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L I S A R . B E L Y E A * and N I L S M A L M E R †
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Abstract

The response of peatlands to changes in the climatic water budget is crucial to predicting potential feedbacks on the global carbon (C) cycle. To gain insight on the patterns and mechanisms of response, we linked a model of peat accumulation to a model of peatland hydrology, then applied these models to empirical data spanning the past 5000 years for the large mire Store Mosse in southern Sweden. We estimated parameters for C sequestration and height growth by fitting the peat accumulation model to two age profiles. Then, we used independent reconstruction of climate wetness and model reconstruction of bog height to examine changes in peatland hydrology. Reconstructions of C sequestration showed two distinct patterns of behaviour: abrupt increases associated with major transitions in vegetation and dominant *Sphagnum* species (fuscum, rubellum–fuscum and magellanicum stages), and gradual decreases associated with increasing humification of newly formed peat. Carbon sequestration rate ranged from a minimum of 14 to a maximum of $72 \, \mathrm{g \, m^{-2} \, yr^{-1}}$, with the most rapid changes occurring in the past 1000 years. Vegetation transitions were associated with periods of increasing climate wetness during which the hydrological requirement for increased seepage loss was met by rise of the water table closer to the peatland surface, with the indirect result of enhancing peat formation. Gradual decline in C sequestration within each vegetation stage resulted from enhanced litter decay losses from the near-surface layer. In the first two vegetation stages, peatland development (i.e., increasing surface gradient) and decreasing climate wetness drove a gradual increase in thickness of the unsaturated, near-surface layer, reducing seepage water loss and peat formation. In the most recent vegetation stage, the surface diverged into a mosaic of wet and dry microsites. Despite a steady increase in climate wetness, C sequestration declined rapidly. The complexity of response to climate change cautions against use of past rates to estimate current or to predict future rates of peatland C sequestration. Understanding interactions among hydrology, surface structure and peat formation are essential to predicting potential feedback on the global C cycle.

Introduction

Compared with most other ecosystems, peatlands globally are a small sink for carbon dioxide (CO_2) (Gorham, 1991; Botch *et al.*, 1995; Clymo *et al.*, 1998; Turunen *et al.*, 2002), a large source of methane (CH_4) (Matthews & Fung, 1987; Bartlett & Harriss, 1993; Huttunen *et al.*, 2003) and dissolved organic carbon

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(Hope *et al.*, 1994; Aitkenhead & McDowell, 2000), and a huge pool of particulate organic carbon (Vitt *et al.*, 2000; Turunen *et al.*, 2002; Kremenetski *et al.*, 2003). Rates of carbon (C) sequestration (i.e., uptake of CO_2) and CH_4 emission depend strongly on height of the peatland surface above the water table (Bubier *et al.*, 1993; Waddington & Roulet, 1996; Alm *et al.*, 1997), and shifts toward increasing surface wetness during the Little Ice Age have been linked to decreases in C accumulation rates (Mauquoy *et al.*, 2002). Scenarios for future climate change predict that high latitude regions

will have higher mean precipitation, but mid-continental regions will become drier in summer due to increased evapotranspiration (Cubasch *et al.*, 2001). Understanding the hydrological and ecological mechanisms controlling peatland response to changes in the climatic water budget is crucial to predicting potential feedbacks on the global C cycle (Moore *et al.*, 1998; Turetsky *et al.*, 2002).

Carbon is sequestered in peatlands so long as formation of new peat exceeds decay losses of all peat accumulated previously. Litter (i.e., the above- and below-ground remains of plants) decomposes rapidly in the thin (~ 0.5 m) surface layer (acrotelm) that is only seasonally water saturated (Clymo, 1984). Peat is formed as litter at the bottom of the acrotelm gradually is engulfed by the rising water table, so becoming part of the thick (several m), lower layer (catotelm) that is permanently water saturated (Clymo, 1984). Height of the peatland surface above the water table (i.e., acrotelm thickness) is a key determinant of plant species distribution (Malmer, 1962), as well as rates of litter production (Wallén, 1987; Wallén *et al.*, 1988) and litter decay losses (Belyea, 1996). As a result of these relationships, peat formation rate is greatest for intermediate microforms (lawns, low hummocks) and least for microforms at the extremes of the water table gradient (high hummocks, pools) (Belyea & Clymo, 2001). Peat decay occurs very slowly in the catotelm. Although recalcitant material may continue to accumulate (Clymo *et al.*, 1998), the primary control on total losses by peat decay is the amount of material available (i.e., catotelm thickness). Hence, C sequestration is controlled by both peatland surface structure (i.e., vegetation composition, acrotelm thickness) and peatland developmental topography (i.e., catotelm thickness).

Peatland surface structure and developmental topography are both linked to hydrology. Hydraulic conductivity is high in poorly decomposed litter near the vegetation surface, but declines as the material becomes more decomposed in its transition to peat (Boelter, 1969; Hoag & Price, 1995). As a result, highest rates of groundwater flow occur at or near the water table (Hoag & Price, 1995). For microforms with an unsaturated layer (i.e., acrotelm thickness greater than zero), water losses increase when the water table rises and decrease when the water table falls, damping seasonal variations in water supply (e.g., range of 2–4 cm for 80% of the frost-free period; Malmer, 1962). If the water table rises above the vegetation surface, water loss occurs rapidly by overland flow. Peatland development (i.e., increase in catotelm thickness) affects hydrology through change in the hydraulic gradient. For the water table to remain near the peatland surface,

development of the groundwater mound must be accompanied by a shift toward surface peat of lower hydraulic conductivity, a shift toward wetter climate, or both. Acrotelm and catotelm thickness, therefore, act together to control water losses by seepage and overland flow.

Changes in the climatic water budget are likely to have large effects on peatland C sequestration, most immediately through acrotelm processes controlling the rate at which litter is transformed into peat (Hilbert *et al.*, 2000; Wieder, 2001; Malmer & Wallén, 2004). In this paper, we linked a model of peat accumulation to a model of peatland hydrology, then reconstructed changes in climate wetness, C sequestration and surface structure over 5000 years at a bog in southern Sweden. We chose Yu *et al.*'s (2003) model of peat accumulation because it allows change in the rate at which peat is formed by the acrotelm. By stratifying the analysis into distinct vegetation stages, we gain insight into the patterns and mechanisms by which surface structure mediates peatland response to climate change.

Materials and methods

Theory

In the model of peat accumulation (Yu *et al.*, 2003), new peat is added to the catotelm at a time-dependent rate and a constant proportion of the peat in the catotelm decays each year:

$$\frac{dH}{dt} = pe^{-\beta t} - \alpha H, \tag{1}$$

where dH/dt is the rate of peat accumulation $[LT^{-1}]$, p is the initial rate of peat formation $[LT^{-1}]$, β is a modifier of this rate $[T^{-1}]$ and α is proportional rate of peat decay $[T^{-1}]$. Later in the text, subscripts specify whether H is measured as length (subscript d) or as cumulative mass of C (subscript C). Integrating forward in time gives the solution (Yu *et al.*, 2003)

$$H = \frac{p}{(\alpha - \beta)} \left(e^{-\beta t} - e^{-\alpha t} \right). \tag{2}$$

Yu *et al.*'s (2003) model of peat accumulation is linked to a simple model of peatland hydrology by the relation that height of the water table defines the top of the catotelm. Hence, the catotelm must increase in thickness at the same rate as the water table rises:

$$\frac{dH_d}{dt} = \frac{1}{\theta}\frac{dW}{dt}, \tag{3}$$

where θ is the specific water yield and dW/dt $[LT^{-1}]$ is the rate of water storage. For a homogeneous, vegeta-

tion-covered surface, water storage is the difference between inputs and seepage losses:

$$\frac{dW}{dt} \approx Q - \frac{T}{l}\frac{H}{L}, \quad (4)$$

where Q $[LT^{-1}]$ is the net rate of water input (i.e., precipitation minus evapotranspiration, plus incoming seepage and overland flow), T is the transmissivity (i.e., hydraulic conductivity integrated over the saturated depth of peat) $[L^2 T^{-1}]$, l is the length $[L]$ of the cell, and H/L is the surface gradient (H $[L]$ is height and L $[L]$ is lateral extent). For simplicity, we ignore vertical flow. In most situations, dW/dt is much smaller than Q. Hence, as the peat deposit grows and surface gradient increases, the quotient of transmissivity and water input, T/Q, decreases:

$$\frac{T}{Q} \approx \frac{lL}{H}. \quad (5)$$

For a heterogeneous surface with some flooded areas, we consider two habitat types: clusters of dry hummocks ('ridges') covering a proportion S_r of the total area and having transmissivity T_r, and flooded hollows covering a proportion $S_h = 1 - S_r$ of the total area and having transmissivity T_h. On the time scale of interest, rates of seepage loss through ridges, hollows, and the total area are all equal as follows:

$$T\frac{H}{L} = T_r\frac{H_r}{L_r} = T_h\frac{H_h}{L_h}, \quad (6)$$

where H_r/L_r is the water table gradient within ridges and H_h/L_h that within hollows. The overall gradient is given by

$$\frac{H}{L} = S_r\frac{H_r}{L_r} + S_h\frac{H_h}{L_h}. \quad (7)$$

Using $L_r = S_r L$ and $L_h = S_h L$, Eqn (7) simplifies to $H = H_r + H_h$ and the first two parts of Eqn (6) can be expressed as

$$T = \frac{T_r}{S_r}\frac{1}{(1 + H_h/H_r)}. \quad (8)$$

Using the last two parts of Eqn (6),

$$\frac{H_h}{H_r} = \frac{T_r}{T_h}\frac{L_h}{L_r}. \quad (9)$$

Overland flow occurs through hollows, so T_h is much larger than T_r, H_h/H_r approaches zero and the second term on the right-hand side of Eqn (9) approaches unity. Hence, an increase in the relative area covered by hollows (i.e., a decrease in S_r) increases overall transmissivity:

$$T \approx \frac{T_r}{S_r}. \quad (10)$$

The hydrological model states that peatlands adjust to abrupt changes in water input (e.g., climate wetness)

and to gradual changes in hydraulic gradient through variations in (ridge) transmissivity, ridge area, or both. Since surface structure has such strong influence on peat formation rate (refer to the Introduction), these adjustments in hydrological properties should affect C sequestration indirectly. On homogeneous surfaces, we expect that C sequestration rate will decrease with decreasing transmissivity, because litter decay losses from lawns and hummocks increase as acrotelm thickness increases. On heterogeneous surfaces, we expect that C sequestration rate will decrease with decreasing ridge area, because litter formation decreases with expansion of hollows.

Study site and peat profiles

We applied Yu *et al.*'s (2003) peat accumulation model to two peat profiles from Store Mosse (57°15′N, 13°55′E; 160–170 m a.s.l.), a large mire complex in the boreonemoral region of southern Sweden. Store Mosse consists of three large bog areas and several smaller fen areas, formed across an extensive sandy area beginning about 6000 BP (Svensson, 1988a; Malmer *et al.*, 1997). After transition from *Carex* fen to ombrotrophic bog at about 5000 BP, the bog developed through three distinct stages dominated by different species of *Sphagnum* (Malmer *et al.*, 1997): fuscum stage (4.5–3 m depth; 5440–2480 BP), rubellum–fuscum stage (3–2 m depth; 2480–940/1000 BP) and magellanicum stage (from 2 m depth; from 940/1000 BP). Through the fuscum (5440–2480 BP) and rubellum–fuscum (2480–940/1000 BP) stages (Svensson, 1988a), the macrofossils showed a homogeneous vegetation, dominated by plants characteristic of hummocks or ridges (S_r: 1.0). Since the start of the magellanicum stage (from 940/1000 BP), the macrofossils showed an obvious differentiation of the vegetation, with some microsites becoming dominated by species characteristic of hollows (Svensson, 1988b) (present-day S_r: 0.563; Malmer & Wallén, 1999). These general trends in stratigraphy and development on Store Mosse have been reported from many bogs around the Baltic and in continental western Europe (for a survey, see, e.g., Svensson, 1988a).

The present surface of the bog plain on Store Mosse slopes asymmetrically at about 1.2 m km^{-1} and has a nonforested hummock and hollow microtopography. The hollows and hummocks are elongated perpendicular to the slope, and hence the surface structure is similar to the ridge and flark structure of aapa mires and patterned fens. Hummock/ridge vegetation is dominated by *Calluna vulgaris*, *Eriophorum vaginatum* and *Sphagnum rubellum*, and hollow/pool vegetation by *Rhynchospora alba*, *S. magellanicum* and *S. cuspidatum*.

Present mean annual precipitation is 720 mm, mean temperature of the warmest month is 15 °C and length of the growing season (temperature >4 °C) is 210 days (Malmer, 1962).

The cores used in this study were collected from near the mid-point of the extensive southern bog area. Both were composed of hummock peat through the fuscum and rubellum–fuscum stages. During the magellanicum stage, Core A remained as hummock peat whereas Core B changed to hollow peat (Malmer & Wallén, 1999). Dry bulk density, von Post humification and concentrations of C and nitrogen (N) were measured on contiguous samples. Within each of the three bog stages, poorly humified peat of low bulk density and high C/N in the lower parts graded to highly humified peat of high bulk density and low C/N in the upper parts. These stratigraphic changes in peat humification record a shift toward increasing litter decay losses in the acrotelm within each stage (Malmer et al., 1997). Peat age was estimated at 2.5 to 5 cm intervals, based on calibrated (Stuiver & Reimer, 1993) radiocarbon dates and C/N quotients (Malmer et al., 1997; Malmer & Wallén, 1999).

Data analysis

To apply Yu et al.'s (2003) model to peat profiles, we rewrite Eqn (1) in terms of depth below the top of the catotelm, Z_i [L], and peat age, Y_i [T]:

$$\frac{dZ_i}{dt} = pe^{-\beta Y_i} - \alpha Z_i. \qquad (11)$$

Integrating backwards in time gives peat depth as a function of peat age:

$$Z_i = \frac{p}{\alpha - \beta}\left(e^{-\beta Y_0} - e^{-\beta Y_0 - (\alpha - \beta)Y_i}\right), \qquad (12)$$

where Y_0 [T] is the peat age at the start of the period of interest.

Parameters p, β and α were estimated separately for each stage and each core by fitting Eqn (12) to profiles of age vs. depth and age vs. cumulative mass of C. A maximum-likelihood type of approach was used to minimize errors in both Z_i and Y_i. Variables were scaled by the quantile between 0.31 and 0.69 of the n data points, and model fit was calculated as the scaled Euclidean distance v_i from the observed point i to its estimate (Clymo et al., 1998). The error term e_i associated with each observation was assumed to be proportional for age (5%) and C mass (2%), and constant (1 cm) for depth. The probability that the data set could have occurred given a particular set of parameters was estimated based on a Lorentzian error distribution (Press et al., 1992). The corresponding function

$$\sum_1^n \frac{1}{n}\log\left(1 + \frac{1}{2}\left(\frac{v_i}{e_i}\right)^2\right) \qquad (13)$$

was minimized using the downhill simplex method (Press et al., 1992). Confidence intervals on parameters were calculated by the bootstrap method (Press et al., 1992), using 100 random selections of the data. Since some of the parameters were highly correlated with one another, deviation from the original estimate was computed as the Euclidean combination of proportional deviations for all parameters. Hence, the methods selected for parameter estimation were robust, conservative and took account of errors in both variables.

We combined results of the peat accumulation model with ancillary data to reconstruct hydrological changes at Store Mosse. Bog height, reconstructed using Eqn (2), was used to approximate changes in surface gradient for the period after the bog reached its present-day lateral extent (i.e., after 5000 BP; Svensson, 1988a). We assumed that changes in Q were climate-driven and directly proportional to changes in lake water levels for this region (Digerfeldt, 1988). We estimated Q as a proportion of the present-day value, Q_p, and standardized T (calculated from Eqn (5)) relative to Q_p. Hence, the derived variable T/Q_p describes a hydrological property of the peatland that is dependent on climate (Q/Q_p) and developmental topography (H/L).

Results

The peat accumulation model provided excellent fits to all dated peat sequences (Fig. 1). Discontinuities in the profiles were reflected in the model by marked changes in parameter values between stages (Tables 1 and 2), particularly for initial peat formation rate, p, and its time-dependent modifier, β. Within each stage, β was generally at least an order of magnitude larger and had proportionately smaller confidence intervals than the proportional decay coefficient, α (Tables 1, 2). Relative to the start of the stage, peat (C) formation, $p_Ce^{-\beta_Ct}$, declined on average by 66% in the fuscum stage, 29% in the rubellum–fuscum stage and 58% in the magellanicum stage. The results at Store Mosse indicate that height growth and C sequestration were controlled primarily by changes in peat formation in the acrotelm, and only secondarily by peat decay losses in the catotelm.

Reconstructions of peat accumulation based on the parameter estimates show two distinct behaviours (Fig. 2). Carbon sequestration, and to a lesser extent height
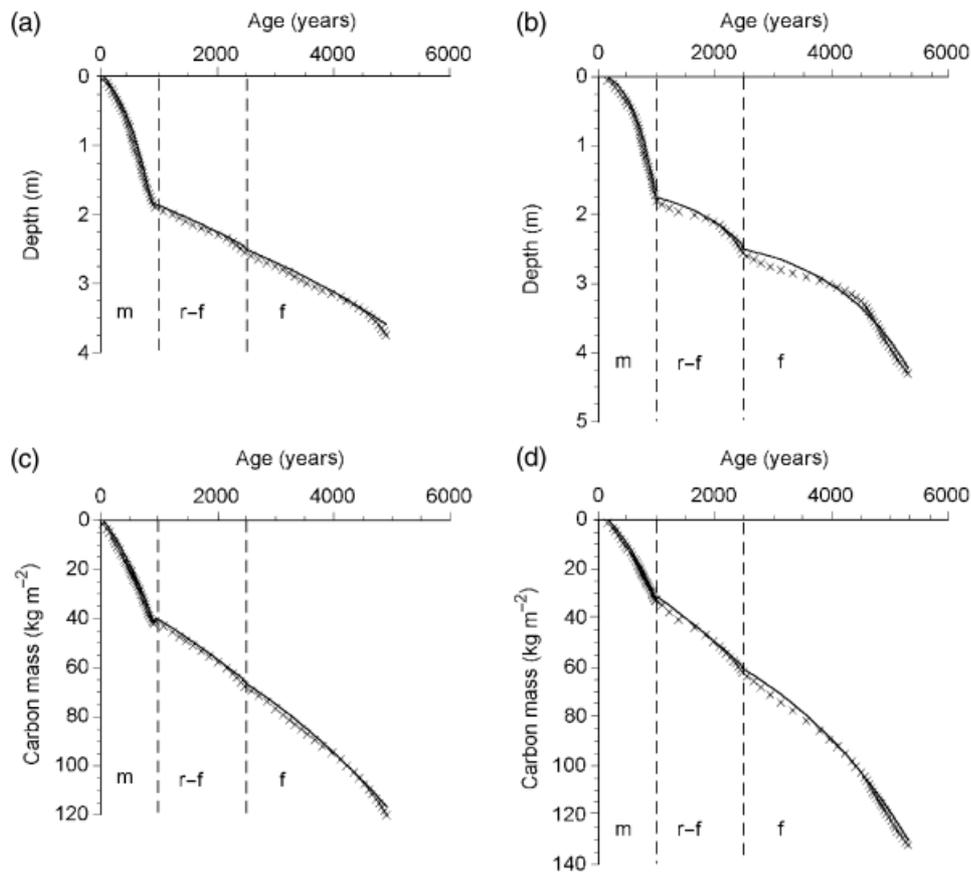
Fig. 1 Age profiles for two cores from Store Mosse mire, southern Sweden. Data (Malmer *et al.*, 1997; Malmer & Wallén, 1999) are plotted as crosses; fitted models (Eqn (12) in the text) are plotted as lines. See Tables 1 and 2 for estimates of parameter values. Broken vertical bars show dates separating three bog stages: m (magellanicum stage), r–f (rubellum–fuscum stage) and f (fuscum stage). (a) Age vs. depth in Core A. (b) Age vs. depth in Core B. (c) Age vs. cumulative mass of C in Core A. (d) Age vs. cumulative mass of C in Core B.

Table 1 Parameter estimates for height growth (dH_d/dt; Eqn (1)) at Store Mosse mire, southern Sweden

Bog stage	p_d (mm yr^{-1})	β_d (10^{-4} yr^{-1})	α_d (10^{-4} yr^{-1})
Fuscum stage			
Hummock A	0.56, **0.66**, 0.76	1.4, **2.2**, 2.9	−0.12, **0.18**, 8.7
Hummock B	1.3, **1.6**, 1.8	6.3, **7.5**, 9.2	−0.68, **0.23**, 1.2
Rubellum–fuscum stage			
Hummock A	0.37, **0.47**, 0.51	−0.18, **1.9**, 2.9	−0.095, **0.39**, 1.5
Hummock B	0.66, **0.94**, 1.1	3.4, **10**, 14	−0.84, **0.50**, 3.5
Magellanicum stage			
Hummock A	5.0, **5.2**, 5.9	18, **19**, 21	−0.83, **0.47**, 2.0
Hollow B	5.8, **5.9**, 6.3	26, **27**, 29	0.16, **0.70**, 1.7

Values on either side of estimate (in bold-face type) indicate 95% confidence intervals. See the text for explanation of model and parameters.

growth, increased abruptly at transitions between vegetation stages. Within each stage, C sequestration, and to a lesser extent height growth, gradually declined. Changes were largest during the magellanicum stage: C sequestration increased three-fold at the start, then declined within 1000 years almost to the original value. These results demonstrate that C sequestration was controlled primarily by abrupt shifts in vegetation, and secondarily by gradual changes in surface structure that enhanced litter decay losses,

Table 2 Parameter estimates for C sequestration (dH_C/dt; Eqn (1)) at Store Mosse mire, southern Sweden

Bog stage	p_C (g m^{-2} yr^{-1})	β_C (10^{-4} yr^{-1})	α_C (10^{-4} yr^{-1})
Fuscum stage			
Hummock A	39, **41**, 44	3.0, **3.3**, 3.9	0.84, **1.1**, 1.5
Hummock B	48, **48**, 51	4.1, **4.1**, 4.8	0.40, **0.66**, 1.1
Rubellum–fuscum stage			
Hummock A	20, **21**, 22	2.3, **2.4**, 3.2	0.37, **0.55**, 1.6
Hummock B	13, **23**, 30	−3.5, **2.0**, 5.3	−0.77, **0.39**, 2.7
Magellanicum stage			
Hummock A	68, **72**, 81	7.4, **8.3**, 10	0.039, **0.83**, 1.6
Hollow B	59, **60**, 65	9.9, **10**, 12	0.49, **0.52**, 1.1

Values on either side of estimate (in bold-face type) indicate 95% confidence intervals. See the text for explanation of model and parameters.
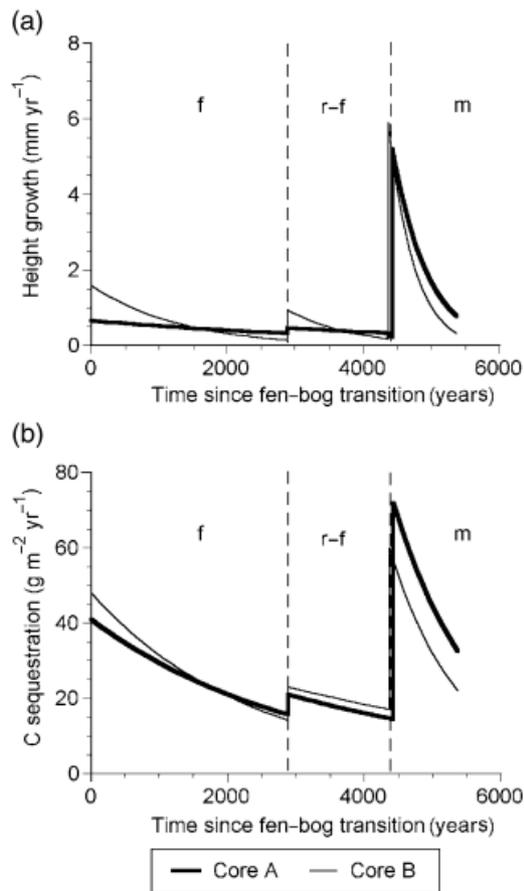
Fig. 2 Rates of peat growth, reconstructed for the past 5400 years at Store Mosse mire, southern Sweden. Broken vertical bars show dates separating three bog stages: m (magellanicum stage), r–f (rubellum–fuscum stage) and f (fuscum stage). (a) Rate of height growth (dH_d/dt; Eqn (1)). (b) Rate of C sequestration (dH_C/dt; Eqn (1)).

thereby inhibiting peat formation rate and increasing peat humification.

Changes in the hydrological property T/Q_P were driven internally by growth of the peat deposit (i.e.,

increasing surface gradient; Fig. 3a, b) and externally by variations in climate wetness (Fig. 3b). Based on Digerfeldt's (1988) lake-level records, climate wetness (Q/Q_P) increased steadily in the late part of the fuscum and rubellum–fuscum stages and throughout the magellanicum stage, and decreased through a small part of the fuscum and most of the rubellum–fuscum stages (Fig. 3b). Surface gradient increased steadily, with that in Core A rapidly overtaking that in Core B at the start of the magellanicum stage (Fig. 3b). Surface gradient had a strong influence on T/Q_P early in bog development (Fig. 3a). The large discrepancies in T/Q_P between the two cores during the fuscum stage (Fig. 3b) resulted from small differences in surface gradient. Hence, the discrepancies in this stage may be too large, reflecting errors in reconstruction of bog height rather than real differences between the cores. Later in development, T/Q_P was driven mainly by changes in climate wetness (Q/Q_P). At transitions between stages, increases in Q/Q_P were sufficiently large to reverse the gradient-induced decline in T/Q. When the peatland surface was homogeneous, T/Q_P underwent net decline, driven by increases in gradient during the fuscum stage and by decreases in climate wetness during the rubellum–fuscum stage. During the magellanicum stage, increasing climate wetness was offset by rapid increase in surface gradient and T/Q_P remained nearly constant. These results show that the hydrological and ecological effects of climate change were contingent on developmental topography and pre-existing surface structure.

Variations in C sequestration (Fig. 2) and hydrological properties of the peatland (Fig. 3b) were related to climate change in a complex way. Major shifts in vegetation and substantial increases in C sequestration rate occurred when T/Q_P was forced to increase during periods of increasing climate wetness. Hollow development was initiated at the beginning of the magellanicum stage, even though climate was drier than at the
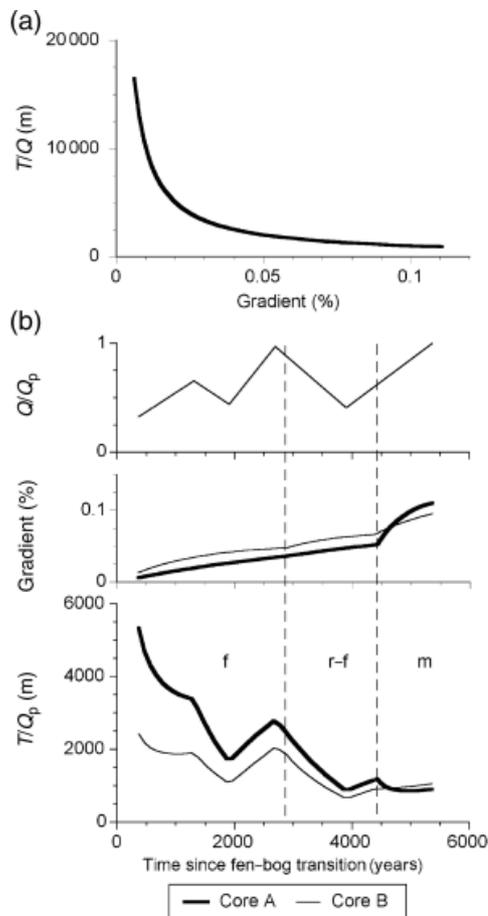
Fig. 3 Inferred changes in bog hydrology at Store Mosse mire, southern Sweden. (a) Transmissivity/water input (T/Q) vs. surface gradient. Values for the two cores overlap completely. (b) Changes over time. Top panel: water input relative to present day (Q/Q_p), based on lake-level data of Digerfeldt (1988). Middle panel: surface gradient (H/L). Bottom panel: transmissivity/present water input (T/Q_p). Broken vertical bars show dates separating three bog stages: m (magellanicum stage), r–f (rubellum–fuscum stage) and f (fuscum stage).

beginning of the rubellum–fuscum stage. Once a dominant vegetation was established, C sequestration rate decreased, even if climate wetness increased further. This response was most pronounced in the magellanicum stage, during development of the ridge and hollow structure. These results demonstrate that peatland C sequestration responded to climate change indirectly, and that surface structure and developmental topography mediated these responses.

Discussion

Past rates of peatland C sequestration determined over long time periods (Turunen et al., 2002) or based on the

assumption of constant peat formation (Clymo et al., 1998) are likely to be unreliable for estimating current rates or for predicting future rates (Malmer & Wallén, 1999; Wieder, 2001; Malmer & Wallén, 2004). Over the past 5000 years, C sequestration rates at Store Mosse ranged from a minimum of 14 to a maximum of $72 \, g \, m^{-2} \, yr^{-1}$, with the most rapid changes occurring in the past 1000 years. Two distinct patterns of behaviour were both linked to the rate of new peat formation: abrupt increases coinciding with major transitions in vegetation, and gradual decreases coinciding with increasing humification of newly formed peat. Both these patterns of behaviour suggest a strong role for surface structure in determining peatland response to hydrological change.

Abrupt transition *between* bog stages might be viewed as a hydrological threshold, at which peatland surface structure shifted from one steady state to another. Vegetation responded to increasing T/Q_p through increased dominance of *Sphagnum* species that occupy niches at progressively lower heights above the water table, with *S. fuscum* occupying the highest and driest niches, followed by *S. rubellum* at intermediate niches and *S. magellanicum* at the lowest and wettest niches. As water input increased, the hydrological requirement for seepage losses to increase also was met by rise of the water table closer to the peatland surface, into peat of higher hydraulic conductivity. The decrease in acrotelm thickness and resulting vegetation switch enhanced peat formation and C sequestration. Although climate change forced the system over the threshold, changes in C sequestration were indirect results of major shifts in surface structure.

The shifts in surface structure enhanced peat formation, either by increasing production of new litter or by reducing litter decay losses. Most likely, decay losses were reduced by abrupt decreases in acrotelm thickness. At the start of each stage, the water table rose more rapidly than the peatland surface increased in height, so that the litter engulfed by the catotelm was younger and less humified than it had been previously. Peat formation was enhanced by instantaneous capture of litter in the lower part of the acrotelm and by decrease in the proportion of mass lost by litter during shortened residence in the acrotelm. Shortening of acrotelm residence time is particularly relevant for hollows, which developed during the magellanicum stage. Although vegetated hollows produce new litter at a slower rate than do hummocks (Malmer & Wallén, 1999), this difference is at least partially offset by lower litter decay losses in hollows, owing to the closer proximity of the water table to the peatland surface (Belyea & Clymo, 2001). Also, indirect evidence (Malmer et al., 1997) suggests that litter production in

hummocks increased at the start of the magellanicum stage, coincident with a phytogeographic shift toward vegetation with stronger oceanic affinities than that in the previous two stages (Svensson, 1988a). Hence, reduced litter decay losses (arising from shortening of litter residence in the acrotelm) and increased litter formation (arising from shift in vegetation) explain how abrupt shifts in vegetation and surface structure may enhance peat formation and C sequestration.

The subsequent, gradual decline in C sequestration *within* each stage resulted from inhibited formation of new peat, without major changes in vegetation. As water input decreased due to reduced precipitation (rubellum–fuscum stage) or surface gradient increased due to growth in bog height (fuscum stage), the hydrological requirement for seepage losses to decrease was met by fall of the water table, into peat of lower hydraulic conductivity. With the resulting increase in acrotelm thickness, litter engulfed by the catotelm became progressively older and more humified. Decay losses were enhanced by exposure of peat at the top of the catotelm to oxic conditions and by increase in the proportion of mass lost by litter during lengthened residence in the acrotelm. Hence, peatland development (i.e., increasing surface gradient) and reductions in climate wetness led to gradual decreases in C sequestration via increases in acrotelm thickness that reduced water loss but also inhibited peat formation.

Carbon sequestration rate declined rapidly through the magellanicum stage, even though effects of surface gradient were minimal and climate wetness continued to increase. Although macrofossil composition across multiple cores showed that the surface vegetation was homogeneous through the fuscum and rubellum–fuscum stages (Svensson, 1988a), small differences in rates of height growth between Cores A and B suggest that the bog surface comprised a mosaic of slightly higher and lower microsites. At some point during the earliest part of the magellanicum stage (Svensson, 1988b), climate wetness increased sufficiently for lower microsites to be flooded. Once overland flow began to occur, constant or decreasing transmissivity was attained by decrease in ridge transmissivity, T_r, matching or exceeding the decrease in ridge relative area, S_r (Eqn (10)). Initial differences in acrotelm thickness were amplified by hummock building on higher microsites and hollow deepening on lower microsites, with C sequestration rate decreasing in both cases. Hence, the large decline in C sequestration rate observed over the past 1000 years resulted from internal processes driving a 'divergent succession' (Sjörs, 1990) of the peatland surface into a system of ridges and hollows.

In recent decades, much effort has been directed at measuring rates of peatland C sequestration in relation to predicted effects of climate change. Field studies show large spatial variation in rates of C cycling, much of which can be attributed to surface structure (Bubier *et al.*, 1993; Waddington & Roulet, 1996; Alm *et al.*, 1997). Most experimental (Moore & Knowles, 1989) and modelling (Walter *et al.*, 1996; Frolking *et al.*, 2001) studies, however, consider only the direct effects of changes in physical controls – temperature, water table depth – on peatland gas flux and C cycling. Few studies (Weltzin *et al.*, 2001, 2003) consider indirect effects on peatland surface structure and their potential feedbacks on hydrology, peat formation and C sequestration. The effects of peatland developmental topography also are incorporated in few studies (Waddington & Roulet, 1996; Hilbert, *et al.*, 2000). The complex responses to increases and decreases in climate wetness observed at Store Mosse show the necessity of understanding mechanisms of change in order to predict future effects.

The physiographic setting at Store Mosse may have made the effects of past climate change more evident than they would be at other peatland sites, but we believe the mechanisms of response identified in this study are broadly applicable to many northern peatlands and provide insight on possible responses to future global climate change. At Store Mosse, the confounding effects of lateral expansion on development of surface gradient were probably minimal because the ombrotrophic bog formed across a large area (nearly 10 km[2]) and reached its present limits to lateral extent very rapidly. Lateral expansion of the extensive peatlands of the West Siberian lowlands has slowed or stopped within the past 3000 years (Kremenetski *et al.*, 2003). We speculate that increased summer droughts (Cubasch *et al.*, 2001) in the oligotrophic bogs of mid-continental regions will lead to increases in acrotelm thickness, inhibiting peat formation and C sequestration. The ridge and hollow system that formed at Store Mosse over the past 1000 years is a surface structure similar to those on the aapa mires and patterned fens that cover large areas of northern Europe and North America (Sjörs, 1990; Turunen *et al.*, 2002). We speculate that patterned peatlands in oceanic regions may respond to predicted increases in precipitation (Cubasch *et al.*, 2001) through expansion of flarks or hollows, inhibiting peat formation and C sequestration and enhancing CH_4 emission. In all peatlands, the magnitude and direction of response to climate change is likely to be contingent on pre-existing surface structure and developmental topography. In order to incorporate peatland response to climate change into models of global C cycling, there is an urgent need to understand how surface structure and vegetation interact with climate and developmental changes in peatland hydrology.

Acknowledgements

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