Feedback control of the rate of peat formation

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The role of peatlands in the global carbon cycle is confounded by two inconsistencies. First, peatlands have been a large reservoir for carbon sequestered in the past, but may be either net sources or net sinks at present. Second, long-term rates of peat accumulation (and hence carbon sequestration) are surprisingly steady, despite great variability in the short-term rates of peat formation. Here, we present a feedback mechanism that can explain how fine-scale and short-term variability in peat-forming processes is constrained to give steady rates of peat accumulation over longer time-scales. The feedback mechanism depends on a humpbacked relationship between the rate of peat formation and the thickness of the aerobic surface layer (the acrotelm), such that individual microforms (hummocks, lawns, hollows and pools) expand or contract vertically in response to fluctuations in the position of the water table. Hummocks (but not hollows) 'evolve' to a steady state where changes in acrotelm thickness compensate for climate-mediated variations in surface wetness. With long-term growth of a topographically confined peat deposit, the steady state gradually shifts to a thicker acrotelm (i.e. taller hummocks) and lower rates of peat formation and carbon sequestration.

Keywords: peatlands; soil organic matter; ecosystem dynamics; carbon cycle

1. INTRODUCTION

Since the most recent deglaciation, peat deposits have sequestered about as much carbon (400–500 Pg) as is currently held in the atmosphere (Clymo *et al.* 1998). At present, however, northern peatlands are a source of methane (Harriss *et al.* 1985) and can switch rapidly from a sink to a source of carbon dioxide, depending on surface wetness (Silvola *et al.* 1996). This apparent inconsistency in the role of peatlands in the global carbon cycle is the predictability of the processes. Peat has accumulated, and hence carbon has been sequestered, at a surprisingly steady rate over long time-scales (Clymo 1984; Clymo *et al.* 1998). Yet, contributing processes of peat formation are very variable on short-term and small-spatial scales (Wallén *et al.* 1988; Hogg *et al.* 1994; Alm *et al.* 1997; Ohlson & Økland 1998). As a result of these discrepancies, estimates of the rates of carbon sequestration and emission derived from small-scale flux studies are difficult to reconcile with long-term estimates derived from radiocarbon studies (Trumbore *et al.* 1999). We must resolve these discrepancies if we are to understand the present and future roles of peatlands in the carbon cycle.

The long-term sequestration of carbon as peat involves both biological and hydrological processes, operating at different spatial scales. Peat formation occurs at the small scale of an individual hummock or hollow ($1 m^2$; figure 1a) through production, decomposition and compression of organic matter derived from *Sphagnum* mosses and vascular plants (Clymo 1984). Plant litter deposited at the bog surface and in the rooting zone forms a porous mass through which air circulates and surplus water drains readily. Each year's cohort of litter undergoes aerobic decay and is buried under the weight of younger material, until eventually the main plant structures collapse. The decrease in the size of the pore spaces reduces the

hydraulic conductivity of the peat, so that incident precipitation is dispersed primarily through the thin porous layer near the mire surface (the acrotelm), while lateral seepage through the denser underlying layer (the catotelm) is impeded. Anaerobic decay in the permanently waterlogged and anoxic catotelm occurs about a thousand times more slowly than aerobic decay in the periodically oxic acrotelm above the water table (Ingram 1978). Hence, carbon is sequestered over long time-scales by submergence of organic matter at the base of the acrotelm or, from the opposite perspective, by thickening of the catotelm and a rising of the water table (Clymo 1984). The catotelm's rate of water storage, ΔW_c, (and hence the rate of submergence) depends mainly on climatic control of effective precipitation, and on large-scale ($10^4 m^2$; figure 1b) hydrological properties controlling the rate of lateral seepage from the peatland (Ingram 1982; Hilbert *et al.* 2000). If the hydraulic conductivity of the catotelm remains constant, seepage varies with developmental changes in the shape of the peat deposit. In peatlands confined by the topography of the surrounding mineral substrate, ΔW_c decreases over time, whereas in peatlands that can expand laterally, ΔW_c remains constant or increases over time. Hence, changes in the shape of the peatland can affect ΔW_c independently of changes in climate (figure 1b).

Much of the spatial variation in peat-forming processes can be explained by the height of the peatland surface above the water table (i.e. the acrotelm thickness). Distinct microforms, ranging from wet depressions (pools and hollows) to dry mounds (hummocks), are common features on northern peatlands, distinguished by species composition, microenvironment and process rates. Litter production increases with acrotelm thickness from hollow to hummock, mainly due to enhanced production by vascular plants (Wallén 1986, 1987; Wallén *et al.* 1988). The innate resistance of plant litter to decay increases across microforms in the order hollow to lawn to hummock (Johnson & Damman 1991; Belyea 1996).
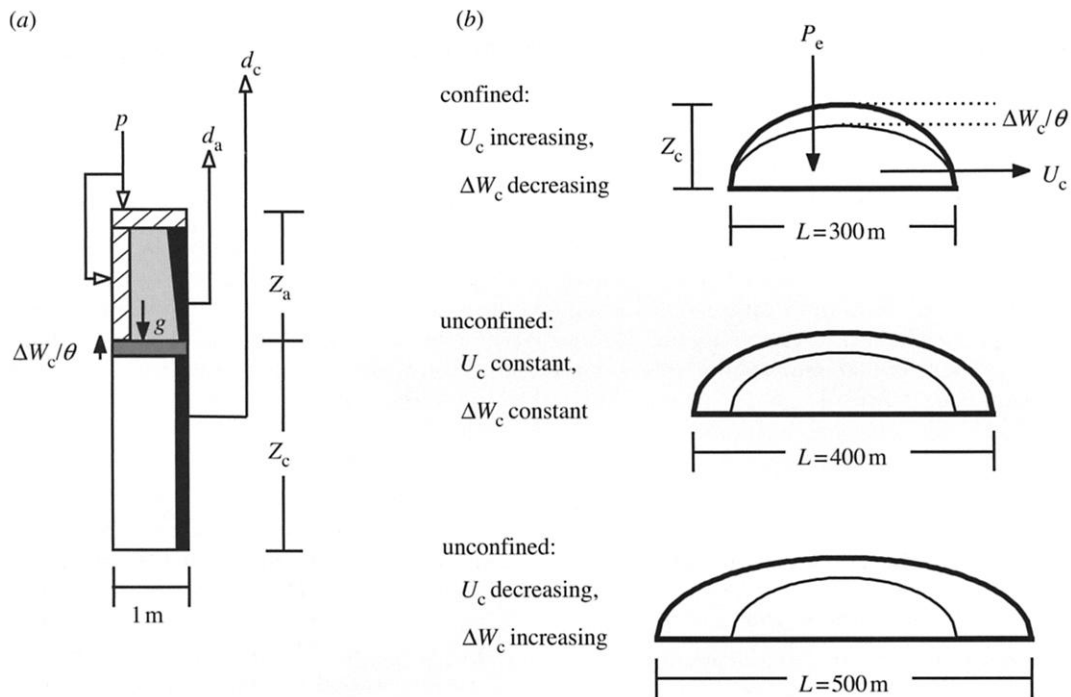
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Figure 1. Peat-forming processes in relation to (*a*) small-scale biological and (*b*) large-scale hydrological processes. (*a*) At the small scale (1 m^2), litter is added to the acrotelm surface and below ground at a rate p (M L^{-2} T^{-1}) and lost by aerobic decay at a cumulative rate d_a (M L^{-2} T^{-1}). Peat in the catotelm of thickness Z_c (L) is lost by anaerobic decay at a cumulative rate d_c (M L^{-2} T^{-1}). Peat at the acrotelm–catotelm boundary has dry bulk density ρ_d (M L^{-3}) and specific water yield θ (L L^{-1}). Under a steady-state acrotelm thickness Z_a (L), ignoring d_c, the rate of peat formation expressed as a thickness increment $g = (p - d_a)/\rho_d$ (L T^{-1}) equals the rate at which acrotelm peat is submerged by the rising water table, $\Delta W_c/\theta$ (L T^{-1}). (*b*) At the large scale (10^4 m^2), the rate of water storage, ΔW_c (L T^{-1}), is the difference between the effective precipitation in dry years (hydrologically limiting conditions), P_e (L T^{-1}), and lateral seepage, U_c (L T^{-1}). P_e is determined mainly by climate, whereas U_c is determined by the hydraulic conductivity of catotelm peat and by the shape of the peat deposit. If hydraulic conductivity remains constant as the mire develops then seepage is related to the summit height, Z_c, and length, L, of the catotelm (Ingram 1982): $U_c \propto (Z_c/L)^2$. In a peatland that is topographically confined (top panel), Z_c increases over time; hence U_c also increases and ΔW_c decreases. In a peatland that can expand laterally, U_c either remains constant (hence ΔW_c remains constant; middle panel) or decreases (hence ΔW_c increases; bottom panel). Note that open arrows show rates (p, d_a and d_c) as a change in mass per unit area whereas filled arrows show rates (g, $\Delta W_c/\theta$, P_e and U_c) as a change in thickness or depth.

Decay is fastest in the zone of water-table fluctuation, intermediate in sites above the water table and slowest in waterlogged peat (Belyea 1996). Methane emissions are higher in open-water pools than in other microforms (Hamilton *et al.* 1994), whilst the net exchange of carbon dioxide is most strongly positive (i.e. net gain) in lawns and about equally positive in hollows and hummocks (Clymo & Reddaway 1971; Alm *et al.* 1997). Taken as a whole, these observations suggest that the rate of peat formation varies in a complicated but systematic way with acrotelm thickness (i.e. depth of the water table).

The balance between the rate of peat formation and the rate of submergence (i.e. rise of the water table) has a reciprocal effect on acrotelm thickness. The rate of peat formation expressed as a thickness increment, g (with dimensions L T^{-1}, where L represents length and T, time), is a function of litter additions to, p (M L^{-2} T^{-1}, where M represents mass, and L and T as before), and losses from, d_a (M L^{-2} T^{-1}), the acrotelm, as well as the dry bulk density, ρ_d (M L^{-3}, where $_d$ refers to the dry-standard term in soil science), of peat at the acrotelm–catotelm boundary: $g = (p - d_a)/\rho_d$ (figure 1*a*). (For comparisons across microforms, the effect on peat accumulation of

losses from the catotelm by anaerobic decay, d_c (M L^{-2} T^{-1}), can be ignored because differences are likely to be small.) The rate of submergence, $\Delta W_c/\theta$ (L T^{-1}), depends on the hydrologically determined rate of water storage, ΔW_c (L T^{-1}), and on the specific water yield of peat at the acrotelm–catotelm boundary, θ (L L^{-1}) (figure 1*b*). Any local imbalance between g and $\Delta W_c/\theta$ causes the acrotelm to increase or decrease in thickness (Belyea & Clymo 1998). If $\Delta W_c/\theta$ is equal to g then the acrotelm maintains a steady-state thickness. If $\Delta W_c/\theta$ is larger than g then the water table rises relative to the vegetation surface, so some peat previously in the acrotelm becomes submerged by the catotelm (i.e. the acrotelm becomes thinner). If $\Delta W_c/\theta$ is smaller than g, only some of the newly formed peat is submerged and the acrotelm becomes thicker. We suggest that the nature of the relationship between the rate of peat formation and acrotelm thickness determines the long-term dynamics of surface microforms and rates of peat formation.

We investigated how peat formation may interact with water-table position to regulate the long-term dynamics of peatlands by measuring rates of peat formation across a range of acrotelm thicknesses. We then used the nonlinear

Table 1. *Regression of peat-forming processes on acrotelm thickness for Ellergower Moss, UK*

(In all equations, the independent variable is acrotelm thickness (cm). All dependent variables were Box–Cox transformed; before transformation, the rate of peat formation was translated by the minimum so that all values were positive. Standard errors of the estimate calculated for mean acrotelm thickness (s.e.$_{est}$) have been back-transformed to the original units).

equation	d.f.	F	r^2_{adj}	s.e.$_{est}$
above-ground productivity and root productivity within the acrotelm (g m^{-2} yr^{-1})				
$\sqrt{y} = 9.3 + 1.33x - 0.022x^2$	3, 21	72.5	0.86	$-157, +183$
cumulative rate of decay through the acrotelm (g m^{-2} yr^{-1})				
$\sqrt{y} = 2.45 + 0.416x$	1, 22	269	0.92	$-28, +36$
dry bulk density at the acrotelm–catotelm boundary (g cm^{-3})				
$\sqrt{y} = 0.108 + 0.0057x$	1, 22	59.9	0.72	$-0.018, +0.025$
rate of peat formation, expressed as a thickness increment (cm yr^{-1})				
$\sqrt{(y - y_{min})} = 0.92 + 0.042x - 0.0012x^2$	2, 21	5.85	0.30	$-0.11, +0.51$

relationship between these two variables to simulate dynamics under a fluctuating climate at different stages of bog development. Our analysis tests the hypothesis that both the persistence of bog microforms and the steady long-term rate of peat accumulation can be explained by feedback between biological and hydrological processes operating near the bog surface.

2. METHODS

(a) The field site and its microforms

We estimated rates of peat formation across the four main microforms spanning the range of acrotelm thickness (and water-table depth) on Ellergower Moss (55°5′ N, 4°23′ W; 230 m above sea level), a precipitation-fed bog in south-western Scotland, UK. The climate is oceanic, with an average annual rainfall of *ca*. 2400 mm and a mean monthly temperature ranging between 12.3 °C and −0.9 °C (Barrow *et al.* 1993). The bog is roughly elliptical in plan (length of 570 m, width of 400 m); the central cupola has a maximum thickness of about 7.2 m and resembles a hemi-ellipse in cross-section, consistent with the predictions of hydrological theory for raised bogs (Ingram 1987).

We estimated rates of peat formation, *g*, in a 2500 m^2 area of the bog that exhibits typical hummock–hollow micro-topography. In this area, distinct microforms occur along a gradient from the highest and driest to the lowest and wettest sites: *Sphagnum rubellum* hummocks (acrotelm thickness of 20–50 cm above the mean water table); *Sphagnum papillosum* lawns (7–20 cm (maximum of 35 cm) above the mean water table); *Eriophorum angustifolium-*, *Narthecium ossifragum-* or *Sphagnum cuspidatum*-dominated hollows (2 cm below to 7 cm above the mean water table); and open-water pools (below the mean water table). Tussocks composed of *Trichophorum cespitosum* and hummocks dominated by *Racomitrium lanuginosum* occur scattered among the other microforms, but are not considered here.

(b) Estimating the rate of peat formation

Organic additions to and losses from the acrotelm were estimated for six microsites of each of the four microform types, spanning the natural range in acrotelm thickness. Here, 'acrotelm thickness' refers to the distance from the moss or bare-peat surface to the level of the lowest water table, inferred from discoloration of polyvinyl-chloride tape (an indicator of

reducing conditions; Belyea 1999). All masses are expressed on a dry (80 °C for 24 h) ash-free (450 °C for 4 h) basis.

Above-ground production on the microforms was measured by direct harvest of one year's increment. On each hummock and lawn microsite 10.8 cm × 10.8 cm of coarse net (mesh size of 3.6 cm) was worked around vascular plants and anchored flush with the moss surface by plastic mesh (Lindholm & Vasander 1990). After one year, a 7.3 cm diameter core was taken from the centre of the plot and all material lying between 1 cm below the netting and 1 cm below the moss surface (i.e. the annual increment excluding moss capitula) was harvested. In hollows and pools, vascular-plant litter falling on a 112.5 cm^2 piece of fine plastic mesh was harvested. In hollows, production of floating-leaved *S. cuspidatum* was measured by the capitulum-correction method (Clymo 1970) on ten stems packed to natural density in a cylinder of plastic mesh. In pools, algal detritus was harvested from sediment traps (diameter of 8.5 cm) after decanting the overlying water and flocculant.

Relative rates of root production were measured using ingrowth cores (diameter of 7.3 cm; length of 45 cm; mesh size of 15 mm) (Backéus 1990) loosely packed with a 50:50 (v:v) mixture of fine sand and expanded volcanic glass. Ingrowth cores were installed in precut holes (with surface vegetation replaced on top) and harvested after one year. Upon retrieval, peat surrounding the cores was carefully removed and protruding roots were cut flush with the mesh. Ingrowth cores were then frozen and cut into 10 cm sections (the basal 5 cm section was discarded). Organic and inorganic materials were dispersed in water; coarse roots were removed by sieving and fine roots were separated by sedimentation of inorganic particles (Pallant *et al.* 1993). To derive the proportion of root production confined to the acrotelm, a negative exponential model (Jackson *et al.* 1996) was fitted to the cumulative proportions at 10 cm, 20 cm and 30 cm and solved for acrotelm thickness. Net primary productivity, *p* (M L^{-2} T^{-1}), was calculated as the annual increment for all above-ground biomass and root biomass confined to the acrotelm.

Cumulative acrotelm mass loss, d_a (M L^{-2} T^{-1}), was estimated by integrating instantaneous rates of decay at various depths throughout the acrotelm. Cores (diameter of 8 cm) collected from each microsite were subsampled at depth intervals 1–3 cm thick, and subsequently repacked with air-dried litter bags (6 cm × 6 cm; mesh size of 330 μm) (Belyea 1996) placed in the original position of the air-dried material. The cores were re-installed in their original positions on the bog
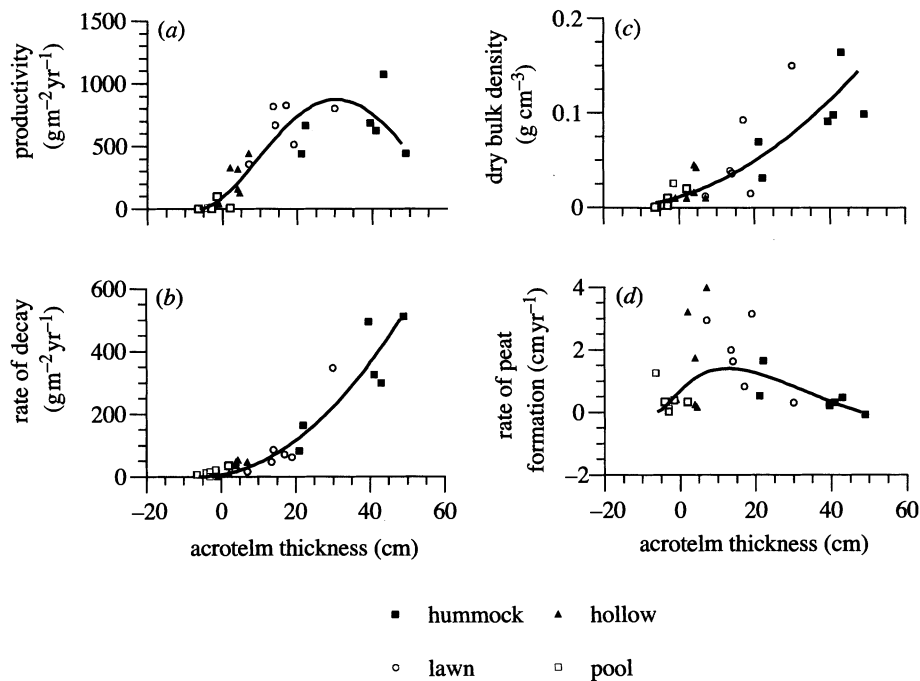
Figure 2. Variation in peat-forming processes in relation to acrotelm thickness for Ellergower Moss, UK: (a) above-ground productivity and root productivity within the acrotelm; (b) cumulative rate of decay through the acrotelm; (c) dry bulk density at the acrotelm–catotelm boundary; and (d) rate of peat formation, expressed as a thickness increment. Peat formed in the acrotelm and about to enter the catotelm, (a) minus (b), was assumed to have density (c). The curves in (a–c) are polynomial regressions (see table 1); the curve in (d) is the arithmetic combination of the regressions in (a–c).

within two months of collection. After one year, ingrown roots were removed, litter bags were re-dried and re-weighed, and mass losses were expressed as proportions of the original ash-free dry masses. At the end of the sampling season, dry bulk density and ash proportion were measured on ten sections of equal thickness through a core (minimum diameter, 8 cm) spanning the acrotelm. Polynomial regressions were used to relate depth of cumulative organic mass to depth in core, and to estimate dry bulk density at the acrotelm–catotelm boundary, ρ_d ($M L^{-3}$). A second polynomial was fitted, piecewise, to the profile of proportion of original mass lost versus cumulative organic mass, and cumulative loss was estimated by analytical integration. The regressions accounted for more than 85% of the variation in mass loss in all but one microsite.

The rate of peat formation, g, was calculated by subtracting cumulative losses from additions to the acrotelm (mass basis) and then dividing by the dry bulk density of organic matter at the acrotelm–catotelm boundary, $g = (p - d_a)/\rho_d$. Catotelm decay was ignored because this component of the rate of peat accumulation is unlikely to vary much across microforms. Process rates were Box–Cox transformed to normalize the distributions and then regressed on acrotelm thickness (table 1).

(c) Simulating long-term dynamics

We examined the effect on acrotelm dynamics of varying ΔW_c on both long (1000 year) and short (one year) time-scales. The regressions on p, d_a and ρ_d were combined to give the net response of the rate of peat formation to acrotelm thickness. This relationship was used to model changes in acrotelm thickness for different rates of water storage. We accounted for the effects of peat structure by specifying specific water yield, θ, as a linearly decreasing function of dry bulk density at the acrotelm–catotelm boundary: $\theta = 0$ for $\rho_d = 1.6 \, g \, cm^{-3}$ (the intrinsic

density of the peat substance) and $\theta = 1$ for $\rho_d = 0 \, g \, cm^{-3}$ (open water). The change in acrotelm thickness, ΔZ_a, was integrated numerically at yearly time-steps, as the difference between the rates of peat formation and submergence: $\Delta Z_a = g - \Delta W_c / \theta$. Hence, ΔZ_a is positive for an increase in thickness and negative for a decrease in thickness. Short-term (i.e. within year) fluctuations in climate were simulated by allowing ΔW_c to vary as a random Gaussian deviate ($0.5 \, cm \, yr^{-1}$) around a fixed (long-term) value. Three fixed values were selected across the observed range of peat-formation rates to show the effects of a long-term decrease in ΔW_c, a trend expected during the development of a topographically confined bog (figure 1b): early in bog development, catotelm growth is rapid and ΔW_c is large; as time goes by, catotelm growth slows and ΔW_c decreases.

3. RESULTS

(a) Rates of peat formation

Relationships between peat-forming processes and acrotelm thickness are presented in figure 2 and table 1. Both additions to (figure 2a) and losses from (figure 2b) the acrotelm, as well as the dry bulk density of peat at the acrotelm–catotelm boundary (figure 2c), increased over most of the range of acrotelm thicknesses. As a result of these processes, the relationship between the rate of peat formation, g, and acrotelm thickness is humpbacked (figure 2d), with maximum g at an acrotelm thickness of 10 cm. The relationship derived by polynomial regression of g on Z_a (table 1) explained 30% of the variation and was practically indistinguishable from the relationship derived by arithmetical combination of regressions of p, d_a and ρ_d on Z_a (figure 2d). Note that even if productivity in
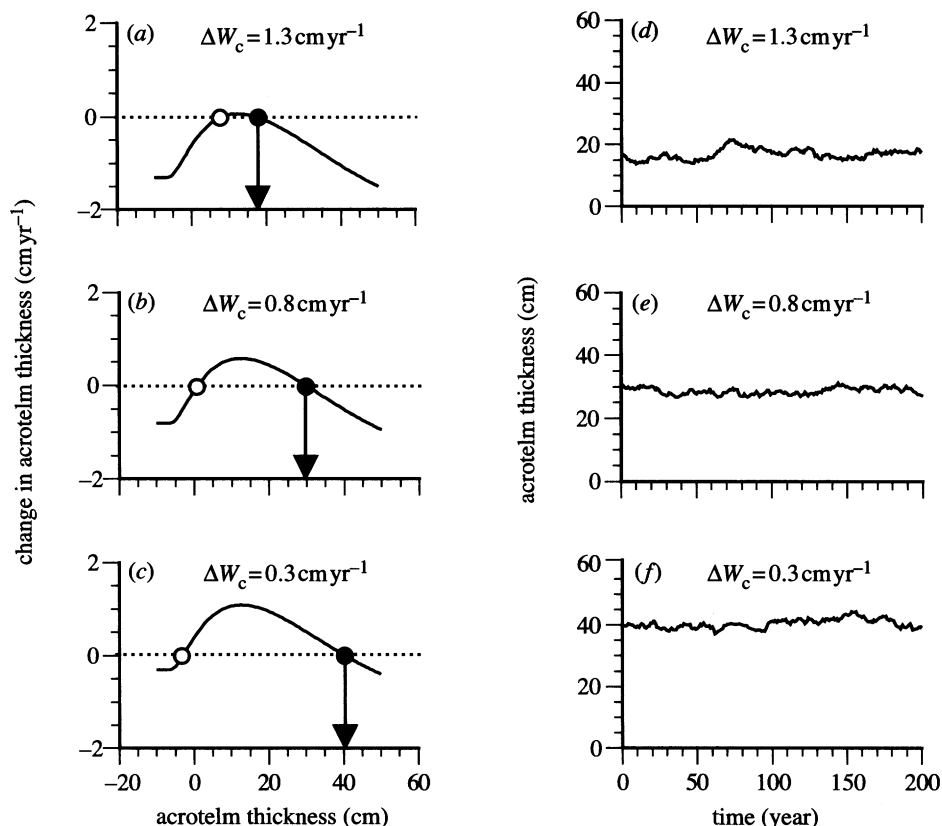
Figure 3. Effects of temporal variation in the rate of water storage, ΔW_c, on acrotelm thickness. (*a–c*) Change in acrotelm thickness at fixed ΔW_c representative of different stages of bog growth. The change in acrotelm thickness, ΔZ_a, was calculated as the difference between the statistically modelled g (figure 2*d*) and fixed ΔW_c, adjusted for specific yield, θ: $\Delta Z_a = g - \Delta W_c/\theta$. The intersection of the curve with the broken line indicates exact balance between the rates of peat formation and submergence. Filled circles and arrows show stable states where the acrotelm thickness is resilient to small variations in ΔW_c; open circles show unstable states. (*d–f*) Change in acrotelm thickness for ΔW_c varying as a random Gaussian deviate (0.5 cm) around a fixed value.

a hummock were to be maintained at its maximum rate as the hummock became taller, the corresponding increase in total acrotelm decay would eventually force the rate of peat formation to decrease.

(b) Simulated dynamics

The humpbacked relationship between the rate of peat formation and acrotelm thickness has interesting consequences for microform dynamics. Change in acrotelm thickness was calculated by subtracting the rate of submergence, $\Delta W_c/\theta$, from the rate of peat formation, g. On the resulting humpbacked curve, there are two points where the change in acrotelm thickness is zero (figure 3*a–c*). At the lower point, the slope is positive and hence the state is unstable: vertical expansion or contraction of the microform will tend to reinforce any slight fluctuation in ΔW_c. Once below this unstable point, microforms will tend toward increasingly deep pools; once above this point, microforms will tend toward hummocks. At the upper point, the slope is negative and hence the state is stable: vertical expansion or contraction of the hummock will tend to compensate for any slight fluctuation in ΔW_c. Microforms that reach this stable state are resilient to year-to-year variations in ΔW_c (Belyea & Clymo 1998): the acrotelm gets thicker if ΔW_c decreases slightly and thinner if ΔW_c increases slightly (figure 3*d–f*). The position of the stable state (and hence the dominant micro-

form) is determined by the mean rate of water storage. When ΔW_c is close to the maximum rate of peat formation, the only stable state is a small hummock (figure 3*a*). As ΔW_c decreases, the stable state shifts to progressively taller hummocks (figure 3*b,c*). Hence, peat-forming processes and water-table depth interact in a negative feedback loop that maintains a stable acrotelm thickness. For a bog that is topographically confined, the stable state gradually shifts over time to a lower rate of peat formation and a thicker acrotelm.

4. DISCUSSION

Our analysis explains how an individual hummock might persist, expanding and contracting, in the same place for centuries (Barber 1981), and how small-scale variability in peat-forming processes (Wallén *et al.* 1988; Hogg *et al.* 1994; Alm *et al.* 1997; Ohlson & Økland 1998) is damped over larger scales. In the short term, an individual microform expands or contracts vertically in response to trends in dry-year effective precipitation (and hence ΔW_c). In the long term, both the dominant microform and the rate of peat formation may shift to compensate for changes in the rate of water storage.

Both the pattern and the gross magnitude of peat-forming processes measured here are consistent with studies that have used different methods. Net primary

productivity increased over much of the range in acrotelm thickness, consistent with studies that emphasize the contributions of vascular plants (Wallén 1986, 1987; Wallén *et al.* 1988). The decrease in productivity at the highest end of the range has not, to our knowledge, been reported previously. Root-ingrowth cores provided a relative measure of below-ground productivity that allowed comparison across a range of acrotelm thicknesses, but absolute values of net productivity (and hence peat formation) should not be compared too closely with those from other sites. Several studies have emphasized differences in instantaneous rates of decay of different source materials and environmental conditions, as well as the inexorable decrease in litter quality that occurs with age (Johnson & Damman 1991; Hogg 1993; Belyea 1996). These differences had little effect on the cumulative rate of decay, which was controlled largely by acrotelm thickness. The maximum rate of peat formation occurred in lawn microforms, as in studies that measured net carbon exchange by gas flux (Clymo & Reddaway 1971; Alm *et al.* 1997). Overall, rates of peat formation were similar to, or larger than, those measured for *Sphagnum*-dominated hummocks using nitrogen as an innate marker (Malmer & Wallén 1993, 1999) but considerably smaller and less variable than those estimated by a method that ignores acrotelm decay (Ohlson & Økland 1998). As acrotelm thickness increased, increases in productivity were offset by increases in cumulative decay. These opposing effects lead to the humpbacked relationship between the rate of peat formation and acrotelm thickness that allows hummocks to persist.

The humpbacked relationship between g and z_a suggests that hollows should be unstable (i.e. 'evolve' to pools or hummocks) because, on the rising limb of the curve, small variations in ΔW_c will be reinforced by a change in the rate of peat formation (figure 3). Hollows do coexist with hummocks, so some other mechanism must ensure compensation for year-to-year variations in ΔW_c. For simplicity, we assumed that ΔW_c was the same across different microforms, and we adjusted this value locally only for differences in specific yield. In essence, we modelled the bog surface as a collection of microforms operating independently of one another, rather than as an assemblage of interacting microforms. Hydrological properties (e.g. specific water yield, hydraulic conductivity and the potential for evapotranspiration), however, differ between microforms (Ivanov 1981; Bragg 1982) in such a way that the rate of submergence should increase with acrotelm thickness. Eventually, water must be redistributed down the small-scale hydraulic gradients created, leading to a net flux of water from hummocks to hollows and pools (A. J. Baird, personal communication). Spatially explicit models will be necessary to ascertain whether such intermediate-scale redistribution of water could maintain hollows alongside other microforms.

In addition to the vertical adjustments suggested here, bog microforms can adjust to fluctuations in surface wetness through lateral expansion and contraction (Barber 1981). The net primary productivity of communities on lawns and small hummocks may be particularly sensitive to year-to-year variations in surface wetness, and the species dominance on these microforms may shift accordingly (Wallén *et al.* 1988; Malmer & Wallén 1993).

Specifically, hollows will expand laterally during wet periods, and hummocks will expand during dry periods, with lawns shifting position in concert. These lateral shifts might provide the system with resilience to changes in hydrology and facilitate the persistence of bog surface pattern through periods of climatic variation (Barber 1981; Wallén *et al.* 1988). The high hydraulic conductivity of hollows would promote more rapid runoff if these microforms expanded laterally during wet periods; conversely, the low hydraulic conductivity of hummocks would retard runoff if these microforms expanded during dry periods. Shifts in the lateral extents of hummocks and hollows are clearly related to changes in surface wetness, but palaeoecological studies that invoke past climate change as the underlying cause (Blackford 2000) are overly simplistic. Such interpretations fail to account for changes in peatland morphology that may have affected lateral seepage and surface wetness independently of changes in climate (figure 1*b*).

Spatial and temporal variations in microform composition and acrotelm thickness have important implications for elucidating the past and present roles of peatlands in the global carbon cycle. Methods of estimating rates of carbon sequestration that are based on age–depth profiles (Clymo *et al.* 1998) generally assume that the rate of peat formation has remained constant throughout peatland development. If g decreases as a peatland develops then these methods will underestimate the rates of carbon sequestration shortly after deglaciation and overestimate the current rates; if g increases as a peatland develops then these errors will be reversed. Short-term measurements of carbon dioxide exchange (Silvola *et al.* 1996; Alm *et al.* 1997) will also fail to provide accurate estimates of current rates of sequestration because carbon entering long-term storage in the catotelm cannot be distinguished from that contributing to short-term vertical adjustments in acrotelm thickness. Moreover, estimates of the overall greenhouse forcing will be compromised by climate-mediated shifts in the lateral extent and vertical height of microforms because the balance between the uptake of carbon dioxide and the release of methane depends very strongly on acrotelm thickness (Moore & Knowles 1989; Bubier *et al.* 1995). All of these limitations in current approaches can be overcome only by including the feedback mechanisms that link carbon sequestration and hydrology to the dynamics of peatland microforms.

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