

Modelling long-term peatland dynamics. II. Processes and rates as inferred from litter and peat-core data

Zicheng Yu ^{a,b,c,*}, M.R. Turetsky ^c, I.D. Campbell ^{a,b,1}, D.H. Vitt ^{c,2}

^a Northern Forestry Centre, Canadian Forest Service, 5320–122 Street, Edmonton, Alta., Canada T6H 3S5

^b Department of Earth and Atmospheric Sciences, University of Alberta, Edmonton, Alta., Canada T6G 2H4

^c Department of Biological Sciences, University of Alberta, Edmonton, Alta., Canada T6G 2E9

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Abstract

The production and decomposition of organic matter are major processes determining peat accumulation dynamics, both of which vary over different time scales. Here we evaluate three types of experimental and observational data related to peatlands, which are from litter, oxic (acrotelm) peat, and anoxic (catotelm) peat. The ²¹⁰Pb-dated peat-core profiles for the last 100–200 years are used to understand the oxic decomposition processes; ¹⁴C-dated peat profiles for the last several millennia are used for understanding anoxic decomposition processes. Analysis of data from litter-bag experiments suggests that a significant portion of the litter is lost in the first few years owing primarily to rapid initial decomposition processes, including movement/leaching of soluble materials. This is also confirmed indirectly by ²¹⁰Pb-dated peat-core data. Several records of acrotelm peat show similar estimated litter-addition ($265 \pm 37.3 \text{ g m}^{-2} \text{ year}^{-1}$) and decay rates ($0.017 \pm 0.0047 \text{ year}^{-1}$), despite the climatic difference among study areas. The litter-addition rate of $265 \text{ g m}^{-2} \text{ year}^{-1}$ is at most about half of measured net primary production. Warmer climate causes higher production but also higher decomposition. The balance of production and decay processes in the litter and acrotelm determines the peat addition rate to the catotelm, where long-term peat accumulation occurs. Our sensitivity analysis shows that change in the peat-addition rate would affect both young and old peat; in contrast, a change in the decay rate has more influence on old peat. We therefore hypothesize that the wiggles often seen in peat age–depth profiles are caused by changes in peat addition rates, which are determined by climatically sensitive processes including photosynthesis and acrotelm decomposition. Evaluating these litter and peat-core data provides insights useful to the design and implementation of a peatland dynamics simulation model. © 2001 Elsevier Science B.V. All rights reserved.

Keywords: Peatlands; Litter; Acrotelm; Catotelm; Decomposition; Climate change; Models

* Corresponding author. Present address: Department of Earth and Environmental Sciences, Lehigh University, Bethlehem, PA 18015, USA.

E-mail address: ziy2@lehigh.edu (Z. Yu).

¹ Present address: Canadian Forest Service, Science Branch, 580 Booth Street, Ottawa, Ont. K1A 0E4, Canada.

² Present address: Department of Plant Biology, Southern Illinois University, Carbondale, IL 62901, USA.

1. Introduction

This is the second article devoted to understanding and modelling the long-term carbon dynamics of northern peatlands. The first article (Yu et al., 2001) briefly reviews the available conceptual and simulation models for peatlands and presents a framework for modelling peatland dynamics, based on a well-accepted conceptual model (Clymo, 1984). The current article presents results from re-analysis of available field data, which provide the basis for the proposed simulation model design. Although these articles are closely related, each addresses and presents its own topic and conclusions.

The production and decomposition of organic matter are the major processes determining peatland carbon dynamics, which vary over different time scales. To fully understand peat addition and decomposition processes in peatlands, we analyze experimental and observational data from the three main components of the peat system: (1) litter, (2) acrotelm peat (above the lowest seasonal water table), and (3) catotelm peat (permanently saturated peat below the water table). Data from litter-bag experiments elucidate decomposition processes during the first few years following litter addition to the surface of peatlands. ^{210}Pb -dated peat-core profiles for the last 100–200 years are used to test models of oxic decomposition processes, whereas ^{14}C -dated peat profiles are used for understanding anoxic decomposition processes. These data analyses provide the basis for the model design as described in Yu et al. (2001). The meta-analysis presented here points to a need for new high-resolution data at and near the boundary between the acrotelm and catotelm.

The objectives of this article are (1) to evaluate these three components (litter, acrotelm, and catotelm) of peatland ecosystems in the same context using same approach; (2) to infer processes linking these components and to estimate parameters needed for peatland dynamic simulations; and (3) to carry out sensitivity analysis for understanding the relative roles of different processes in determining long-term peat accumulation.

2. Decay rules and their significance

The selection of a decay model is one of the distinguishing features in both conceptual and simulation peatland models. Two criteria to guide this selection are biologically meaningful and mathematically tractable behaviours. Wieder and Lang (1982) reviewed different statistical methods for analyzing decomposition data. If the proportion of initial mass remaining at time t is $X=f(t)$, then two decomposition rates can be defined as (1) absolute decomposition rate, which is the first derivative of X with respect to t , (dX/dt) , and (2) relative decomposition rate, $((dX)/(dX))$ (Wieder and Lang, 1982).

The most realistic decomposition models appear to be one of the exponential models, in terms of both mathematical and biological behaviour (Wieder and Lang, 1982). In dealing with litter-bag decomposition data, a single exponential decay function (Jenny et al., 1949; Olson, 1963) has a formulation of $X=e^{-kt}$. The consequences of this model are (1) the absolute decay rate decreases as the amount of substrate remaining declines, and (2) the relative decay rate remains constant. A double exponential decay model has the form of $X=A \exp(-k_1t) + (1-A)\exp(-k_2t)$ (Wieder and Lang, 1982), which assumes that litter can be partitioned into two components: a relatively easily decomposed or labile fraction (A) and a more recalcitrant fraction ($1-A$). Each fraction decomposes at a different rate (k_1 , k_2), with $k_1 > k_2$. The consequences are (1) the overall relative rate tends to decline over time, approaching k_2 , and (2) the overall absolute rate decreases non-linearly over time.

A double exponential decay model appears to be biologically more realistic (e.g. Wieder and Lang, 1982) and could be adapted to make the peatland model more compatible with the ‘standard’ upland soil ecosystem models, such as the CBM-CFS2 forest carbon budget model (Kurz et al., 1992; Kurz and Apps, 1999). The CBM-CFS2 model uses four pools to represent soil organic carbon: very fast, fast, medium and slow pools. Each pool consists of different plant materials and has a different decomposition rate. In a forested peatland, the ability to implement two or more

compartments (moss, sedge, forest litter, etc.) is certainly desirable, especially when more detailed data are available. The appropriate peat decay constants are in the range of 0.01–0.8 year⁻¹ for the acrotelm and 0.7–5.5 × 10⁻⁴ year⁻¹ for the catotelm, if a single exponential model is used (Clymo, 1984). In comparison, the decay constants for the four pools in the upland soils in the CBM-CFS2 model are 0.5 (very fast), 0.14 (fast), 0.037 (medium) and 0.0068 year⁻¹ (slow), all of which are closer to the ones for the oxic acrotelm than anoxic catotelm peats.

For analyzing the peat-core data, the general formulation is $dM/dt = p - \alpha M$, where M is cumulative dry peat mass (g m⁻²), p is peat-mass input rate (g m⁻² year⁻¹), and α is decay rate (year⁻¹). Its solution is dependent on the selection of decay rules (e.g. constant, linear, or non-linear rules; Clymo et al., 1998; Yu et al., 2001) and the selection of a function for changing the peat addition rate (p). The simplest case with constant decay coefficient has a general solution in the form of $M = (p/\alpha)[1 - \exp(-\alpha T)]$ (where T is the time span of accumulated peat mass M), when both p and α are constant (Clymo, 1984). Different decay rules imply different processes and will generate slightly different results.

3. Litter inputs and initial decomposition

3.1. Net plant productivity and environmental controls

Net primary production (NPP) is the initial input to peatlands through fixation of atmospheric CO₂ by photosynthesis. In spite of very different plant communities and vegetation covers, NPP as reported in the literature does not vary widely for different types of peatlands. Campbell et al. (2000)'s compilation shows a mean NPP of 522 g m⁻² year⁻¹ (348 ± 184 aboveground NPP, and an additional 50% (174 g m⁻² year⁻¹) assumed for belowground NPP) for non-permafrost peatlands (bogs and fens) in continental Canada. However, recently reported data suggest much large contribution from belowground NPP at least for fens (Saarinen, 1996).

Mitsch and Gosselink (1993) estimated NPP at 560 g m⁻² year⁻¹ for northern bogs. Using Gorham's (Gorham, 1991) estimates of peat-addition rates to the catotelm of ≈ 40 g m⁻² year⁻¹ and Clymo's (Clymo, 1984) overall average percentage of input from the acrotelm to catotelm (10–20%), the productivity atop the acrotelm would be 400–800 g m⁻² year⁻¹. Thus, in mature peatlands, we can assume that the litter production rate of dead organic material is equal to NPP, which requires that there be no removal of vegetation by other means including animals.

Climate and other environmental factors influence the NPP in a peatland. Moore (1989) combined his own field data and other data from the literature and found that a 1-degree increase in mean annual temperature (MAT) could cause a 17 g m⁻² year⁻¹ increase in *Sphagnum* NPP. He reported the regression relation: *Sphagnum* NPP = 187 + 17.2MAT (g m⁻² year⁻¹; $n = 60$; $r^2 = 0.307$; $P < 0.001$) (Fig. 1A). Thormann et al. (1998) also reported a positive relation between moss NPP and summer (growing season) temperatures, suggesting a 41 g m⁻² year⁻¹ increase in moss NPP with a 1-degree increase in summer temperature. These relationships are, however, quite weak. Thormann et al.'s study consisted of four summarized points from a single site observed for 4 years. Moore's data (1989) are heavily leveraged by the small number of sites at the cold end of the spectrum—the more numerous warmer sites show greater variation than do the few cold sites.

Thormann et al. (1998) found a positive effect of water table on NPP for a lacustrine sedge fen (extreme-rich fen) in central Alberta. Their field data from 1991 to 1994 suggested an 11 g m⁻² year⁻¹ increase in total NPP per 1-cm rise in water table. Thormann and Bayley's (Thormann and Bayley, 1997a) results show that a 22.4-cm rise in water table caused a 326% increase in herb NPP in 1993–1994; whereas Szumigalski and Bayley (1996) showed a 14-cm decline in water table causing a 40% decrease in herb NPP at the same site in 1991–1992. The NPP and water table measurements in a bog at Ellergower Moss, southwestern Scotland, show various relations for different species groups (Fig. 1B; Belyea and

Clymo, 1999; Belyea, 1995). Herb NPP tends to increase with rising water tables, but the reverse is

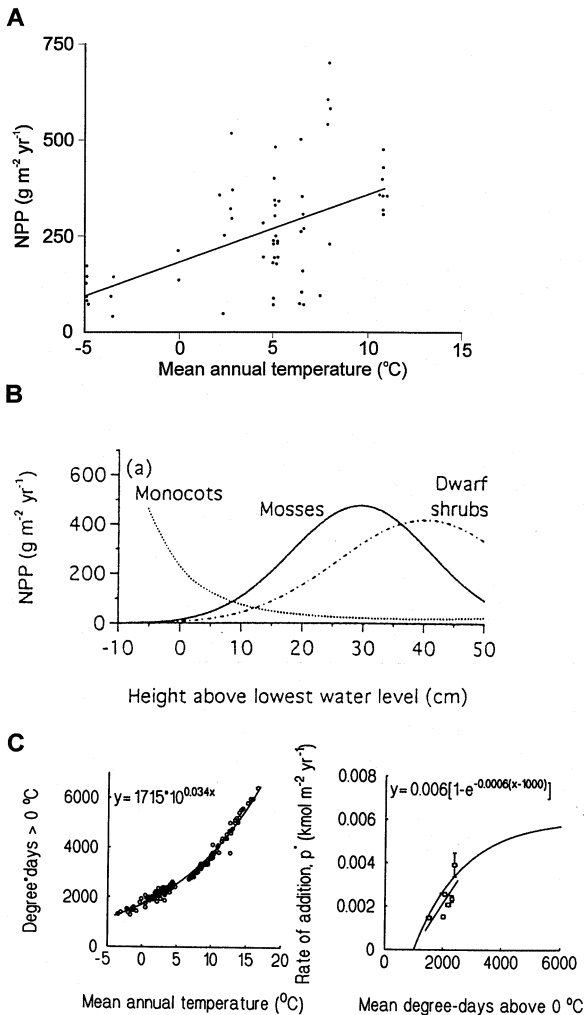


Fig. 1. (A) An example of the statistical relationship between net primary production (NPP) and environment factors (temperature in this case) (modified from Moore, 1989). Solid line is originally reported regression line (see text for discussion). (B) Relationship of water level with NPP of linear-leaved plants ('Monocots'), *Sphagnum* mosses, and ericaceous dwarf shrubs at Ellergower Moss, southwestern Scotland (from Belyea and Clymo, 1999; Belyea, 1995). Curves are second-order polynomial regressions of log-transformed. (C) Relations between degree-days above zero and mean annual temperature (left) and relation between peat-addition rate and degree-days above zero (right). The points and corresponding regression line are based on data for five regions in Finland and the mid-Boreal region of Canada (Canadian data from Zoltai, 1991; graphs adapted from Clymo et al., 1998).

true for dwarf shrubs. For *Sphagnum* mosses, the second-order polynomial regression shows a 'bell-shaped' curve, with a peak NPP at a WTD of ≈ 30 cm. The results from fens in Alberta as discussed above appear to capture only certain portions of this overall relationship.

Hilbert et al. (2000) hypothesized a quadratic peat productivity function, suggesting that plant growth peaks at some intermediate value of the limiting environmental condition and decreases to zero for either greater or lower environmental values. Their functional relation is in the form of $P = k(E - E_{\min})(E_{\max} - E)$, where k is a coefficient determining the maximum productivity, and E_{\max} and E_{\min} are maximum and minimum environmental conditions at which growth equals zero. They specifically used WTD as the major environmental variable.

In the proposed model, $550 \text{ g m}^{-2} \text{ year}^{-1}$ will be taken as the base NPP value. The effective moisture and subsequent WTD will be the major environmental drivers. Environmental relations can be treated either empirically or hypothetically, but the extrapolation of relationships built upon a limited range of environmental variability could easily result in unstable model behaviours. In contrast, a purely hypothetical growth function would run the risk of being unverifiable through field data. Therefore, the middle ground and a compromise approach is the preferred route: theoretically based extrapolation of an empirical relationship (e.g. Fig. 1C; see Clymo et al., 1998).

3.2. Initial decomposition of litter

In the first few years, litter will experience very rapid initial decomposition caused by processes such as leaching of soluble organic materials. We used data from a litter-bag experiment using *Rubus chamaemorus* leaves (Heal et al., 1978) to test the relative suitability of single exponential, double exponential and linear decay models (Fig. 2). The single exponential model assumes that material is homogeneous. However, this model produces the poorest fit to the data set, suggesting that *Rubus* leaves are not homogeneous in terms of decay. In contrast, the double exponential model produces the best fit, implying the litter

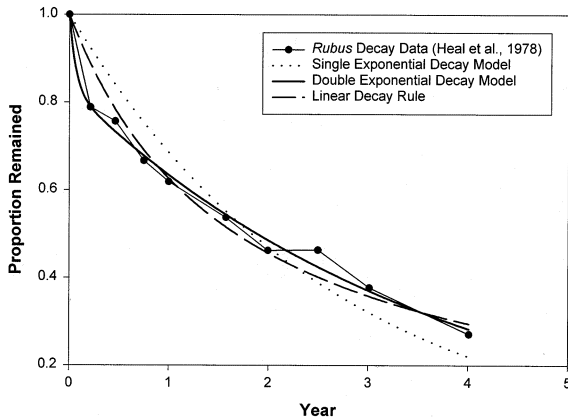


Fig. 2. Decomposition of *Rubus* leaves (data from Heal et al., 1978) and fitted curves using single exponential decay ($\alpha = 0.38 \text{ year}^{-1}$; also analyzed by Clymo, 1984) and double exponential ($\alpha_1 = 15.4 \text{ year}^{-1}$; $\alpha_2 = 0.27 \text{ year}^{-1}$), and linear models ($\alpha = 0.6 \text{ year}^{-1}$). The exercise seems to support the use of a double exponential decay model, which provides a second decay term significantly greater than zero.

consists of two components: a fast decay component with a decay coefficient of 15 year^{-1} ($\approx 20\%$ of litter mass), which thought to be leachable solutes, and a slow component of 0.27 year^{-1} ($\approx 80\%$ of litter mass).

Litter-bag experiments in peatlands tend to have a limited number of data points and are conducted mostly for short time periods. These study designs prevent us from analyzing more litter data using a double exponential model. The *Carex aquatilis* decomposition data from an open rich fen in central Alberta, with four data points over 100 days (Thormann, 1995), suggest a decay rate of 5.4 year^{-1} in a single exponential model. *Carex* in another open rich fen shows a decay rate of 0.60 year^{-1} with three data points over a 2-year period (Szumigalski and Bayley, 1996).

We realise that *Rubus* leaves decay much faster than *Sphagnum* or woody tissues (Clymo, 1965; Coulson and Butterfield, 1978), but the observed pattern is probably similar to other types of litter with different decay rates, showing rapid initial mass loss (e.g. Rochefort et al., 1990). If the pattern from *Rubus* leaves is typical of litter in peatlands, then a double exponential decay model should be used to capture the initial decomposition process. The initial loss of matter is so rapid

for *Rubus* (40% of litter is removed in the first year) that a linear decay model does not fit the data (Fig. 2). The product of this initial decay is likely not in the form of gases CO_2 and CH_4 but of liquids such as dissolved organic carbon (DOC) derived from leaching processes (e.g. Sallantausta, 1992; Waddington and Roulet, 1997). This DOC will be likely subject to further decomposition in the acrotelm to CO_2 and CH_4 (see next section for further discussion).

The decomposition rates of litter are believed to be a function of temperature fluctuations (variability) and mean temperatures (Clymo, 1984). There are limited data, however, to build a reliable functional relationship. The oxygen consumption rate of decomposing *Rubus* leaves, as a proxy of decomposition, shows an exponential relation between decomposition and temperature, $\alpha_T = 142(-0.86 + e^{0.0324T})$, where α_T is the temperature-dependent decomposition rate and T is temperature (Rosswall, 1974; Clymo, 1984).

4. The acrotelm

Several peat profiles dated by ^{210}Pb can be analyzed to detect patterns in terms of organic matter addition and decomposition during the first 100–200 years (usually the top 20–30 cm of peat; i.e. acrotelm). Although there are no on-site water-level monitoring and measurements at these sites, the ^{210}Pb -dated portion is assumed to be acrotelm only. Seven profiles from five bog sites in central and northern Alberta (Turetsky et al., 2000) and Minnesota and West Virginia (Wieder et al., 1994) are used here. All profiles show concave peat age–depth/mass curves (Fig. 3), suggesting continuous decomposition in the peat column. Both single and double exponential models were fitted to the profile, but the double model does not produce a second decay term statistically different from zero, indicating that a single exponential model is sufficient to explain the data.

Using a single exponential model, the five sites produce quite similar estimates of decay coefficients ($0.017 \pm 0.0047 \text{ year}^{-1}$) and litter addition rates ($265 \pm 37.3 \text{ g m}^{-2} \text{ year}^{-1}$) (Table 1), despite the range of climate conditions represented at

these sites. The most southern site (Big Run Bog in West Virginia) has a mean annual temperature of 8.3 °C and annual precipitation of 1215 mm; whereas the Minnesota site (Marcell S-2 Bog) has a mean annual temperature of 4.2 °C and precipitation of 670 mm (Wieder et al., 1994). The sites in Alberta have even lower temperatures (−0.2 to 1.4 °C) and lower precipitation (471.9–490 mm) (Environment Canada, 1982). On the basis of similar rates of net peat accumulation over the last 150–200 years at four sites along a latitudinal

gradient from West Virginia to Ontario (over 8 degrees), Wieder et al. (1994) suggested that the recent peat accumulation may be relatively insensitive to broad-scale regional climatic differences.

The estimated litter addition rates of 265 g m^{−2} year^{−1} to the acrotelm are at most only half of the measured NPP in the Alberta sites (Thormann and Bayley, 1997b) and much less than that in the southern sites (aboveground NPP of 1045 g m^{−2} year^{−1} at Big Run Bog; Wieder et al., 1989). This suggests that the initial decomposition of litter in the first few years is responsible for the loss of that portion of organic matter, likely in the form of DOC by leaching. Two bog cores from Bleak Lake Bog (Fig. 3B) show quite different values of estimated litter addition rates and decay rates. The two coring sites are only about 15 m apart, so this suggests a significant within-bog variation (see Waddington and Roulet, 1996).

The similarity of estimated decay and litter-addition rates for sites in different climate conditions suggests weak environmental controls of litter addition rates and decomposition rates even in the acrotelm, while the results from two cores at Bleak Lake Bog suggest local, presumably hydrological, factors may be more important than general climatic context. Strong environmental controls on litter production and decomposition, however, likely exist. Warm climate and high precipitation at Big Run Bog (West Virginia) result in high NPP (Wieder et al., 1989), but at same time the high temperature would also promote rapid initial litter decomposition as well as a high leaching rate due to flushing by the abundant precipitation. The opposite applies to the northern sites in Minnesota and Alberta, and consequently the inferred processes and rates in the acrotelm are quite similar. If this analysis is correct, then the processes associated with litter production and decay over a short time scales are critical in determining peat accumulation at longer time scales.

As the mathematical behaviour of the single exponential model suggests, changing the decay coefficients would shift the concavity of the peat age–mass curves (high decay rate causing greater concavity; Fig. 4A), whereas changing litter-addition rates would modify the peat mass/depth ac-

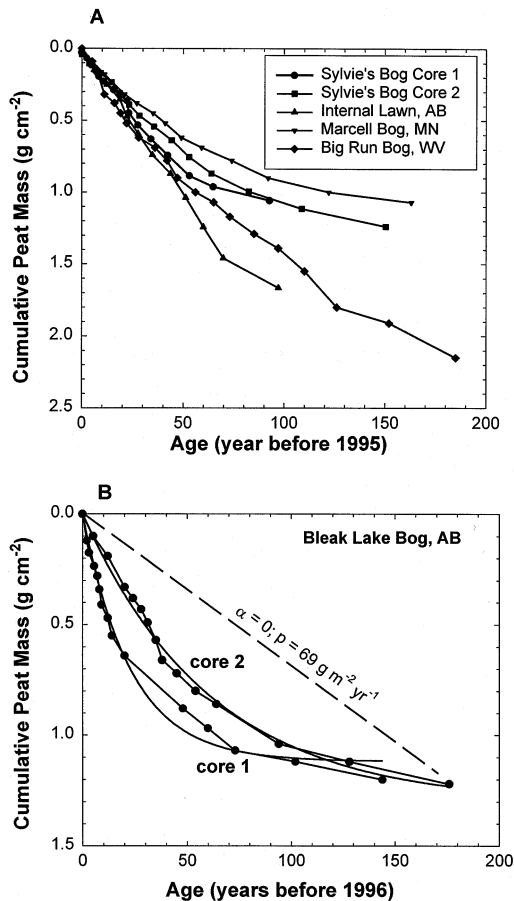


Fig. 3. ²¹⁰Pb-dated peat profiles and fitting exercises. (A) Sylvie's Bog, Core 1 and Core 2, AB; Internal Lawn Bog, AB; Marcell S-2 Bog, MN; and Big Run Bog, WV; (B) Comparison of Core 1 and Core 2 from Bleak Lake Bog, AB. The straight dashed line in B shows the case when there is no decomposition ($\alpha = 0$). Data for Alberta (AB) sites are from Turetsky et al. (2000), and for West Virginia (WV) and Minnesota (MN) from Wieder et al. (1994).

Table 1

Summary of decomposition coefficients and litter-addition rates in the acrotelm based on fitting of ^{210}Pb -dated peat profiles using a single exponential decay model

Site	Location (lat., long.)	Annual temperature (°C)	Annual precipitation (mm)	Decay coefficients (year ⁻¹)	Litter-addition rate (g m ⁻² year ⁻¹)
Sylvie's Bog Core 1, AB ^a	56°N; 112°32'W	-0.2	472	0.0176	241
Sylvie's Bog Core 2, AB ^a	56°N; 112°32'W	-0.2	472	0.0139	199
Internal Lawn Bog, AB ^a	56°N; 112°32'W	-0.2	472	0.0062	238
Bleak Lake Bog Core 1, AB ^a	56°30'N; 113°W	1.4	490	0.0433	484
Bleak Lake Bog Core 2, AB ^a	56°30'N; 113°W	1.4	490	0.0164	213
Marcell S-2 Bog, MN ^b	47°32'N; 93°28'W	4.2	670	0.0117	259
Big Run Bog, WV ^b	39°07'N; 79°35'W	8.3	1215	0.0082	221
Mean				0.017	265
S.E.				0.0047	37.3

^a Data from Turetsky et al. (2000);

^b Data from Wieder et al. (1994).

cumulated (Fig. 4B). Based on results in Fig. 3B and the sensitivity analysis in Fig. 4, we know that many combinations of two parameters (α , p) can achieve the same end-point peat mass accumulated at an individual site, but with different time course. What really happens in nature does matter for reconstructing the past peat accumulation as well as for projecting possible future change.

5. The catotelm

5.1. Fitting the ^{14}C -dated peat profiles

Most of the potential peat organic mass produced as NPP by living plants is decayed atop the acrotelm as litter and in the acrotelm prior to entry into the catotelm. The rate of peat addition to the catotelm has been estimated at 10–20% of NPP, with a range of 36–78 g m⁻² year⁻¹ (Clymo, 1984; Gorham, 1991). For a single exponential decay model, the constant decay rate is in the range of $0.7\text{--}5.5 \times 10^{-4}$ year⁻¹, based on the compilation by Clymo (1984).

Here we use the data from Draved Mose in Denmark (Aaby and Tauber, 1975) as an example to examine the peat accumulation pattern, to infer the underlying processes and to estimate parameters. We performed curve fitting exercises using program SigmaPlot (SSPS Inc.) on this data set, which includes 55 ^{14}C dates, using single exponential ($M = (p_c/\alpha_c)(1 - \exp(-\alpha_c t))$), double exponential ($M = (p_{c1}/\alpha_{c1})(1 - \exp(-\alpha_{c1} t)) + (p_{c2}/\alpha_{c2})(1 - \exp(-\alpha_{c2} t))$), and linear decay models ($M = (p_c/\alpha_c)\ln(1 + \alpha_c t)$) (see Clymo et al., 1998; Yu et al., 2001). In the models, the rates of peat addition, or catotelm production (p_c) determine the general slope of the curve, and the decay constants (α) determine the curvature. Draved Mose demonstrates a concave age–depth/mass curve (Fig. 5; data from Aaby and Tauber, 1975). Using these dates calibrated with the program CALIB Rev. 4.0 (Stuiver et al., 1998) and assuming a constant bulk density of 0.1 g cm⁻³ as estimated from humification (Clymo, 1984), the estimated values from a single exponential model are 69 g m⁻² year⁻¹ for the peat addition rate (p_c) and 0.00024 year⁻¹ for the constant decay rate (α). The estimates are similar to those reported in

Clymo (1984) with same model, $64 \text{ g m}^{-2} \text{ year}^{-1}$ and $0.00019 \text{ year}^{-1}$. The fitting exercise suggests that despite the greater degree of realism it theoretically carries, a double exponential decay model is not needed because the second fitted decay parameter is not statistically different from zero. This is most likely due to inadequate data, preventing biological meaningful

evaluation of different models. Clymo et al. (1998) maintain that constant decay is as good as other models.

Based on a Finnish peatland database of 310 bogs and fens, Clymo et al. (1998) estimated that the peat addition rate to the catotelm is $0.0021 \text{ kmol C m}^{-2} \text{ year}^{-1}$ (equivalent to $48.5 \text{ g m}^{-2} \text{ year}^{-1}$ in terms of peat mass) and the decay rate

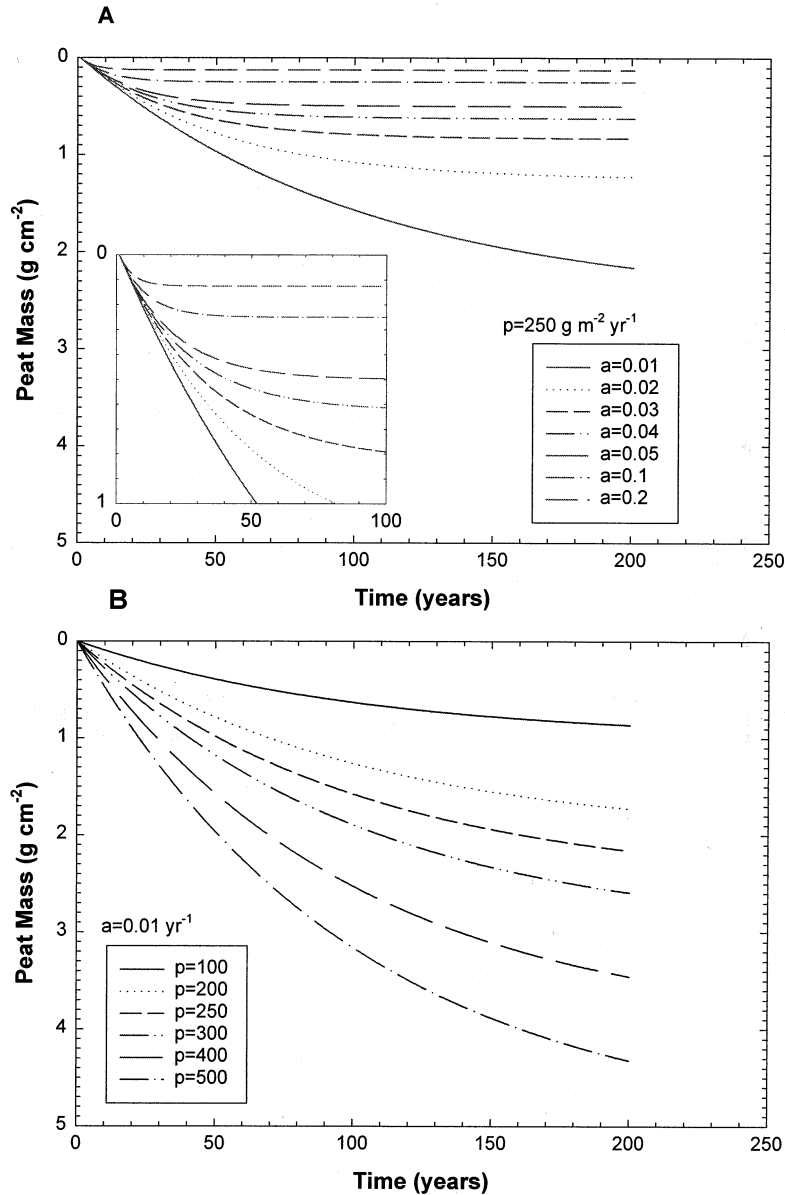


Fig. 4. Sensitivity test of effects of changing decay (A) and litter-addition rates on the acrotelm peat mass (B).

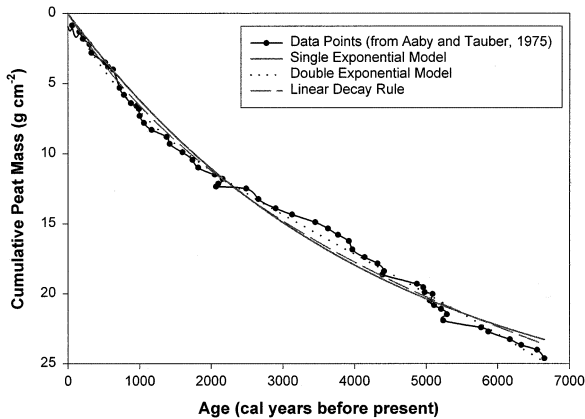


Fig. 5. Peat age–mass plot for Draved Mose, Denmark (data from Aaby and Tauber, 1975) and fitted curves using single (see also Clymo, 1984) and double exponential, and linear decay models.

is $3.7 \times 10^{-5} \text{ year}^{-1}$ using a linear decay model (assuming a proportional decay constant decreasing linearly with remaining peat mass). They find that different decay models (constant, linear or quadratic) do not make much difference to the goodness of fit for individual peat profiles, in part because of the small number of data points in the majority of individual profiles and thus less variation. However, if using pooled basal dates from different peat profiles, the greater variation, presumably caused by site-specific factors, causes noticeable difference of estimates using different models.

There are 14 peat profiles with a minimum of three ^{14}C dates (maximum of six dates at Slave Lake site) in continental western Canada (Yu and Campbell, 1998; Vitt et al., 2000). Although four data points are not really enough to convincingly fit two parameters, we use these data to estimate peat addition rates to the catotelm and decay rates based on a single exponential decay model. Ten of the 14 profiles show concave age–depth (mass) curves for this model. The remaining four profiles show convex curves and yield biologically meaningless negative decay rates, when the peat-addition rate is held constant through time. The estimated values from individual sites and from a combined data set are reported in Table 2. At Slave Lake bog (Kuhry and Vitt, 1996), the con-

vex age–mass curve suggests a continuously decreasing peat-addition rate over the last 10,000 years. Multiple proxy data from the Beauval Bog site in west central Saskatchewan indicate progressively decreasing moisture over the last 4000 years (Kuhry, 1997). Drying conditions may have decreased NPP and increased litter and acrotelm-peat decay, consequently reducing the peat-addition rate to the catotelm (see Yu et al., 2000).

5.2. Effects and significance of changing peat addition and decay rates

Based on Clymo's conceptual model, there are two variables determining long-term peat accumulation in the catotelm: the rate of peat addition and the decay rate. Both variables likely change over time, but the peat addition rate is likely to be more sensitive to vegetation type and environmental parameters, and therefore be more variable than the decay rate. The addition rate is determined at the acrotelm–catotelm interface, which usually lies 20–50 cm below the peat surface, where variations in environmental conditions such as temperature and moisture would certainly affect the peat addition rate, through changes in NPP and acrotelm decay. In contrast, the catotelm decay rate is determined all along the peat profile. During the 6-year observations of soil temperatures in northern Minnesota that has a seasonal temperature variation of $> 30 \text{ }^\circ\text{C}$, Nichols (1998) found that temperatures in peatlands (bogs and fens) are dampened more than in uplands soils. At 2 m depth, peat temperatures vary only about 2–4 $^\circ\text{C}$ seasonally, while nearby upland temperatures vary by about 12 $^\circ\text{C}$. In a detailed survey of temperature variations within a raised bog in Finland, Puranen et al. (1999) found that at the bog surface the temperature could vary 15 $^\circ\text{C}$ seasonally, but at depths greater than about 4 m downward the temperatures remain constant at 6 $^\circ\text{C}$. This suggests the low and invariable temperatures in deep peat would limit changes in decomposition rates.

The peat addition rate and decay rate have different influences on overall peat accumulation, specifically the shape of the peat age–depth curve. The peat addition rate significantly affects the

amount of young peat as well as old peat (Fig. 6A), and decreasing the addition rate will move the curves upward (less peat accumulation). If the fitted curve is considered as representing the long-term average of peat-addition rate (p), then the data points above the curve suggest an interval with lower than average addition rate. In contrast, the decay rate affects older peat much more significantly than it does younger peat (Fig. 6B), though increasing the decay rate will similarly shift the curve upward and cause the data points to lie above the fitted curve. Overall, the shape of the curve is more sensitive to changes in the rate

of addition; therefore, the decay rate is more ‘conservative’, more determined by old peat, and therefore ‘smoothed’ over time.

What causes the often-seen wiggles, or departures from a smooth curve, in peat age–depth/mass curves? Based on the above analysis, we hypothesize that changes in the peat addition rate play a significant role. If the assumption that the anoxic decay rate remains constant over thousands of years is valid, then changes in the peat addition rate could be used to explain the century-scale or millennial-scale variation in peat age–depth curves, assuming the wiggles are not caused

Table 2

Parameter estimates for the catotelm from sites in continental western Canada using a single exponential decay model (Some preliminary results are presented in Yu and Campbell (1998), Vitt et al. (2000); see the latter for data source)

Site Name	Peat type	# ^{14}C dates	Location (lat., long.)	Catotelm peat-addition rate ($\text{g m}^{-2} \text{ year}^{-1}$)	Catotelm decay rate ($\times 10^{-4} \text{ year}^{-1}$)
<i>Concave sites</i>					
Gypsumville Bog, MB	Bog	3	51°46'N; 98°30'W	33.8	1.9
Legend Lake, AB	Bog	3	57°26'N; 112°57'W	17.3	2.6
Mariana Lakes site 16, AB		3		18.7	0.16
89-18A, AB	Plateau	4	58°18'N; 119°17'W	20.3	0.89
Wathaman Bog, SK	Bog	3	56°57'N; 103°34'W	26.1	0.99
Steve 81-18A, AB	Patterned fen	3	54°45'N; 115°52'W	44.2	1.4
Steve 89-16A (Zama), AB		3	59°7'N; 118°9'W	27.6	1.7
Buffalo Narrows, SK		3	55°56'N; 108°34'W	17.6	1.3
Steve 81-8A (site 4), AB	Fen	3	52°51'N; 116°28'W	23.9	0.43
Steve 81-11A (site 5), AB	Fen	3	53°20'N; 117°28'W	47.7	2.3
Mean (and if plot all together)				27.72 (23)	1.37 (0.64)
<i>Convex sites</i>					
Beauval Bog, SK (Kuhry, 1997)	Bog, fen	3	54°40'N; 107°49'W		
Steve WC2 (site 7a), AB	Horizontal fen	3	53°26'N; 116°04'W		
La Ronge, SK	Bog	3	54°57'N; 105°15'W		
Slave Lake site, AB (Kuhry and Vitt, 1996)	Bog, fen	6	55°01'N; 114°09'W		

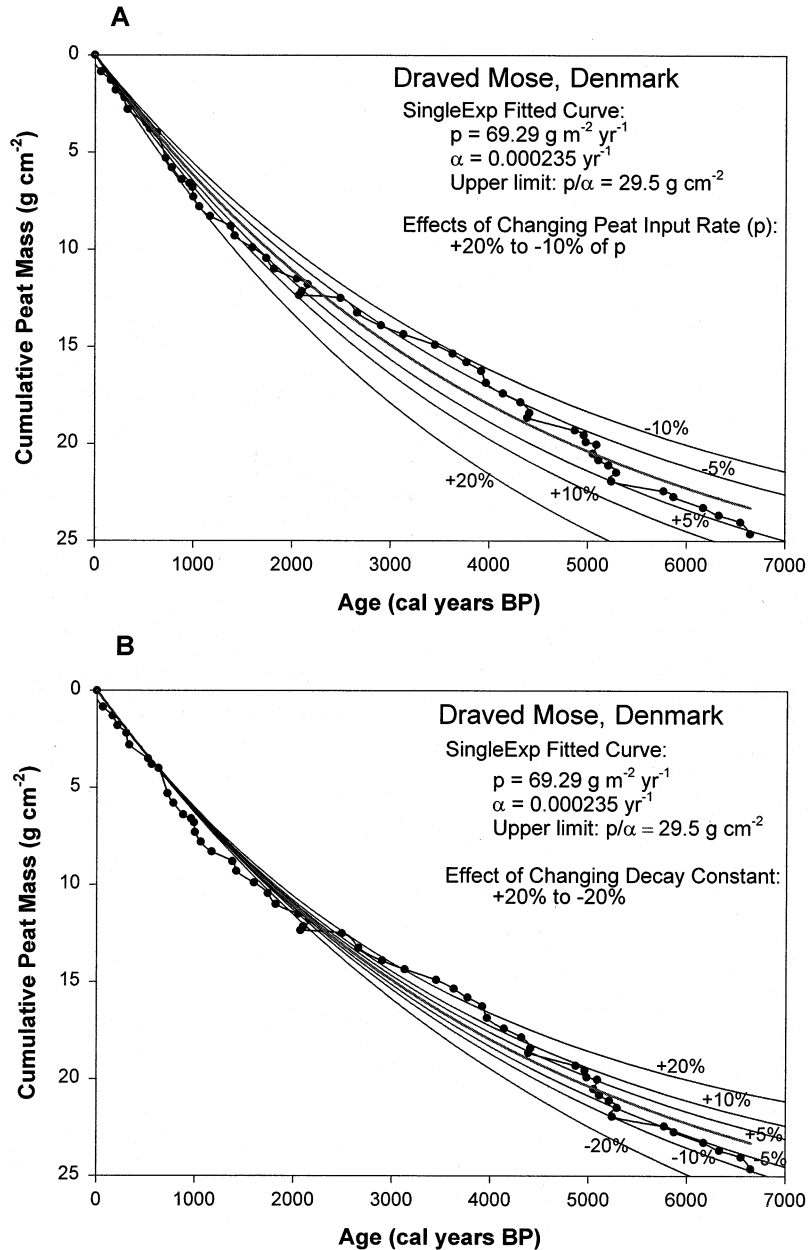


Fig. 6. (A) Effects of changing the peat addition rate to the catotelm on the shape of peat age–mass profile, using the Draved Mose peat profile as an example (data from Aaby and Tauber, 1975). Increasing the addition rate causes deeper peat, i.e. the curve moves downward. The central thick curve is fitted by a single exponential model. (B) Effects of changing the peat decay rate in the catotelm on the shape of peat age–mass profile, using the Draved Mose peat profile as an example (data from Aaby and Tauber, 1975). Increasing the decay rate causes shallower peat, i.e. the curve moves upward. Changing addition rate tends to affect both young and old peat, but changing decay rate tends to affect more significantly old peat.

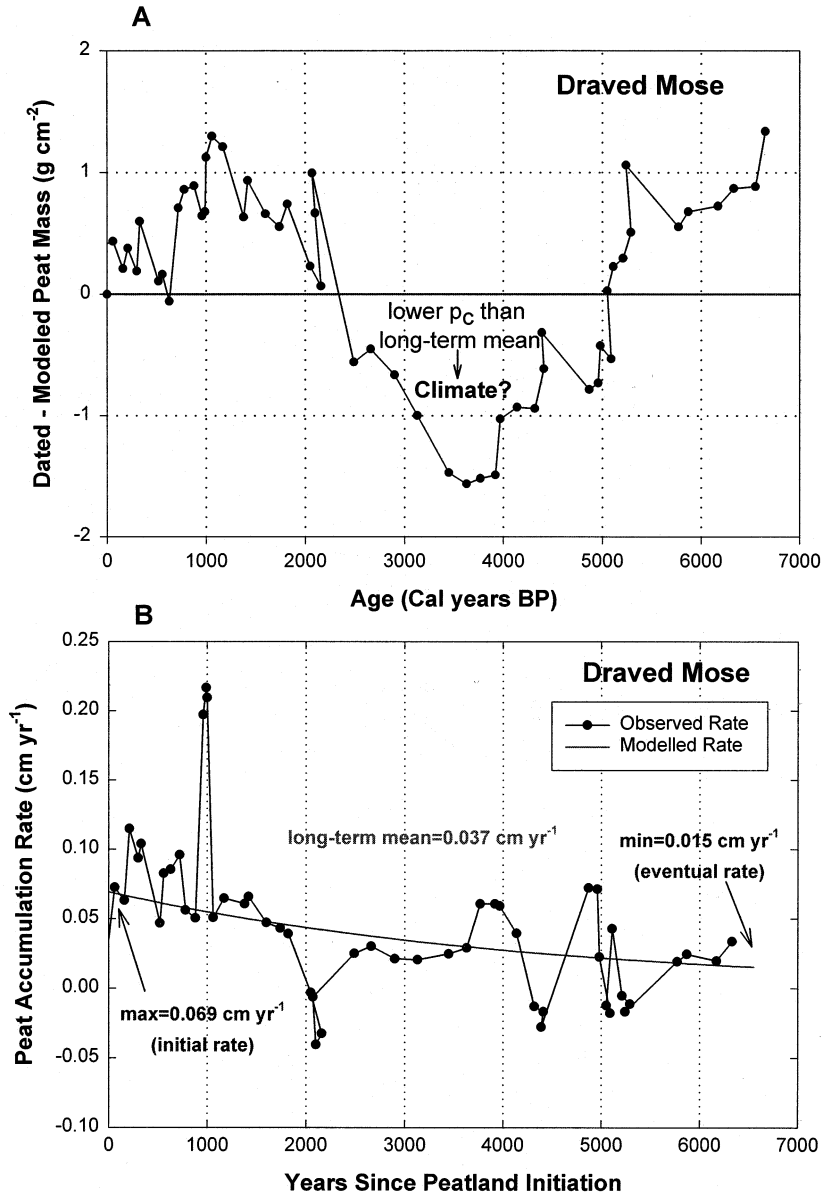


Fig. 7. (A) Difference between dated peat mass and modeled peat mass (using a single exponential model, see Figs. 5 and 6) at Draved Mose (data from Aaby and Tauber, 1975). Assuming a constant decay rate and the fitted curve representing a long-term average of addition rate for the last 7000 years, the lower peat mass accumulation from 5000 to 2500 BP may suggest a lowered peat addition rate, possibly caused by lowered NPP, lowered water table, higher acrotelm decay rate or any combination of these factors. (B) Change of peat accumulation rates over time, using Draved Mose as an example (data from Aaby and Tauber, 1975). The wiggled line is calculated from each adjacent pair of dated horizons, and the smooth curve is derived from modeled results using a single exponential model. This figure shows that the accumulation rate decreases over time due to increased decomposition of ever accumulating peat from an initial maximum peat addition rate of $0.069 \text{ cm year}^{-1}$ to an eventual rate of $0.015 \text{ cm year}^{-1}$, with a mean of $0.037 \text{ cm year}^{-1}$. The rates are based on the calculated smooth curve. Note different time scale in B, which is an analogous representation of long-term dynamics by present steady snapshot. Few data points around 2000 cal BP are reversed due to dating reversal.

by dating errors (but see Kilian et al., 2000). Fig. 7 illustrates the possible climate inference and interpretation of this peat age–depth profile. The results from Draved Mose (Fig. 7) suggest that peat addition rates are lower from ca. 5000 to 2500 cal year BP than the overall mean, most likely caused by either lower NPP or higher litter and acrotelm decomposition; either condition could be caused by a relative lowering of the water table, which would in turn suggest a drier climate. The high-frequency 260-year climatic cycles as inferred from peat humification at the same site (Aaby, 1976) might have superimposed on this general climate pattern.

The sensitivity analyses as shown above would also help to explain the convex peat age–mass curves demonstrated at a few well-dated sites in Finland (e.g. Ikonen, 1993) and in continental Canada (Charman et al., 1994; Kuhry and Vitt, 1996; Yu et al., 2000), where the peat addition rate likely changes with changes in the peatland height and hydrology. The assumption of relatively constant peat-addition rates as in Clymo's peat growth model is certainly violated at these sites. This was caused by continuous decrease of peat-addition rates, most likely due to changes in local hydrological conditions. The continuous growth of a peatland would potentially keep the living plants further away from occasional input of nutrients from groundwater (see Glaser et al., 1997) thus limiting their growth. This convex relation would be expected to occur more often in a continental climate, such as in continental Canada, than in oceanic climates.

5.3. Temporal variation of peat accumulation rates

We can further analyze the Draved Mose peat profile to gain some understanding of long-term peat accumulation rates. Fig. 7B illustrates the change of peat accumulation rates as calculated from paired data points (mass divided by age span) and based on a single exponential model, assuming a constant peat addition rate of $69 \text{ g m}^{-2} \text{ year}^{-1}$, which is only about 10–20% of NPP

after litter and acrotelm decomposition. From the model, the mean apparent accumulation rate over the last 6650 years is $0.037 \text{ cm year}^{-1}$ (equivalent to $37 \text{ g m}^{-2} \text{ year}^{-1}$). The accumulation rate at the top of the peat column is $0.069 \text{ cm year}^{-1}$ ($69 \text{ g m}^{-2} \text{ year}^{-1}$), which represents an initial rate without decay loss from the peat; the apparent rate at the base of the peat profile is $0.015 \text{ cm year}^{-1}$ ($15 \text{ g m}^{-2} \text{ year}^{-1}$), which represents the current rate taking into account of decomposition of the entire peat profile. Similar trends can be seen in the graph of cumulative peat mass through time (Fig. 5); its rate of accumulation (slope of the curve) appears to increase through time to the present, as a result of this same decay process operating on an ever-increasing peat column. This is a direct consequence of the continuous exponential decay processes of catotelm peat. Thus the usual practice of calculating peat accumulation rates by dividing peat depth/mass by the time span between two dated horizons can be misleading, particularly when comparing peat cores of different depths and ages (e.g. Tolonen et al., 1992). If the peat-addition rate (balance of NPP and litter and acrotelm decay) has kept constant over the course of peat accumulation, then the ever-accumulating peat and its long-term catotelm decomposition would decrease net accumulation rates and thus, diminish the efficiency of peatlands as atmospheric carbon sinks over time.

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