions, their model can be solved analytically for the mean quality of an aggregated continuum of litter cohorts of varying quality, and this quality can be related to chemical fractionations of the organic matter (Ågren and Bosatta 1996a).

There are two characteristics of peatlands, however, that favor an explicit modeling of individual cohorts. First, accumulating organic matter in a peatland develops a well-defined stratigraphy, with minimal bioturbation, so age–depth profiles are generally monotonic, with the oldest peat at the base of the profile. Second, there is a very steep and relatively stable gradient in the conditions for decomposition because the deeper peat is continuously saturated, while the shallowest peat is often drained. In a typical northern bog, the top 0.2–0.4 m will be oxic for much of the year, whereas the peat below about 0.4–0.6 m will be anoxic. Therefore, there is a strong correlation between cohort age (and thus degree of decomposition) and the conditions to which the cohort is exposed. Because of this, we chose to develop an annual cohort model of decomposition in which the fate of each year's litter input (a cohort) is tracked as the peat continues to accumulate above it.

PDM operates at an annual time step, with aboveground litter input deposited as an annual litter cohort at the top of the existing peat profile. Root litter inputs also occur every year and are added to upper cohorts, down to the bottom of the rooting zone. These amended cohorts now contain litter of multiple ages, mixing older surface litter with younger root litter, and hereafter are called "peat layers". The vegetation is assumed to be in steady state, so aboveground litter production equals aboveground NPP, and root litter production equals root NPP. Annual peat layers in the rooting zone lose mass through decomposition, but they also gain mass from the root litter input. All peat

layers below the rooting zone only lose mass. PDM variables for each peat layer are mass, bulk density, depth, age, and decomposability. PDM was developed assuming constant NPP. Constant initial decomposition rates were used for each litter type, and these rates decreased as a simple function of peat layer mass loss, representing an increasing recalcitrance or decreasing quality (Ågren and Bosatta 1996a, b) of the remaining mass of the peat layer as it moves deeper into the peat. Decomposition rates are subsequently modified to reflect the influence of the soil climate at the depth of each peat layer. These simplifying assumptions permit an analytical solution of the equations of state of the peat layer mass and thickness, which can be solved iteratively from the top to the bottom of the peat profile. Input variables are aboveground and belowground NPP, water table and rooting depths, and the peatland age (Table 1), all based on field observables. Model parameters are the initial decomposability of the litter types, degree of anaerobicity at depth, and effect of temperature with depth (Table 1), again all based on field and laboratory measurements. The model has no free parameters to be used to fit age–depth profile data; hence, the model is not calibrated. PDM output is the mass and decomposability of peat for each age peat layer. Using a prescribed density profile, PDM can calculate peat layer thickness. The mass and thickness of each peat layer can be summed to obtain total mass and depth of accumulated peat or used to generate age–depth profiles.

## Decomposition

A general formulation for decomposition of a mass of organic matter,  $m$ , is

$$\frac{dm(t)}{dt} = -k_0 m_0 \left( \frac{m(t)}{m_0} \right)^\alpha \quad (3)$$

where  $m_0$  is the initial mass and  $k_0$  is the decomposition or mass loss rate at  $t = 0$ . If the parameter  $\alpha$  equals 1.0, this simplifies to simple exponential decay, as in the second term in Eq. (1). Otherwise, a general solution is given by

$$m(t) = \frac{m_0}{[1 + (\alpha - 1)k_0 t]^{1/(\alpha-1)}} \quad (4)$$

Clymo and others (1998) have shown that when fitting peat core data from 310 bogs and fens from southern Finland, they can get roughly equivalent goodness of fit with  $\alpha = 1, 2$ , or 3. Because there is strong evidence that the fractional loss rate of a decomposing tissue declines with time (Heal and

**Table 1.** Model Parameters and Values for Base Case Scenarios

Parameter	Description	Units	Values for Base Case*		Model Sensitivity**		References
			Bog	Fen	Bog	Fen	
$m_{s,a}$	Vascular vegetation surface litter input	$kg\ m^{-2}\ y^{-1}$	0.2	0.3	+	+	Thormann and Bayely 1997
$m_{r,a}$	Vascular vegetation root litter input	$kg\ m^{-2}\ y^{-1}$	0.2	0.3	+	+	Backéus 1990
$Z_R$	Vascular vegetation rooting depth below water table	$m$	0.0	0.25	+	—	Backéus 1990; Saarinen 1996
$k_{o,a}$	Vascular vegetation initial mass loss rate	$y^{-1}$	0.2	0.2	—	—	T.R. Moore unpublished
$m_{s,b}$	Moss surface litter input	$kg\ m^{-2}\ y^{-1}$	0.2	0.1	++	+	Moore 1989
$k_{o,b}$	Moss initial mass loss rate	$y^{-1}$	0.05	0.08	—	—	T.R. Moore unpublished
$Z_{WT}$	Mean water table depth	$m$	0.3	0.05	—	0	Ingram 1983; Verry and others 1988; Siegel 1993
$Z_{anox}$	Thickness of oxic–anoxic transition zone below root zone	$m$	0.05	0.0	—	n.a.	Lähde 1967
$f_{anox}$	Anaerobic: aerobic decomposition ratio	—	0.025	0.1	—	—	Scanlon and Moore 2000
$\Delta T$	Reduction in rate of decomposition due to temperature profile	—	0.2	0.2	0	0	P. Lafleur unpublished
$A$	Peat age	$y$	8000	8000	+	+	—
$P_o$	Bulk density at surface (minimum)	$kg\ m^{-3}$	50	50	—	—	Boelter 1968, Ivanov 1981; Irwin 1968
$P_{bot}$	Bulk density at depth (maximum)	$kg\ m^{-3}$	100	100	0	0	Boelter 1968, Ivanov 1981; Irwin 1968

++, strong positive correlation; +, moderate positive correlation; 0, weak correlation; —, weak negative correlation; —, strong negative correlation; n.a., not applicable

\*These default values are not meant to represent any specific peatland, but rather to be generally representative of these two broad peatland classes bog and fen.

\*\*Sensitivities are for changes in each parameter value of up to  $\pm 30\%$ , with other parameters held constant.

others 1997),  $\alpha$  should be greater than 1. For simplicity we have chosen  $\alpha = 2$ , so the model has a solution of the peat layer mass as a function of time:

$$m(t) = \frac{m_0}{1 + k_0 t} \quad (5)$$

and an effective decomposition rate of

$$k(t) = k_0 \frac{m(t)}{m_0} = \frac{k_0}{1 + k_0 t} \quad (6)$$

Note that after 1 year of decomposition  $m(1) = m_0/(1 + k_0)$ . In the first few years of decomposition, this function is similar to the simple exponential decay, but the decomposition rate slows as decomposition progresses (that is, it slows with time). If this formulation is combined with a constant input (as in the first term in Eq. [1]), it would lead

logarithmically to an infinite accumulation of peat, given infinite time. This time-dependent functional form of the decomposition rate is the same form as the decline in litter quality with time in one representation of the more general decomposition model of Ågren and Bosatta (1996b) with  $\alpha = 2$ .

Litterbag decomposition studies provided initial mass loss rates,  $k_o$ , for various peatland tissue types. Because litterbag studies are typically of only a few years duration, the litterbags are exposed to soil climate conditions representative of near-surface conditions. Deeper in the peat, decomposition rates should reflect the confounding factors of cooler temperatures and saturation of the peat leading to anoxic conditions that do not occur at the peat surface. These additional effects are modeled as multiplicative factors, and actual decomposition of a peat layer is modeled as



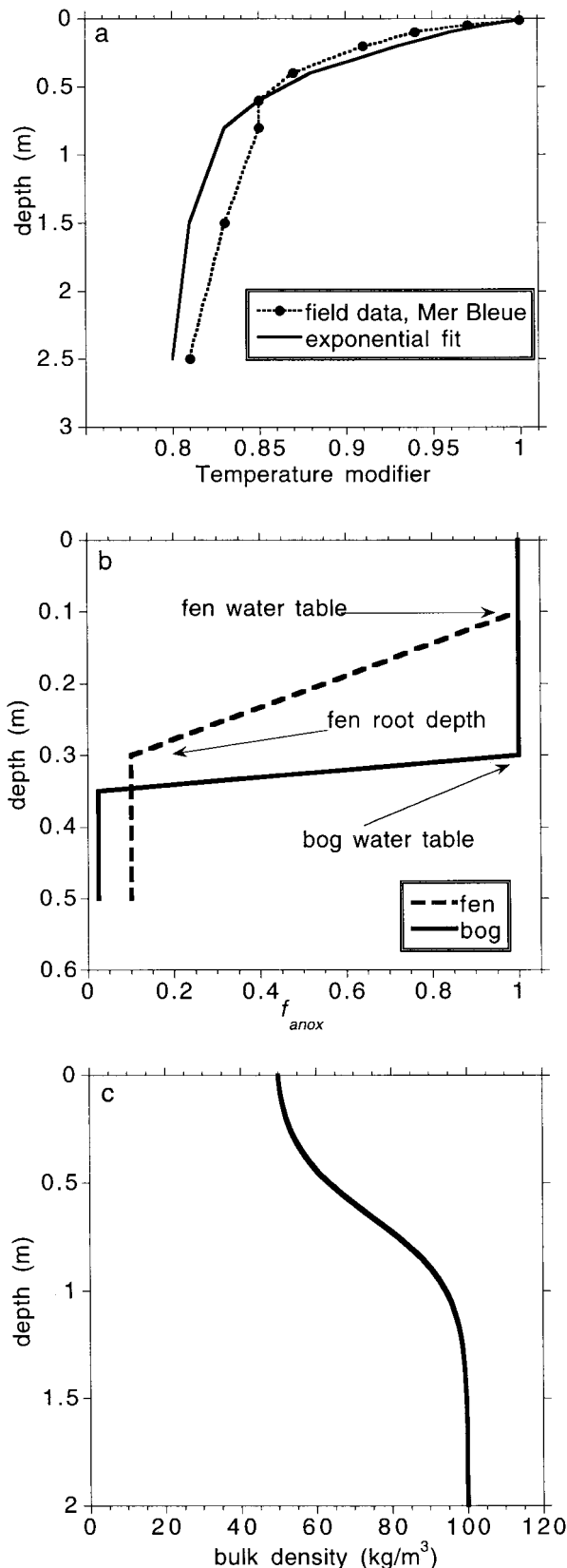


Figure 1. (a) Mean annual temperature effect on decomposition,  $f_T(z)$ , as a function of depth. Monthly average

$$\frac{dm(t)}{dt} = -k_0 \frac{m(t)^2}{m_0} \cdot f(T) \cdot f(W) \quad (7)$$

We assumed that the annual effect of the soil climate multipliers  $f(T)$  and  $f(W)$  were constant from year to year but varied with depth,  $z$ , with both  $f(T) = f_T(z)$  and  $f(W) = f_w(z)$  equal to 1.0 at the surface. The temperature modifier,  $f(T)$ , is based on an observed peatland temperature profile and an assumed and simple temperature effect ( $Q_{10} = 2$ ) (see Scanlon and Moore 2000). We applied this function to monthly means of hourly soil temperature measurements from Mer Bleue bog near Ottawa, Canada (Lafleur and others 2001) to calculate a general monthly modifier, then averaged these for the year, and normalized the values to the surface value. We then fit (by eye) a simple exponential curve to these data to get a decomposition temperature modifier that was only a function of depth (Figure 1a).

The moisture modifier,  $f(W)$ , is set to one for the surface oxic zone and decreases below the water table (Figure 1b). For bogs, which have a deeper water table, we assume that there is a rapid linear transition between oxic and anoxic conditions just below the mean long-term water table depth. For fens, which have a shallow water table and a deeper rooting depth, we assume that there is a linear decline in oxic status from the mean water table depth to the bottom of the rooting zone. For all of the following discussion, decomposition rates are implicitly assumed to be multiplied by  $f_T(z)$  and  $f_w(z)$ , and these terms are left out of the equations for simplicity (that is,  $k \cdot f_T(z) \cdot f_w(z) \rightarrow k$ ). A simple bulk density profile (Figure 1c) was based on bulk density data from two bogs in southeastern Canada (P. J. H. Richard and S. D. Muller unpublished).

soil temperatures were calculated from hourly average temperature profile data recorded continuously at Mer Bleue bog, near Ottawa, Ontario (Lafleur and others 2001) and used to calculate a monthly temperature multiplier ( $= 2^{T/10}$ ), which was then normalized so that the surface value was 1.0. The curve fit is an exponential decay with depth, having an asymptotic value of 0.8 and an initial value of 1.0. (b) Modeled effect of peat water table and fen roots on  $f_{anox}$ . This multiplier on decomposition rates accounts for the effect of anoxicity. (c) Shape of model's peat bulk density profile. Surface and deep peat values based on references in Table 1; shape based on unpublished data from P. J. H. Richard.

## Root Inputs

Most peatland plants (except bryophytes) have large root:shoot ratios (see, for example, Wallén 1986; Saarinen 1996; Moore and others 2001); thus, some fraction of their annual litter input into the peat will be root litter. To develop a litter/peat profile with root inputs, we considered the analytical solution to steady-state conditions (as above) but incorporated the effect of roots. We made the following two simplifying assumptions: (a) Root decomposability equals that of aboveground tissue of the same plant type, and (b) root density and root litter input rates are uniform to the rooting depth and zero below that depth. This simplified rectangular root distribution is a rough approximation to the typical profile (for example, see Wallén 1986). The model rooting depth input variable,  $Z_r$ , thus represents the depth to which the bulk of the root turnover takes place but not the maximum observable rooting depth.

Annual peat layers get a fresh input (root litter) every year until they are buried below the rooting zone. Adding this fresh litter increases the peat layer's net decomposability because fresh litter decomposability is always greater than partially decomposed peat layer's decomposability (see Eq. [6]). Consider a peat layer of mass  $m^*$  (the mass remaining from all previous inputs, including both surface litter and shallower roots, with total previous inputs equal to  $M$ ) and decomposability  $k^*$ , receiving a root litter input of  $m_r$  with decomposability  $k_0$ . The new peat layer mass will be  $m' = m^* + m_r$ . PDM updates the peat layer's decomposability,  $k'$ , with the following equation:

$$k' = k_0 \frac{m^* + m_r}{M + m_r} \quad (8)$$

which gave a better approximation to the exact solution of tracking all root litter cohorts independently than did a mass-weighted average ( $k' = (m^* k^* + m_r k_0) / (m^* + m_r)$ ).

## Calculating the Litter/Peat Profile

Because peatland plant tissues decompose at different rates, we generalized the solution above to two tissue types that do not interact—vascular, rooted vegetation (tissue type  $a$  with initial decomposition rate  $k_{0,a}$ ) and bryophyte (rootless) vegetation (tissue type  $b$  with initial decomposition rate  $k_{0,b}$ ). Let  $m_{s,a}$  be the surface vascular litter input,  $m_{r,a}$  be its root litter input ( $NPP_a = m_{0,a} = m_{s,a} + m_{r,a}$ ),  $Z_r$  be the rooting depth,  $\beta_a$

( $= m_{r,a} / Z_r$ ) be the root input per unit depth,  $m_{s,b}$  be the surface litter input for the nonvascular vegetation ( $NPP_b = m_{0,b} = m_{s,b}$ ), and  $z_i$  be the thickness and  $\rho_i$  the bulk density of the  $i^{th}$  peat layer. Then the surface peat layer ( $i = 0$ ) can be described by the following set of equations:

$$\begin{cases} m_0 = m_{0,a} + m_{0,b} = m_{s,a} + \beta_a z_0 + m_{s,b} \\ z_0 = \frac{m_0}{\rho_0} \\ k_{0,a} = k_{0,a} \\ k_{0,b} = k_{0,b} \end{cases} \quad (9)$$

Combining the equations for  $m_0$  and  $z_0$ , this can be solved as

$$\begin{cases} z_0 = \frac{m_{s,a} + m_{s,b}}{\rho_0} \left( \frac{1}{1 - \beta_a / \rho_0} \right) = (m_{s,a} + m_{s,b}) \left( \frac{1}{\rho_0 - \beta_a} \right) \\ m_0 = z_0 \rho_0 \end{cases} \quad (10)$$

The 1-year-old peat layer's mass will equal the mass remaining from the surface peat layer after 1 year of decomposition plus the fresh root litter input into the 1-year-old layer. The peat layer can be described by a similar set of equations, as follows:

$$\begin{cases} m_1 = \frac{m_{0,a}}{1 + k_{0,a}} + \beta_a z_1 + \frac{m_{0,b}}{1 + k_{0,b}} \\ z_1 = \frac{m_1}{\rho_1} \\ k_{1,a} = k_{0,a} \frac{m_{1,a}}{m_{0,a} + \beta_a z_1} \\ k_{1,b} = k_{0,b} \frac{m_{1,b}}{m_{0,b}} \end{cases} \quad (11)$$

These can be solved in a similar manner:

$$\begin{cases} z_1 = \left( \frac{m_{0,a}}{1 + k_{0,a}} + \frac{m_{0,b}}{1 + k_{0,b}} \right) \left( \frac{1}{\rho_1 - \beta_a} \right) \\ m_1 = z_1 \rho_1 \\ m_{1,b} = \frac{m_{0,b}}{1 + k_{0,b}} \\ m_{1,a} = m_1 - m_{1,b} \end{cases} \quad (12)$$

This methodology can be used to construct the peat profile down from the top in annual peat layers, and the  $i^{th}$  peat layer will be described by

$$\begin{cases} z_i = \left( \frac{m_{i-1,a}}{1 + k_{i-1,a}} + \frac{m_{i-1,b}}{1 + k_{i-1,b}} \right) \left( \frac{1}{\rho_i - \beta_a} \right) \\ m_i = z_i \rho_i \\ k_{i,a} = k_{0,a} \frac{m_{i,a}}{m_{0,a} + \beta_a \sum_{j=1}^i z_j} \\ k_{i,b} = k_{0,b} \frac{m_{i,b}}{m_{0,b}} \end{cases} \quad (13)$$

and solved in the same manner. Once below the rooting depth, the calculation proceeds as above, but without root inputs (that is,  $\beta_a = 0$ ).

We characterized bogs by rooting depth equal to the mean water table depth (for example, see Backéus 1990) and fens by rooting depth deeper than their characteristically shallow mean water table depth (see, for example, Saarinen 1996). We modeled the oxic/anoxic effect for bogs as previously described—that is, a linear drop in decomposability to a fixed factor ( $f_{anox}$ ) in a narrow band below the water table. Because fens have living roots that function below the water table, we considered the fen root zone to be partially oxic and prescribed a linear decline in decomposition rate from the oxic rate at the fen water table to  $f_{anox}$  at the bottom of the rooting zone. Because deep peat in bogs is more hydrologically isolated (Verry and others 1988; Siegel 1993) and more acidic (Gorham and Jannsens 1993) than deep peat in fens, we assigned bogs an  $f_{anox}$  value one-fourth the fen value.

### Aggregating the Annual Peat Layers

The total mass in a collection of peat layers between ages  $T_1$  and  $T_2$  is given by

$$M_{1,2} = \int_1^2 dm = \int_{T_1}^{T_2} \tilde{m}(t) \cdot dt = \int_{T_1}^{T_2} \frac{m_0}{1 + k_0 t} \cdot dt$$

$$= \frac{m_0}{k_0} \cdot \ln\left(\frac{1 + k_0 T_2}{1 + k_0 T_1}\right) \quad (14)$$

where  $\tilde{m}$  is the mass per unit time interval, or the peat layer mass when the time interval is 1 year. The mass loss rate of this aggregated peat layer can be approximated by

$$\overline{k}_{1,2} = \frac{\int_{T_1}^{T_2} m(t)k(t)dt}{\int_{T_1}^{T_2} m(t)dt} = k_0 \frac{\left(\frac{1}{1 + k_0 T_2} - \frac{1}{1 + k_0 T_1}\right)}{\ln\left(\frac{1 + k_0 T_2}{1 + k_0 T_1}\right)} \quad (15)$$

Because this integration over time (age) is also an integration over some depth interval, this approximation depends on the temperature and moisture factors implicit in  $k$  being approximately constant over the depth interval. We used this aggregated peat layer approximation for deep peat (generally older than 500–1000 years) so the model did not need to keep track of each annual peat layer for all

5000–12,000 years of the peat profile. For depths from about 1–2 m, we aggregated the peat into 10-year peat layers, typically about 1–2 cm thick. Below this, we aggregated the peat into 150-year peat layers, typically 1–10 cm thick. The mean decomposition rate (Eq. [15]) was not used to calculate the peat profile, but only to characterize the peat layers' decomposability.

## RESULTS

### Baseline Bog and Fen Scenarios

We developed very general parameterizations for a bog and a fen from typical values reported in the literature for peatland productivity, decomposition rates of various tissues, root biomass and depth, and typical values for long-term mean water table depth (Table 1). Annual NPP for the bog scenario was  $0.6 \text{ kg m}^{-2} \text{ y}^{-1}$ , with one-third from moss, one-third from aboveground vascular productivity, and one-third from belowground vascular productivity (Thormann and Bayley 1997; Backéus 1990). Annual NPP for the fen scenario was  $0.7 \text{ kg m}^{-2} \text{ y}^{-1}$ , with 14% from moss, 43% from aboveground vascular productivity, and 43% from belowground vascular productivity (Thormann and Bayley 1997; Saarinen 1996). Throughout this paper, all mass values are given as biomass, not carbon.

PDM generated depth profiles of peat mass, moss and vascular tissue fractions, decomposability, and age for the bog and fen baseline scenarios. The fen material had a faster initial decomposition rate; thus, fen peat layer mass fell more rapidly with depth (age) than bog peat layer mass (Figure 2a). However, root inputs for the fen were larger than those for the bog. Thus, below about 0.2 m, the fen peat layer mass increased above that of the bog. At the transition to the fully anoxic zone ( $Z_{WT} + Z_{anox} = 0.35 \text{ m}$  for the bog,  $Z_r = 0.3 \text{ m}$  for the fen), the bog peat layer mass was  $0.059 \text{ kg m}^{-2}$  (10% of annual surface plus root litter inputs), and the fen peat layer mass was  $0.17 \text{ kg m}^{-2}$  (24% of annual surface plus root litter inputs). Below this, in the fully anoxic zone, bog peat layers lost mass more slowly than fen peat layers. The effective decomposability of each peat layer, calculated as the mass-weighted mean of the  $k_i$  value for each tissue type, declined with depth (Figure 2b). For the bog peat layers, there was a rapid drop in decomposability to anaerobic rates in the 0.05 m below the mean water table depth. Decomposability continued to decline down the catotelm profile due to continuing mass loss (see Eq. [6]), and effective decomposability at the base of the peat, approximately  $0.0001 \text{ y}^{-1}$

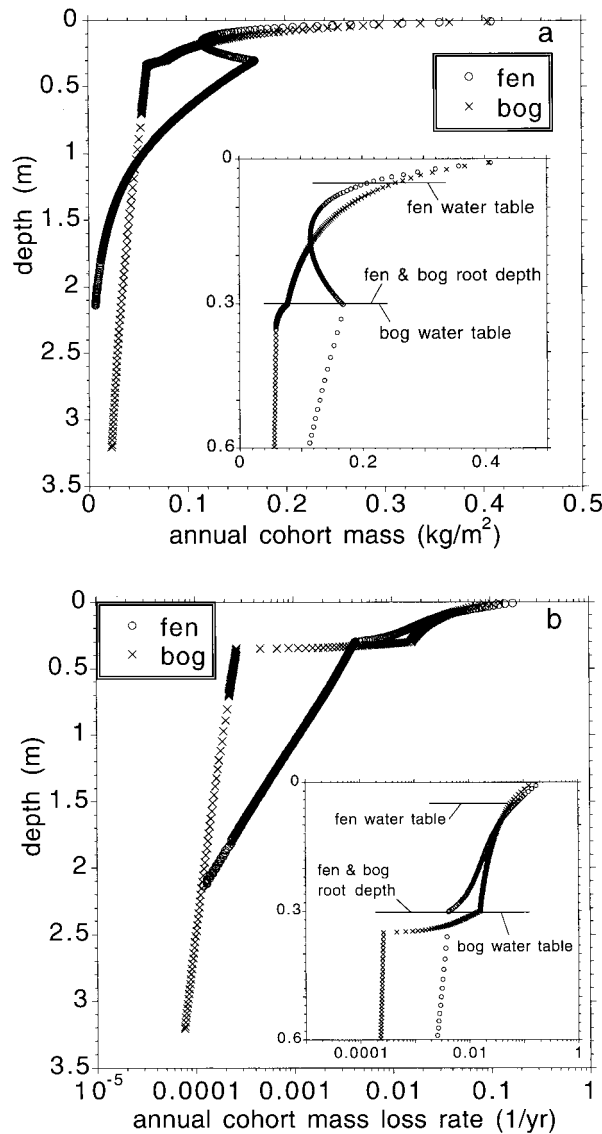


Figure 2. (a) Peat layer mass versus depth for the bog (x) and fen (o) base case scenarios. The inset panel highlights the top 0.6 m of the profile. Above 0.3 m (the bog water table and the fen rooting depth), each symbol represents a single peat layer. (b) Peat layer effective decomposability vs depth (or age) for the bog (x) and fen (o) base case scenarios. The inset panel highlights the top 0.6 m of the profile. Above 0.3 m (the bog water table and the fen rooting depth), each symbol represents a single peat layer. The rapid shift in bog decomposability between 0.3 m and 0.35 m is the transition from the oxic acrotelm to the anoxic catotelm. The fen scenario has a more gradual transition from the water table down to the bottom of the rooting zone.

(Figure 2b) was around three orders of magnitude lower than the surface rate.

After 8000 years, fen peat thickness was 2.1 m ( $180 \text{ kg m}^{-2}$ ); whereas after 8000 years, bog peat

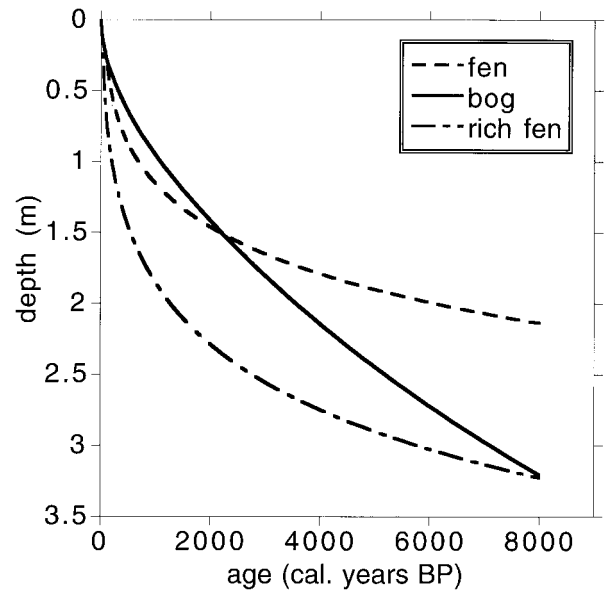
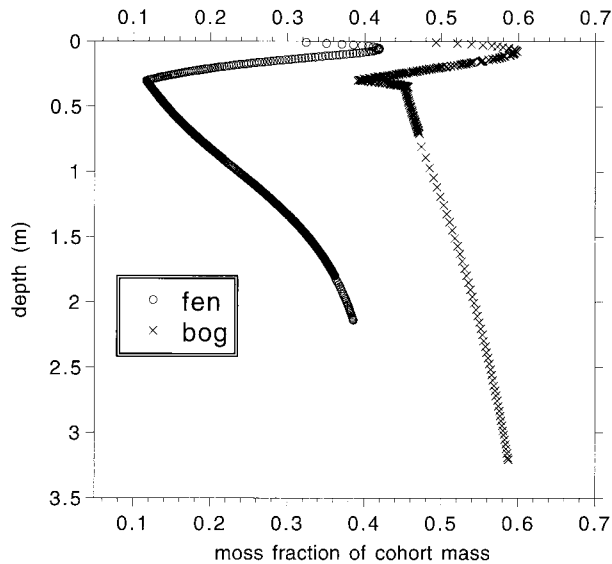


Figure 3. Age depth profiles for bog and fen base scenarios and for a rich-fen scenario. Model parameters for bog and fen are in Table 1. Changes from the fen to rich-fen scenario were  $m_{s,a} = 0.35 \text{ kg m}^{-2} \text{ y}^{-1}$ ;  $m_{f,a} = 1.0 \text{ kg m}^{-2} \text{ y}^{-1}$ ;  $k_{o,a} = 0.38 \text{ y}^{-1}$ ;  $m_{s,b} = 0.15 \text{ kg m}^{-2} \text{ y}^{-1}$ ; and  $k_{o,b} = 0.07 \text{ y}^{-1}$ . This rich-fen scenario was used for the deeper peat in some of the model comparisons with core data. Although the bog and rich-fen scenarios accumulate about the same amount of peat in 8000 years, the current rate of accumulation is given by the slope of the curve at 8000 years and is much greater for the bog than for either of the fen scenarios.

thickness was 3.2 m ( $290 \text{ kg m}^{-2}$ ) (Figure 3). These figures imply mean accumulation rates of  $0.022 \text{ kg m}^{-2} \text{ y}^{-1}$  for the fen and  $0.036 \text{ kg m}^{-2} \text{ y}^{-1}$  for the bog. The model assumed constant conditions, so that each additional year effectively added an additional layer to the bottom of the profile, leading to current accumulation rates of  $0.006 \text{ kg m}^{-2} \text{ y}^{-1}$  (fen) and  $0.02 \text{ kg m}^{-2} \text{ y}^{-1}$  (bog). Because of higher NPP rates and deeper roots, the fen peat age at a depth of 1 m was about 700 years, whereas the bog peat age at 1 m was about 1100 years. Because fen decomposition rates were faster at depth, at depths below 1.5 m bog peat was younger than fen peat (Figure 3).

The moss fraction of each peat layer was higher for the bog than the fen (Figure 4), due to a higher percentage of moss inputs, both at the surface and overall (Table 1). Because moss initial decomposition rates were slower than vascular tissue rates for both bog and fen, the moss fraction increased with depth (and peat layer age). However, from a depth





**Figure 4.** Fraction of peat layers that is moss (nonvascular) peat for bog and fen base case scenarios. For most of the profile, this fraction increases with depth as moss decomposability is less than that of vascular tissue. Near the surface this trend is reversed as significant root litter inputs from vascular plants decreases the moss fraction of the peat layer.

of about 0.05–0.2 m for the bog and 0.1–0.3 m for the fen, the moss fraction declined because of vascular root inputs in this zone.

### Model Sensitivities

**Sensitivities to individual parameters.** The sensitivity of peat accumulation to model parameters was explored by varying each parameter by  $\pm 15\%$  and  $\pm 30\%$  from its baseline value (Table 1). Parameter sensitivities were approximately linear, ranging from strongly positive (a 30% change in the parameter value caused more than a 25% change of the same sign in peat accumulation) to weak (a 30% change in a parameter value caused less than a 10% change in accumulated peat) to strongly negative (a 30% change in the parameter value caused more than a 25% change of opposite sign in peat accumulation). Both bog and fen showed moderate positive sensitivity to changes in vascular plant productivity ( $m_{s,a}$ ,  $m_{r,a}$ ). Sensitivity to moss productivity ( $m_{s,b}$ ) was higher for bog than for fen because moss productivity was a greater fraction of total productivity and bog moss decomposability was slow ( $k_{0,b}$ ). As expected, the bog scenario showed moderate negative sensitivity to changes in decomposition rates ( $k_{0,a}$ ,  $k_{0,b}$ ,  $k_{anox}$ ); slower decomposition rates led to more peat accumulation. Fen sensitivity to  $k_{anox}$  was greater than bog sensitivity

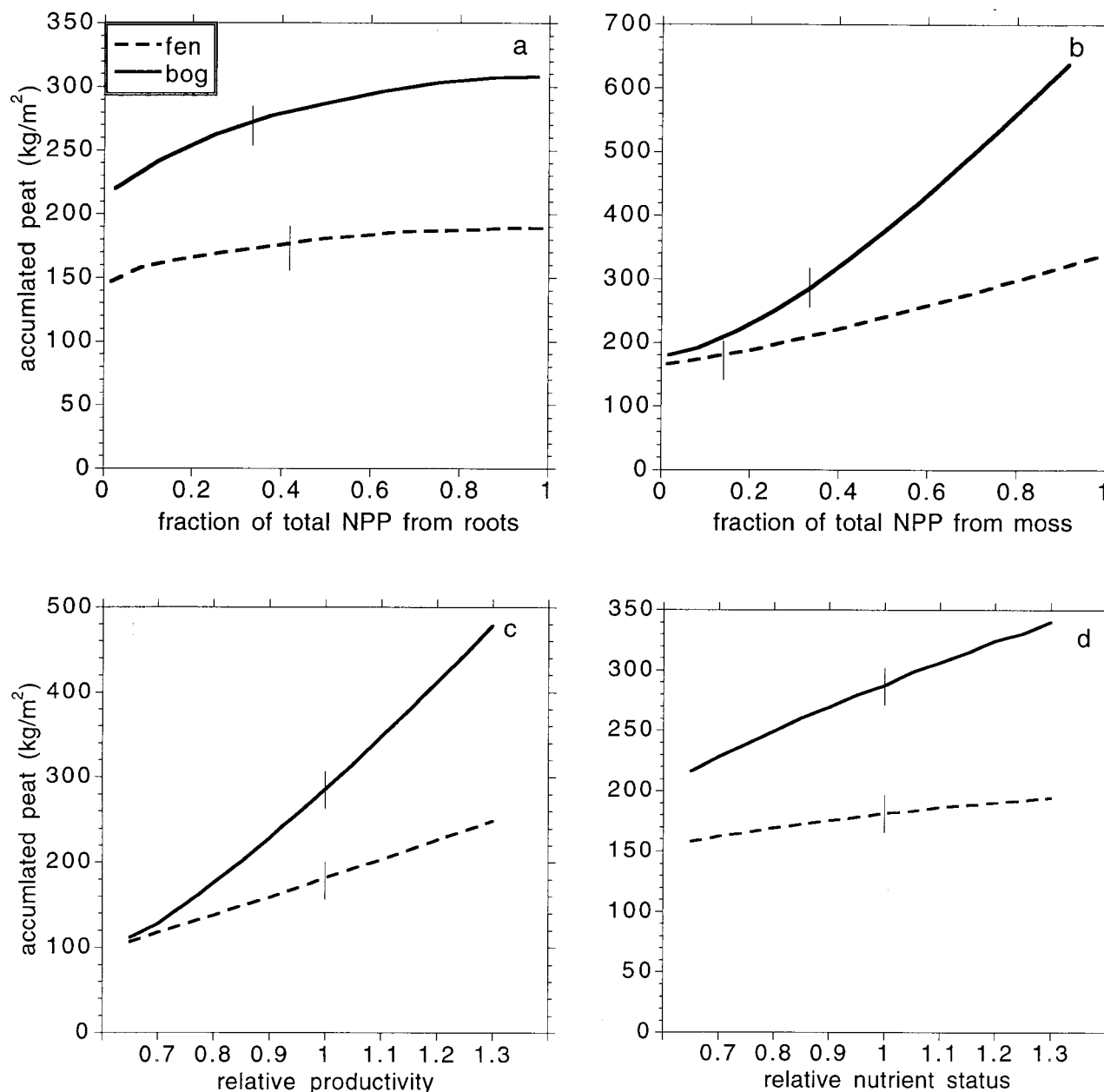
because the base value for the fen was four times greater than that for the bog, so a fixed percentage change was larger and had a greater effect.

Decreasing the surface peat bulk density ( $\rho_0$ ) increased the thickness of each and thus also buried the peat below the water table more quickly, leading to increased accumulation. Bog sensitivity was about three times that of fen sensitivity, as the ratio of anoxic to oxic decomposition rates was smaller for the bog than the fen scenario. Changing  $\Delta\rho$ , the increase in bulk density with depth in the peat had very little effect on mass accumulation for either bog or fen because most of the change took place below 0.5 m, where conditions were relatively constant (see Figure 2). Changing  $\Delta\rho$  did modify the total depth of peat accumulated in a very predictable way.

The bog scenario was very sensitive to the water table depth ( $Z_{WT}$ ). A shallower water table led to significantly greater peat accumulation because peat layers reached the anoxic zone with more mass intact. The fen scenario had little sensitivity to water table depth; as the change in decomposition rate for the fen was much less abrupt at the water table, and the anoxic zone decomposition rate was generally higher for the fen than for the bog scenario (see Figure 2b). Increasing rooting depth in the fen decreased accumulation as it extended the partially oxic zone deeper into the peat. Decreasing rooting depth in the bog decreased accumulation because less fresh litter was input deeper in the profile, closer to the transition to anoxia, and thus peat transfer to the catotelm was smaller. Because  $Z_{anox}$  had a small magnitude (0.05 m), 15% and 30% changes were also small and bog peat accumulation sensitivity was small. In additional simulations with  $Z_{anox}$  at 0.0 m and 0.1 m, bog peat accumulations showed strong negative sensitivity.

**Sensitivities to vegetation productivity.** Using the base case scenarios for bog and fen (Table 1), we adjusted the fraction of vascular plant litter input that was root tissue, keeping total vascular NPP constant ( $0.6 \text{ kg m}^{-2} \text{ y}^{-1}$  for fens,  $0.4 \text{ kg m}^{-2} \text{ y}^{-1}$  for bogs). As the root fraction increased, peat accumulation also increased because more litter was input closer to the anoxic zone and thus had less time to decompose aerobically (Figure 5a). For both bog and fen, the sensitivity was stronger for low root fractional inputs and weaker if most vascular litter was input as roots.

We also adjusted the base case bog and fen scenarios by changing the moss fraction of total NPP, again holding total NPP and the vascular aboveground:belowground NPP ratio fixed. Because moss litter had a lower decomposition rate



**Figure 5.** (a) Sensitivity of peat accumulation to fraction of vascular litter input as roots for bog and fen base case scenarios. Total vascular NPP was unchanged ( $0.6 \text{ kg m}^{-2} \text{ y}^{-1}$  for the fen,  $0.4 \text{ kg m}^{-2} \text{ y}^{-1}$  for the bog). (b) Sensitivity of peat accumulation to moss fraction of total NPP for bog and fen base case scenarios. Total NPP was unchanged ( $0.7 \text{ kg m}^{-2} \text{ y}^{-1}$  for the fen,  $0.6 \text{ kg m}^{-2} \text{ y}^{-1}$  for the bog). (c) Sensitivity of peat accumulation to total NPP (moss + vascular). Moss:vascular and aboveground:belowground

productivity ratios were unchanged (see Table 1). (d) Sensitivity of peat accumulation to nutrient status. Improved (diminished) nutrient status was modeled by increasing (decreasing) both NPP and decomposition rates by the same fraction. Moss:vascular and aboveground:belowground productivity ratios were unchanged (see Table 1). In each panel, the vertical lines represent baseline scenario values. Note the different scales on some panels.

than vascular litter as the fraction of total NPP due to mosses increased, the total accumulated mass of peat also increased (Figure 5b). The bog scenario was more sensitive to this ratio because the initial

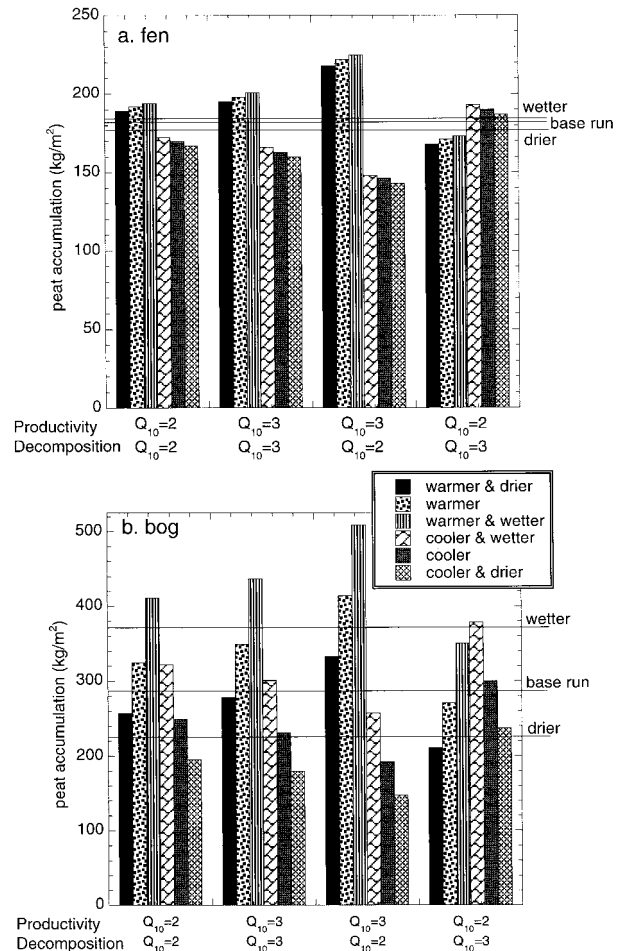
decomposition rate of bog moss litter was lower than the rate for fen moss litter, although both scenarios had the same initial decomposition rate for vascular litter.

In a third test, we adjusted total productivity for both the bog and fen scenarios (Figure 5c). Peat accumulation in the fen scenario had a linear response to total productivity, with a 10% increase in productivity leading to a 12% increase in peat accumulation. Peat accumulation in the bog scenario had a stronger sensitivity to total productivity and a slightly nonlinear response.

Finally, to approximate changes in nutrient status, we adjusted both total productivity and decomposition rates up and down by the same proportions. Higher nitrogen and other nutrient input leads to increased productivity (Aerts and others 1992; Jauhiainen and others 1999) and to more readily decomposable fresh litter (Johnson and Damman 1993; Verhoeven and Toth 1995); however, there is some suggestion that chronic nitrogen loading may alter the decomposer community (Williams and Silcock 1997; Gilbert and others 1998). Again, responses were roughly linear (Figure 5d) over a  $\pm 30\%$  range, with bog peat accumulation more sensitive than fen peat accumulation.

**Sensitivities to climate.** To evaluate the model's sensitivity to climate, we considered eight climate scenarios—(warmer, cooler, wetter, drier, warmer/wetter, warmer/drier, cooler/wetter, and cooler/drier)—and four scenarios of ecophysiological sensitivity to temperature—(low and high sensitivity for both productivity and decomposition). Temperature changes were  $\pm 3^\circ\text{C}$  and moisture changes were  $\pm 25\%$  in water table depth. Ecophysiological sensitivities were modeled by assuming an exponential response (low;  $Q_{10} = 2$ ; high,  $Q_{10} = 3$ ) for both total productivity or litter inputs ( $m_{s,a} + m_{r,a} + m_{s,b}$  in Table 1) and total decomposition rate ( $k_{o,a}$  and  $k_{o,b}$  in Table 1). Thus, for example, in the warmer/wetter scenario with high sensitivity for productivity and low sensitivity for decomposition rate, the simulation would multiply baseline values of  $m_{s,a}$ ,  $m_{r,a}$ , and  $m_{s,b}$  by 1.390, multiply baseline values of  $k_{o,a}$  and  $k_{o,b}$  by 1.231, and multiply  $Z_{WT}$  by 0.75; by contrast, in the cooler/drier scenario, the multipliers would be 0.719, 0.812, and 1.25. Note that these scenarios do not represent sensitivity to climate variability or change, since the modified conditions were in effect for the entire period of peat development.

The fen scenario showed very little sensitivity to changes in water table depth (Figure 6a, and Table 1), so the effect of a water table shift was very small. The bog scenario had much larger sensitivities to both temperature and water table differences (Figure 6b). In both scenarios, warmer and wetter conditions were most conducive to peat accumulation. Both bog and fen sensitivities to wetter or drier



**Figure 6.** Sensitivity to climate of peat accumulation for (a) fen and (b) bog under four ecophysiological scenarios representing high and low sensitivity to temperature for both productivity (total NPP) and decomposition rates. In each panel, each group of six bars represents the sensitivity to climate of a particular ecophysiological scenario, modeled as a  $Q_{10}$  response of 2 (low sensitivity) or 3 (high sensitivity). Climate scenarios were changes of  $\pm 3^\circ\text{C}$  and  $\pm 25\%$  in water table depth. The base scenario value (standard climate) is represented by a horizontal line labeled “base run”. Because the ecophysiological scenarios represented sensitivity to temperature change only, the wetter and drier scenarios (with no temperature change) are also represented by horizontal lines.

conditions were relatively insensitive to the effect of warming or cooling on the ecophysiological scenario. When productivity and decomposition rate sensitivities to temperature were the same (both low or both high), productivity effects dominated and warmer conditions led to enhanced accumulation whereas cooler conditions led to reduced accumulation. Only when decomposition rates had a  $Q_{10}$  of 3 and productivity had a  $Q_{10}$  of 2 did cooler

**Table 2.** General Site Characteristics for the Peatland Sites with Peat Core Data used to Test the PDM Model

Site	Frontenac	Mer Bleue	Mirabel	Malbaie			
Physiographic region	Appalachians	St. Lawrence Lowlands		Laurentians			
Latitude	45°58'N	45°25'N	45°68'N	47°36'N			
Longitude	71°08'W	75°40'W	74°07'W	70°58'W			
Elevation (m)	360	65	75	800			
Mean annual temp. (°C) <sup>a</sup>	4.2	5.8	6.1	0.0			
Mean July temp. (°C) <sup>a</sup>	18.5	20.8	20.8	14.8			
Mean January temp. (°C) <sup>a</sup>	−11.4	−10.8	−10.3	−15.3			
Degree-days > 5°C <sup>a</sup>	1500	2050	2070	850			
Total precipitation (mm) <sup>a</sup>	1130	910	740	1530			
Annual snowfall (%) <sup>a</sup>	24	30	29	39			
Regional vegetation type	Maple/Birch/Fir	Sugar Maple/Hickory	Sugar Maple/Hickory	Spruce/Fir			
Peatland size (km <sup>2</sup> )	1	28	2	1			
Peatland types	Domed bog, fen	Bog	Bog	Bog with pools			
Regional topography	Incised plateau	Terraces	Terraces	Hilly plateau			
Local topography	Tilted	Horizontal	Horizontal	Tilted			
Basin margins	Smooth-sided	Steep-sided	Smooth-sided	Smooth-sided			
Underlying deposit	Till	Marine clay	Marine clay	Till			
Initial conditions	Scattered pools	Shallow lake	Shallow lake	Scattered pools			
Peatland/core identifier		<i>FRON-</i>	<i>MB-</i>	<i>MIR-</i>	<i>MAL-</i>		
Core number	1	2	3	930	1	2	3
Number of dates <sup>b</sup>	8	8	6	13	8	5	4
Pond sediment age (ky)	8.4	12.8	12.2	8.7	9.0	10.3	—
Peat inception age (ky)	7.5	11.6	9.9	8.4	7.4	8.0	8.9
Fen-to-bog transition (ky)	—	5.3	5.0	6.5	6.8	5.0	2.4

<sup>a</sup>Environment Canada 1994.<sup>b</sup>Dates are either radiocarbon dates or from pollen correlation with well-dated events in the area.

temperatures lead to enhanced accumulation and warmer temperatures cause reduced accumulation.

### Comparison with Peat Core Data

PDM simulations were compared to age–depth profiles from cores collected in four peatlands in eastern Canada, selected because of their various past and present environmental conditions and because we have firsthand information about their developmental history. Mer Bleue and Mirabel bogs are located approximately 150 km apart in the St. Lawrence Lowlands, near Ottawa and Montreal, respectively. Frontenac peatland is found another 150 km to the east of Montreal, in the Lower Appalachian physiographic region, near Sherbrooke. Finally, Malbaie bog lies in the central part of the Laurentian Highlands about 100 km north of Québec City.

The individual peatlands span a range of climate conditions (Table 2). Malbaie differs strikingly from the other peatlands in that it is a bog patterned by numerous pools. It is also the peatland where precipitation is highest and temperature lowest. Like Fron-

tenac peatland, Malbaie bog occupies a tilted basin in the regional topography; in both areas, peat has accumulated over an irregular till plain with scattered local pools. Frontenac peatland is covered by a domed bog (80%) to which a poor fen (20%) is adjoined down-slope. Mirabel and Mer Bleue are both slightly domed bogs without pools, lying in flat topography. In all peatlands, black spruce (*Picea mariana* (Mill.) BSP) and larch (*Larix laricina* (Du Roi) Koch.) are dispersed over a microtopographic pattern of hummocks and hollows. Shrub heath communities are dominant (*Chamaedaphne calyculata*, *Kalmia angustifolia*, *Ledum groenlandicum*). Sedge lawns are widespread only further away from the dome at Frontenac (Ball 1996). The bryophyte layer is composed almost entirely of *Sphagnum* mosses.

The postglacial development of these four peatlands is well known through previous or ongoing studies. Peat thickness and type were observed at 50–140 spots at Frontenac, Malbaie, and Mirabel; and a 300-m transect of peat depth from the margin of the bog to the center is available at Mer Bleue. The peat



cores were analyzed with a set of paleoecological techniques (loss on ignition, radiocarbon dating, and analyses of pollen and spores, testate amoebae, mosses, and plant macrofossils) to reconstruct local and regional vegetation history, local hydrological conditions at the peat surface, net sediment accumulation rate and decomposition events, and the overall developmental history of the peatlands since deglaciation (Lavoie 1998; Lavoie and Richard 2000a; S. D. Muller and P. J. H. Richard unpublished). Additional paleohydrological information (lake level changes) was available to assess the regional water balance in the area (Lavoie and Richard 2000b; S. D. Muller and P. J. H. Richard unpublished).

For comparison with the PDM results, we selected peat cores for which an adequate chronology of peat accumulation was available. All dates reported are calibrated radiocarbon dates (Stuiver and others 1998) or dates obtained through pollen correlation with well-dated events in pollen diagrams from neighboring sites (Mott and Camfield 1969). The palynological and plant macrofossil record for these cores indicated that the Mer Bleue and Mirabel bogs, located in the St. Lawrence Lowlands, began as large ponds left after the drainage of the postglacial Champlain Sea. Rich fens developed over the organic deposits left by marshes (telmatic peat), then changed to bogs at some point in their development (Table 2). Frontenac and Malbaie developed directly as fens on till plains (glacial deposits) with only small pools around and then evolved into bogs, except at the Frontenac poor-fen site.

We adopted two approaches for the development of model profiles for the two-stage peatlands. In each case, we generated a bog peat profile from the present (surface) back to the transition time (2400–6800 BP, depending on the core). To generate the underlying fen peat, in one case we simply generated a fen peat profile from the present (surface) back to the basal date of the core (8000–11,600 BP, depending on the core) and took the lower portion of this fen peat from the transition time to the base. We call this the “bog/fen scenario (*b/f*)”. Our second method of generating a fen peat profile was to “bog the fen.” Deeper fen peat was subjected to bog-anoxic conditions (that is,  $f_{anox} = 0.025$  rather than 0.1). A linear transition from fen-anoxic to bog-anoxic conditions occurred in the 0.45 m below the fen root zone; this layer, extending from 0.3 m to 0.75 m, corresponded to about 200 years of accumulation. The portion of this bogged-fen peat from the transition time to the base was then placed under the bog peat to generate a bog/bogged fen profile (*b/b-f*).

We also generated a bog/bogged rich fen (*b/b-rf*)

profile, where initial fen parameters were set to values representative of current rich fen data. We chose to test a rich-fen parameterization for the initial fen stage because higher base cation (Ca, Mg, K) concentrations in bulk peat samples from the deep portion of the Mer Bleue core (P. J. H. Richard unpublished) indicate that the site initially had conditions appropriate for a rich fen. Similar initial conditions are deduced from palynological and paleobotanical analyses of the other cores, indicating higher nutrient availability after ice retreat (Frontenac, Malbaie) or after draining of the postglacial Champlain Sea (Mer Bleue, Mirabel). The parameter changes from Table 1 were  $m_{s,a} = 0.35 \text{ kg m}^{-2} \text{ y}^{-1}$ ;  $m_{r,a} = 1.0 \text{ kg m}^{-2} \text{ y}^{-1}$ ,  $k_{o,a} = 0.38 \text{ y}^{-1}$ ,  $m_{s,b} = 0.15 \text{ kg m}^{-2} \text{ y}^{-1}$ ; and  $k_{o,b} = 0.07 \text{ y}^{-1}$ . These were based on NPP estimates for rich fens in western Canada (Thormann and Bayley 1997) and mass loss decomposition rates for rich-fen species (T. R. Moore unpublished). Overall peat accumulation for the rich-fen scenario was significantly greater than for the standard-fen scenario (Figure 2), but most of this additional peat was less than 2000 years old.

In each case we compared PDM simulations with our default parameterizations (Table 1 or rich-fen values above) to the core date profiles. We did not try to adjust parameters to fit site data because there are no measurements at these sites to constrain water table depth or total and component NPP rates. All of these values are site specific and have a strong influence on peat accumulation.

**Frontenac peatland.** The PDM baseline fen scenario compares well to the Frontenac fen core for the last 6000 years (FRON-1), (Figure 7a). However, PDM greatly underestimated the peat remaining from the peatland's first 1500 years. Accumulation rates inferred from the core were then much higher (perhaps related to higher NPP due to higher nutrient levels). We tested a second scenario in which the oldest peat (6000–7500 BP) was from a rich-fen simulation (see Figure 2). However, this made little difference and the discrepancy between PDM simulation and core data remained (Figure 7a).

We generated the following three model scenarios for the FRON-2 bog core: (a) *b/f*: 5300 years of bog peat over 6500 years of fen peat, (b) *b/b-f*: 5300 years of bog peat over 6500 years of bogged-fen peat, and (c) *b/b-rf*: 5300 years of bog peat over 6500 years of bogged-rich-fen peat. For the FRON-3 bog core, we used only the *b/b-rf* scenario. The bog portion of these scenarios generated a very good portrayal of net peat accumulation behavior observed in the FRON-2 and FRON-3 cores for their bog period to 5300 BP (Figure 7b). The *b/f* scenario underestimated the peat remaining from peatland's

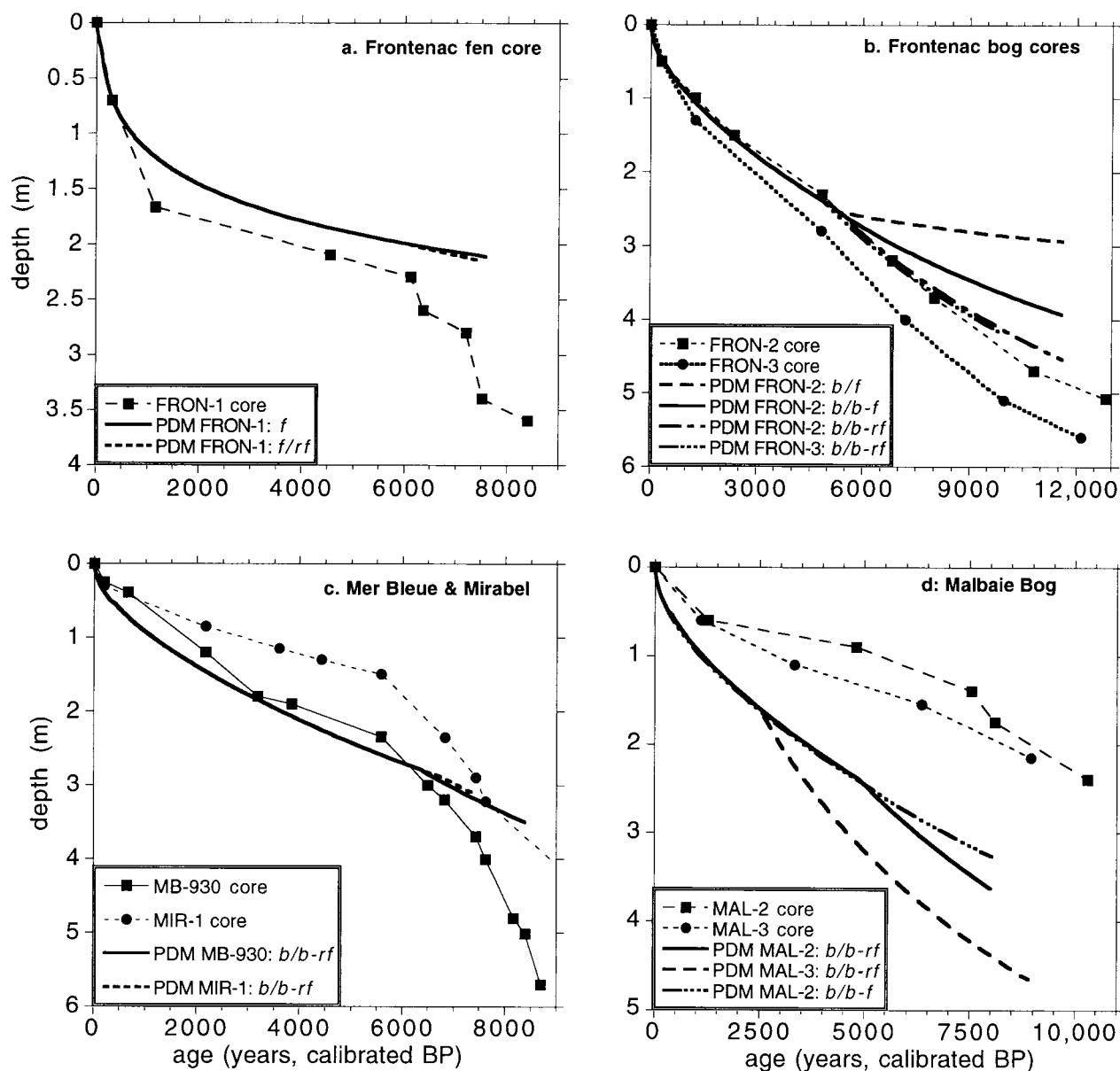


Figure 7. PDM profiles (lines) compared to dated peat cores (dated depths correspond to points on each panel) for (a) Frontenac fen core; (b) Frontenac bog cores; (c) Mer Bleue and Mirabel bog cores, and (d) Malbaie bog cores. See Table 2 for site descriptions. Notation for model

profiles (heavy lines) is as follows:  $f$  = fen,  $f/rf$  = fen over rich fen,  $b/f$  = bog over fen,  $b/b-f$  = bog over bogged-fen, and  $b/b-rf$  = bog over bogged-rich fen (see Table 2 for fen-to-bog transition dates).

first 6500 years as a fen, but subjecting this fen peat to bog-anoxic conditions ( $b/b-f$ ) improved the model fit to the data. The  $b/b-rf$  scenario gave the best approximation to the observed age–depth profile of the FRON-2 core and had reasonable agreement with the FRON-3 core (Figure 7b).

**Mer Bleue and Mirabel bogs.** We generated a  $b/b-rf$  scenario for both the Mer Bleue and Mirabel sites (Figure 7c). The default bog scenario was in

very good agreement with field observations at Mer Bleue (over the last 6500 years), but the observed rich-fen peat accumulation was much higher than that simulated by the model between 8400 to 6500 years ago (Figure 7c). The thickness of the underlying bogged-rich-fen peat as simulated by PDM was more similar to that observed 7200 years ago in the case of Mirabel core (Figure 7c) when submitted to bog conditions 6800 years ago, but the model

overestimated the bog peat accumulated in that core. The most important characteristic that distinguishes the two cores is their position relative to groundwater (and nutrient) supply. The Mer Bleue bog core is located laterally with respect to the entire peatland, in the northernmost fingerlike expanse through which the peatland drains westward, while the Mirabel bog core is centrally located within a much smaller system (Table 2). The Mirabel core was the only one in which we found evidence for local fires (conspicuous charcoal layers, for example, at 25 cm and 80 cm) (S. Muller unpublished); the core age–depth curve may thus depict reduced peat accumulation, either because of the peat that burned, or due to postfire conditions not immediately conducive to peat growth, or both.

**Malbaie bog.** We compared model *b/b–f* and *b/b–rf* scenarios to MAL-2 and the *b/b–rf* scenario to MAL-3, again using our baseline parameterizations. The bog scenario accumulated peat more rapidly throughout the profile than indicated by two cores (Figure 7d). At MAL-2, the apparent fen peat accumulation rate was similar for the model and the core data, but the model had generated 2.5 m of bog peat in the past 5000 years, whereas the core contained only about 1 m of bog peat (Figure 7d). For MAL-3, the model accumulated peat at about twice the observed rate through the bog and fen stages (Figure 7d). The fact that the observed peat accumulation rates during both (rich) fen and the overlying bog stages are lower than at the other sites strongly points to a climate effect, with temperature dominating because Malbaie is both colder and wetter than the other sites (Table 2). This conclusion is also supported by the results of model sensitivity to climate, unless decomposition is more sensitive to temperature than productivity (Figure 6). Clymo and others (1998) also reported lower peat accumulation rates in cooler climates. In addition, the widespread pools found all over Malbaie bog may well have consumed some of the peat accumulated in the past by causing decomposition with little production. The position of the pools has shifted constantly during the peatland's history (Lavoie and Richard 2000a). The absence of slowly-decomposing *Sphagnum* tissues until 1000 years ago at MAL-2 probably means that tissue decomposition rates were faster before that time and thus also deeper than 1000 years (around 0.8 m) into the peat. Faster decomposition rates lead to lower accumulation rates.

## DISCUSSION AND CONCLUSIONS

Several features in PDM distinguish it from previously published models of peat accumulation. PDM

used observed vegetation productivity and fresh litter decomposition rates as key parameters. The model then included three mechanisms for slowing decomposition rate with depth in the peat profile. First, as litter decomposed, it became more resistant to decomposition. By the bottom of the profile, cohorts had lost about 96.5% (bog) to 98.5% (fen) of their initial mass, reducing decomposition rates by this same amount. Second, a temperature effect, based on observed monthly mean temperature profiles and a  $Q_{10} = 2$  temperature rate multiplier function, reduced decomposition rates by 20% below a depth of about 1 m. depth. Finally, there was a reduction in decomposition rates by a factor of 10 (fen) or 40 (bog) due to anoxic conditions. The product of these three effects was to reduce decomposition rates from 0.05–0.2  $y^{-1}$  (surface) to 0.00012  $y^{-1}$  (bottom of fen) and 0.000076  $y^{-1}$  (bottom of bog), or by about a factor of 1000, similar to the estimate of Belyea and Clymo (1999). This relation of decomposition to observable processes at any depth in the peat profile allows PDM to predict a peat profile based on surface conditions and does not require fitting any parameters to peat core age–depth data sets.

A second new feature in PDM is the explicit inclusion of roots and fresh root litter input into the peat column. For both bog and fen scenarios, the mean water table depth determined the depth of the fully oxic zone. In the bog scenario, the mean water table depth was also the rooting depth. In the fen scenario, a partially oxic zone extended from the mean water table depth down to the rooting depth. Root litter inputs affected peat accumulation primarily by incorporating fresh litter at some depth in the peat profile, closer to the anoxic zone. This root material had a shorter transit time through the oxic zone, and more of the material was transferred to the anoxic zone. In both the bog and fen scenarios, increasing the proportion of vascular NPP that was deposited as litter below the surface led to increased total peat accumulation. A third new feature in PDM was the explicit treatment of litter tissue from two different vegetation types (vascular and moss), with different initial decomposition rates. Total peat accumulation depended on the fraction of total NPP attributed to mosses and vascular plants.

With these three features, PDM was able to develop scenarios representing both bog and fen conditions. Although fen productivity was 17% higher, peat accumulation was less for the fen scenario after 2000 years, primarily because the assumption of more severe anaerobic conditions at depth in the bog reduced mass loss by the deeper peat. Two

**Table 3.** Comparison of Characteristics of Peat Accumulation as Simulated by the PDM Model and as Developed by Clymo and Others (1998)

Parameter	Units	Present study		Clymo and Others 1998
		Bog	Fen	
Age	y	8000	8000	<1000–~11,000
$P^*$	$kg\ m^{-2}\ y^{-1}$	0.059	0.17	0.072 <sup>a</sup>
$\alpha^*$	$y^{-1}$	0.00014	0.0011	0.0004 <sup>a</sup>
LARCA	$kg\ m^{-2}\ y^{-1}$	0.036	0.031	0.024–0.072 <sup>b</sup>
TRACA	$kg\ m^{-2}\ y^{-1}$	0.022	0.010	0.054 <sup>c</sup>

The Clymo and others (1998) values are based on fitting curves to peat age–depth profile data for several hundred peat cores from Finland.

<sup>a</sup>Based on Clymo and others (1998; Figure 17) and a mean annual temperature of 5°C

<sup>b</sup>Based on Clymo and others (1998; Figure 15a) for peat ages of around 8000 years

<sup>c</sup>Based on  $P^*$  value for the linear decay model and Figure 15b of Clymo and others 1998

other parameters also contributed to greater peat accumulation in the bog: One was a higher initial mass loss rate for fen moss than bog moss; the other was a higher proportion of NPP by moss for the bog. These were offset to some degree by the greater proportion of total NPP from roots for the fen scenario.

Clymo and others (1998) described three different measures of a peatland carbon balance: the long-term apparent rate of carbon accumulation ( $LARCA$  = total peat mass divided by basal age), the current rate of carbon accumulation ( $TRACA$ ), and the rate of carbon transfer from the oxic zone to the anoxic zone ( $P^*$ ) (see Eq. [1]). They also estimated the mean decay rate of the peat in the anoxic zone ( $\alpha^*$ , equivalent to a mass-weighted average  $k$  in our model). They generated  $P^*$  and  $\alpha^*$  parameters by fitting to peat core data a simple model with constant  $P^*$  and decomposition as in Eq. (3) ( $\alpha = 1$  or 2). All of these indicators of peat accumulation can be derived in PDM without curve fitting.  $LARCA$  values for PDM were similar, whereas  $TRACA$  values were lower for both the bog and the fen scenarios than reported by Clymo and others (1998) in their analysis of 795 peat cores from Finland (Table 3). Peat transfer rate to the anoxic zone was similar for the bog scenario, but the fen scenario had much greater transfer to the anoxic zone, primarily because of its significant root inputs into its partially anoxic zone between the water table and the bottom of the root zone. PDM mean decomposition rates for the anoxic zone were faster for the fen and slower for the bog than the curve-fit values Clymo and others (1998) derived for a linear decay model (as used in PDM) and a mean annual temperature of 5°C. Overall, we conclude that with surface observations of NPP and decomposition rates and a simple formulation for the change in tissue decom-

posability as peat moves down the profile, PDM can generate critical peat-producing parameters similar to those observed in northern peatland systems.

When PDM peat accumulation results were compared with observed peat core age–depth profiles, there were cases of both good and poor agreement. Although we used a very general parameterization and did not fit any parameters, PDM generated very realistic profiles for the most recent 5000–6000 years at one fen (FRON-1) and three bog sites (FRON-2, FRON-3, and MB-930). This same parameterization also overestimated peat accumulation during the past 2500–5000 years at three other sites (MAL-2, MAL-3, and MIR-1). There are several factors that may have contributed to these overestimations, some of which are demonstrated by the PDM sensitivity results (Table 1 and Figures 5 and 6).

First, PDM overall accumulation was quite sensitive to total vegetation NPP, particularly for bogs. Peatland NPP generally decreases with cooler temperatures (Moore 1989), so it is likely that Malbaie has relatively low productivity and thus lower accumulation. Moore and others (2001) presented a relationship between NPP and mean annual air temperature that suggests that Malbaie NPP should be about 55%–70% of that at the other sites. Second, variations in the relative NPP of mosses to vascular plants will also influence productivity rates. This ratio is not known for many peatlands, nor is its variability over millennial time scales. Third, bog accumulation rates are very sensitive to water table depth, and little is known about its historical variability. Mirabel shows evidence of local fires, which may have interrupted or temporarily reversed peat accumulation. Finally, from 2000 to 7000 cal. BP, the MAL-2 core shows very high regional pollen concentrations (excluding



peatland plants) (Lavoie 1998; Lavoie and Richard 2000a), indicating for MAL-2 either high decomposition rates (relative to production) or intermittent periods of peat consumption. When pools are present in a peatland, there will be significant decomposition in the peat under the pool, but negligible productivity in the pool (Seppälä and Koutaniemi 1985). This could lead to both enhanced pollen concentrations in the underlying peat and an age–depth profile similar to that observed in the MAL-2 core.

Because PDM is essentially a static model, the only dynamic feature we could simulate was a single transition from fen to bog, a common phenomenon in northern peatlands (Davis 1984; Janssens and others 1992; Kuhry and others 1993) that occurred at all of our bog core sites. For the Frontenac bog cores, PDM successfully simulated the underlying fen peat accumulation when this peat was subjected to bog-anoxic conditions, and its productivity and root:shoot ratio were adjusted to rich-fen values. The same adjustment failed to produce better simulations for the Mer Bleue and the Mirabel bog cores. At the Malbaie core 2 site, the underlying bogged-fen peat accumulation was similar to that observed. For the Malbaie 3 core, PDM overestimated fen peat accumulation; whereas at Mirabel and Mer Bleue, PDM underestimated fen peat accumulation. In all PDM sensitivity scenarios, fen peat accumulation was less responsive than bog peat accumulation. Nonetheless, changes in root contribution to total productivity, moss contribution to total productivity, temperature, or total productivity itself could each change fen peat accumulation by  $\pm 20\%$  or more, so scenarios of greater or lesser accumulation could be derived.

Although the representation of fen-to-bog transitions in PDM is very simplistic, it generally improves model performance, suggesting that future development in this area would be fruitful. Among the additional complexities that may be important are details of the nature and rate of shifts in productivity and decomposition during the vegetation transition from fen to bog, and rate of development of bog-anoxic conditions down the underlying fen peat. The extremely high rate of accumulation from 6000 to 8000 cal. BP observed in the Frontenac fen core (FRON-1) is coincident with a transition from brown moss to herbaceous peat. A rich-fen parameterization could accumulate peat rapidly (Figure 2), but conditions for decomposition of this early peat would have had to be much less favorable to preserve such a large amount of this old peat. The transition from initial marsh (telmatic peat) to true fen peat, when it applies, is also a matter of concern

because of the tremendous differences in productivity and decomposition.

The PDM value for  $f_{anox}$  for the bog scenarios (0.025) is lower than reported values, and the fen scenario  $f_{anox}$  value (0.10) is at the low end of reported values. Scanlon and Moore (2000) reported a mean aerobic/anaerobic decomposition rate ratio of 0.1 for 12-day incubations of intact cores. In short-term slurry incubations, Moore and Dalva (1997) and Bridgham and Richardson (1992) observed values around 0.4. Longer incubations also show a range in values—for example, Magnusson (1993): 26 weeks, 0.09–0.2; Updegraff and others (1995): 80 weeks, 0.25–0.5; Bridgham and others (1998): 59 weeks, 0.13–0.25. Based on the PDM model results, we hypothesize that these observations underestimate the degree of anoxicity in deep peat, particularly for bogs. All laboratory incubations involve significant disturbance of the in situ peat. The isolation of deep peat from the surface for centuries to millennia, due to extremely low hydraulic conductivities (see, for example, Ivanov 1981), cannot be re-created in the lab. In addition, the longer incubations may underestimate optimal aerobic decomposition due to developing substrate limitations. Another possible explanation of the apparent success of the low anoxic decomposition rates in PDM is that they compensate for an underestimation in the decline of cohort decomposability with mass loss (that is,  $\alpha > 2$  in Eq. [3]).

One important factor affecting peat accumulation at any site that was not included in PDM was the impact of varying environmental conditions over the millennia of peatland development and the effects of autogenic processes such as microtopographic development. Retreat of the ice sheet left bare soils whose nutrient content was initially high, then was progressively diminished through leaching (Willis and others 1997; Iversen 1954). There have been significant changes in climatic conditions in eastern Canada over the past 10,000 years (for example, see Wright and others 1993; Richard 1994; Lavoie and Richard 2000b). These changes have probably influenced peatland plant productivity (and thus litter input rates), peat soil climate profiles (and thus decomposition rates), and the composition of peatland vegetation (and thus tissue decomposability). Variation in any or all of these ecosystem function rates would lead to significant variation in peat accumulation rates over time (see Figures 5 and 6) (Clymo and others 1998). In the PDM results presented here, however, total NPP, the proportions of NPP from vascular and moss vegetation, and initial decomposition rates were all assumed to be constant

through time; and thus, model age–depth profiles are always a smooth, monotonic curve. To more fully explore the influence of the climatic variations on peat accumulation, the model would require dynamic water table and thermal regimes. These would influence plant demographics and both productivity and decomposition rates and thus most parameters in PDM.

Dynamics could be incorporated by merging PDM with the Peat Accumulation Model (PAM) of Hilbert and others (2000). PAM includes a simple water balance model that simulates the position of the water table as a function of the inputs and outputs of water and the changing surface elevation of the peatland. PAM also includes a simple description of the relationship between the position of water table and NPP of a peatland. At present, PAM does not consider the impact of variations in temperature, does not distinguish between moss and vascular plants or belowground and aboveground litter inputs, and has an overly simplified decomposition submodel.

To examine the impact of variations in climate, two additional pieces of information are required. First, an approximation of the date of peatland initiation is needed. In most major peatland regions there are estimates of the basal dates for the initiation of peat accumulation. The second requirement is a realistic chronology of the relative variations in moisture input to the peatland from the time of initiation to the present day, obtained from a data source independent of the peatlands. These independent chronologies are not readily available in most peatland areas, but regional reconstructions based on palynological and macrofossil analyses of lake sediments in some peatland regions are forthcoming (for example, see Lavoie and Richard 2000b; S. D. Muller and P. J. H. Richard unpublished).

## ACKNOWLEDGMENTS

This work has been supported by grants from the NASA Terrestrial Ecology Program's BOREAS Guest Investigator Program to S. F. and an NSERC Strategic Grant to N.T.R. Paleocological results were acquired through the NSERC-funded program Climate System History and Dynamics (Team 4: Konrad Gajewski, University of Ottawa, and P. J. H. R.). We thank Peter Lafleur for access to unpublished data. We also thank Göran Ågren and an anonymous reviewer for suggestions and comments that helped to focus and improve the manuscript.

## REFERENCES

- Aerts R, Wallen B, Malmer N. 1992. Growth-limiting nutrients in *Sphagnum*-dominated bogs subject to low and high atmospheric nitrogen supply. *J Ecol* 80:131–140.
- Ågren GI, Bosatta E. 1996a. Quality: a bridge between theory and experiment in soil organic matter studies. *Oikos* 76:522–528.
- Ågren GI, Bosatta E. 1996b. Theoretical ecosystem ecology: understanding element cycles. Cambridge (UK): Cambridge University Press. 234 p.
- Backéus I. 1990. Production and depth distribution of fine roots in a boreal open bog. *Ann Bot Fennici* 27:261–5.
- Ball T. 1996. Seasonal transitions in fluxes of carbon dioxide and methane from an ombrotrophic peatland, Frontenac Bog, southern Quebec [thesis]. Montreal: Geography Department, McGill University. 142 p.
- Bartsch I, Moore TR. 1985. A preliminary investigation of primary production and decomposition in four peatlands near Schefferville, Québec. *Can J Bot* 63:1241–8.
- Belyea LR. 1996. Separating the effects of litter quality and macroenvironment on decomposition rates in a patterned peatland. *Oikos* 77:529–39.
- Belyea LR, Clymo RS. 1999. Do hollows control the rate of peat bog growth? In: Meade R, Standen V, Tallis JH, editors. Patterned mires: origin and development, flora and fauna. London: British Ecological Society, Mires Research Group. p 1–15.
- Boelter DH. 1968. Important physical properties of peat material. Proceedings of the Third International Peat Congress., National Research Council of Canada, Quebec City. p. 150–156.
- Bridgman SD, Richardson CJ. 1992. Mechanisms controlling soil respiration ( $\text{CO}_2$  and  $\text{CH}_4$ ) in southern peatlands. *Soil Biol Biochem* 24:1089–99.
- Bridgman SD, Updegraff K, Pastor J. 1998. Carbon, nitrogen, and phosphorus mineralization in northern wetlands. *Ecology* 79: 1545–61.
- Brinson MM, Lugo AE, Brown S. 1981. Primary productivity, decomposition, and consumer activity in freshwater wetlands. *Annual Rev Ecol Syst* 12:123–61.
- Clymo RS. 1984. The limits to peat bog growth. *Philos Trans R Soc London B* 303:605–54.
- Clymo RS. 1992. Models of peat growth. *Suo* 43:127–36.
- Clymo RS, Turunen J, Tolonen K. 1998. Carbon accumulation in peatland. *Oikos* 81:368–88.
- Davis AM. 1984. Ombrotrophic peatlands in Newfoundland, Canada: their origins, development and trans-atlantic affinities. *Chem Geol* 44:287–309.
- Environment Canada. 1994. Canadian monthly climate data and 1961–90 normals on CD-Rom (version 3.0). Ottawa: Atmospheric Environment Service.
- Frolking S, Bubier JL, Moore TR, Ball T, Bellisario LM, Bhardwaj A, Carroll P, Crill PM, Lafleur PM, McCaughey JH, and others. 1998. Relationship between ecosystem productivity and photosynthetically-active radiation for northern peatlands. *Global Biogeochem Cycles* 12:115–26.
- Gilbert D, Amblard C, Bourdier G, Francez A-J. 1998. Short-term effect of nitrogen enrichment on the microbial communities of a peatland. *Hydrobiologia* 373/374:111–9.
- Gorham E. 1995. The biogeochemistry of northern peatlands and its possible response to global warming. In: Woodwell GM, MacKenzie FT, editors. Biotic feedbacks in the global

- climatic system: will the warming speed the warming? New York: Oxford University Press. p 169–87.
- Gorham E. 1991. Northern peatlands: role in the carbon cycle and probable responses to climatic warming. *Ecol Appl.* 1:182–95.
- Gorham E, Janssens JA. 1993. The paleorecord of geochemistry and hydrology in northern peatlands and its relation to global change. *Suo* 43:117–26.
- Heal OW, Anderson JM, Swift MJ. 1997. Plant litter quality and decomposition: an historical overview. In: Cadisch G, Giller KE, editors. *Driven by nature: plant litter quality and decomposition*. New York: CABI. p 3–30.
- Hilbert D, Roulet NT, Moore TR. 2000. Modelling and analysis of peatlands as dynamic systems. *J Ecol* 88:230–42.
- Hogg EH. 1993. Decay potentials of hummock and hollow *Sphagnum* peats at different depths in a Swedish raised bog. *Oikos* 66:269–78.
- Ingram HAP. 1983. Hydrology. In: Gore, AJP editor. *Mires: swamp, bog, fen, and moor; vol 4A*. Amsterdam: Elsevier Scientific Publishing p 67–158.
- Irwin RW. 1968. Soil water characteristics of some (southern) Ontario peats. *Proceedings of the Third International Peat Congress, National Research Council of Canada, Quebec City*.
- Ivanov KE. 1981. Water movement in mirelands. New York: Academic Press. p. 165–168.
- Iversen J. 1954. The late-glacial flora of Denmark and its relation to climate and soil. *Danmarks Geol Undersgelse* 11(80):87–119.
- Janssens JA, Hansen BCS, Glaser PH, Whitlock C. 1992. Development of a raised-bog complex. In: Wright HE, Jr, Coffin BA, Aaseng NE, editors. *The patterned peatlands of Minnesota*. Minneapolis: University of Minnesota Press. p 189–221.
- Jauhiainen J, Silvola J, Vasander H. 1999. The effects of increased nitrogen deposition and CO<sub>2</sub> on *Sphagnum angustifolium* and *S. warnstorffii*. *Ann Bot Fennici* 35:247–56.
- Johnson LC, Damman AWH. 1993. Decay and its regulation in *Sphagnum* peatlands. *Adv Bryol* 5:249–96.
- Kuhry P, Nicholson BJ, Gignac LD, Vitt DH, Bayley SE. 1993. Development of *Sphagnum* dominated peatlands in boreal continental Canada. *Can J Bot* 71:10–22.
- Lafleur PM, Roulet NT, Admiral S. 2001. The annual cycle of CO<sub>2</sub> exchange at a boreal bog peatland. *J Geophys Res.* 106:3071–3081.
- Lähde E. 1967. Seasonal variation in the depth of the aerobic limit and the ground water table in virgin and in drained Myrtillus spruce swamp. *Acta Forestalia Fennica* 81:1–15.
- Lavoie M. 1998. *Dynamique de l'entourbement et fluctuations des niveaux lacustres postglaciaires au Québec méridional* [thesis.]. Montreal: Département de géographie, Université de Montréal.
- Lavoie M, Richard PJH. 2000a. Paléoécologie de la tourbière du lac Malbaie, massif des Laurentides (Québec): évaluation du rôle du climat sur l'accumulation de tourbe. *Geogr Phys Quat.* 54:165–181.
- Lavoie M, Richard PJH. 2000b. Postglacial water-level fluctuations of a small lake in Southern Québec. *Holocene* 10: 621–34.
- Lavoie M, Richard PJH. 2000c. The role of climate on the developmental history of Frontenac peatland, Southern Quebec. *Can J Bot* 78:668–84.
- Magnusson T. 1993. Carbon dioxide and methane formation in forest mineral and peat soils during aerobic and anaerobic incubations. *Soil Biol Biochem* 25:877–83.
- Moore TR. 1989. Growth and production of *Sphagnum* at five fen sites, subarctic eastern Canada. *Can J Bot* 67:1203–7.
- Moore TR, Bubier JL, Frolking S, Roulet NT. 2001. Plant biomass and production and CO<sub>2</sub> exchange in an ombrotrophic bog. *J Ecol.* Forthcoming.
- Moore TR, Dalva M. 1997. CO<sub>2</sub> and CH<sub>4</sub> exchange potentials of peat soils aerobic and anaerobic laboratory incubations. *Soil Biol Biochem* 29:1157–64.
- Mott RJ, Camfield M. 1969. Palynological studies in the Ottawa area. Paper 69–38. Ottawa: Geological Survey of Canada. 16 p.
- Paustian K, Ågren GI, Bosatta E. 1997. Modelling litter quality effects on decomposition and soil organic matter dynamics. In: Cadisch G, Giller KE, editors. *Driven by nature: plant litter quality and decomposition*. New York: CABL. p 313–35.
- Puranen R, Mäkilä M, Säävuori H. 1999. Electric conductivity and temperature variations within a raised bog in Finland: implications for bog development. *Holocene* 9:13–24.
- Richard PJH. 1994. Postglacial palaeophytogeography of the eastern St. Lawrence River watershed and the climatic signal of the pollen record. *Palaeogeog Palaeoclimatol Palaeoecol* 109: 137–63.
- Saarinén T. 1996. Biomass and production of two vascular plants in a boreal mesotrophic fen. *Can J Bot* 74:934–8.
- Scanlon D, Moore TR. 2000. CO<sub>2</sub> production from peatland soil profiles: the influence of temperature, oxic/anoxic conditions and substrate. *Soil Sci* 165:153–60.
- Seppälä M, Koutaniemi L. 1985. Formation of a string and pool topography as expressed by morphology, stratigraphy and current processes on a mire in Kuusamo, Finland. *Boreas* 14:287–309.
- Siegel DI. 1993. Groundwater hydrology. In: Wright HE, Jr, Coffin BA, Aaseng NE, editors. *The patterned peatlands of Minnesota*. Minneapolis: University of Minnesota Press. p 163–72.
- Stuiver M, Reimer PJ, Bard E, Beck JW, Burr GS, Hughen KA, Kromer B, McCormac FG, van der Plicht, Spurk M. 1998. *INTCAL98 radiocarbon age calibration, 24,000–0 cal. BP*. *Radiocarbon* 40:1041–83.
- Thormann MN, Bayley SE. 1997. Above-ground net primary production along a bog-fen-marsh gradient in southern boreal Alberta, Canada. *Ecoscience* 4:374–84.
- Tolonen K, Vasander H, Damman AWH, Clymo RS. 1992. Preliminary estimate of long-term carbon accumulation and loss in 25 boreal peatlands. *Suo* 43:277–80.
- Updegraff K, Pastor J, Bridgman SD, Johnston CA. 1995. Environmental and substrate quality controls over carbon and nitrogen mineralization in a beaver meadow and a bog. *Ecol Appl* 5:151–63.
- Verhoeven JT, Toth E. 1995. Decomposition and *Carex* and *Sphagnum* litter in fens: effect of litter quality and inhibitions by living tissue homogenates. *Soil Biol Biochem* 27:271–5.
- Verry ES, Brooks KN, Barten PK. 1988. Streamflow response from an ombrotrophic mire. Vol. 1. *International Symposium on the Hydrology of Wetlands in Temperate and Cold Regions*, The Publications of the Academy of Finland, Helsinki. p. 52–59.

- Wallén B. 1986. Above and below ground dry mass of the three main vascular plants on hummocks of a subarctic peat bog. *Oikos* 46:51–6.
- Williams BL, Silcock DJ. 1997. Nutrient and microbial changes in the peat profile beneath *Sphagnum magellanicum* in response to additions of ammonium nitrate. *J Ecol* 34:961–70.
- Willis KJ, Braun M, Sümegi P, Tóth A. 1997. Does soil change cause vegetation change or vice versa? A temporal perspective from Hungary. *Ecology* 78:740–50.
- Wright HE, Kutzbach JE, Street-Perrott FA, Ruddiman WF, Webb T III. 1993. *Global climates since the last glacial maximum*. Minneapolis: University of Minnesota Press.