

Ecological Monographs, 76(3), 2006, pp. 299–322
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BEYOND “THE LIMITS TO PEAT BOG GROWTH”: CROSS-SCALE FEEDBACK IN PEATLAND DEVELOPMENT

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Abstract. The postglacial development of peatland systems has had a strong influence on the global carbon cycle. Peatland effects on carbon cycling involve changes in both large-scale structure and community composition. The rate of C sequestration declines as a peat deposit grows, and methane emission increases as wet microhabitats expand in area. We examine the theoretical basis, underlying assumptions, and empirical evidence for two highly influential models of peatland form and development: Clymo’s bog growth model (BGM) and Ingram’s groundwater mound hypothesis (GMH). Our detailed theoretical analysis reveals previously unrecognized consequences of the models and, for the BGM, unrealistically stringent conditions for application. Our review of model assumptions and empirical evidence identifies the principal limitations of these models: they ignore spatial heterogeneity in peatland structure and function, fast processes occurring near the peatland surface, and interactions between peat accumulation and hydrological conditions. As a result, these models are unable to predict the effects of bog growth on hydrological conditions or peat-forming processes.

We introduce five conceptual models of peatland development that differ in how bog size and shape change over time, and we examine the consequences of each model for hydrological conditions. This exercise shows how bog height growth and lateral expansion change the boundary conditions constraining peatland dynamics, and so determine the direction of ecosystem development. We link peatland properties to the four general properties of “complex adaptive systems” (CAS): spatial heterogeneity, localized flows, self-organizing structure and nonlinearity. We also present a framework for modeling peatlands as CAS. In this framework, the system is disaggregated, both vertically and horizontally, into a set of components that interact locally through flows of energy and resources. Both internal dynamics and external forcing drive changes in hydrological conditions and microhabitat pattern, and these autogenic and allogenic changes in peatland structure affect hydrological processes, which, in turn, constrain peatland development and carbon cycling. We conclude by outlining four areas in which further empirical research is urgently needed.

Key words: bog growth; carbon cycle; complex systems; cross-scale feedback; ecosystem development; hydrology; peat accumulation; peatland; self-organization.

INTRODUCTION

The postglacial development and expansion of northern peatlands has resulted in transfer from the atmosphere to the soil (peat) of large amounts of carbon (270 to 370 Pg; Turunen et al. 2002), mainly over the past 5000 years (Gajewski et al. 2001). The long-term role of

peatlands in organic carbon storage, however, contrasts with their present role as significant sources of atmospheric CH₄ (Wang et al. 2004) and exporters of dissolved organic carbon to the oceans (Hope et al. 1994). Present rates of CH₄ emission are controlled largely by temperature, water table depth below the peatland surface, and the supply of readily decomposed substrate (Christensen et al. 2003). As a result, vegetation and microtopography are strong predictors of emission rates (Bubier et al. 1995), and fluxes can vary more within a few meters than across peatland regions (Moore et al. 1998). Emissions of CH₄ along succes-

Manuscript received 26 August 2005; revised 30 January 2006; accepted 10 February 2006. Corresponding Editor: J. B. Yavitt.

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sional gradients vary in relation to the effects of developmental stage on soil temperature, hydrological regime, and plant composition and productivity, with highest rates of emission occurring from areas where peat is degrading to form small, shallow pools (e.g., Moore et al. 1994). Hence, models that seek to explain glacial–interglacial cycles of atmospheric CH₄ (Kaplan 2002, Valdes et al. 2005) or to predict carbon cycle effects on the climate system (Gedney et al. 2004, Shindell et al. 2004) must account for developmental changes in surface structure at a range of spatial scales.

Current approaches to understanding and modeling peatland form and development have been strongly influenced by two papers from the 1980s. The major impact of Ingram's (1982) paper on the "groundwater mound hypothesis" (GMH) and Clymo's (1984) paper on the "limits to peat bog growth" model (BGM) is reflected in their high numbers of citations: 82 for the GMH and 227 for the BGM (ISI citations as of 10 January 2006). Both papers have had a clear influence on the types of research questions posed and the methods of study used by a generation of peatland scientists. Both the GMH and the BGM developed from work in a maritime climate (i.e., in the UK) and were formulated specifically for raised bogs. In their presentation of the models, both papers promoted the view of a two-layer bog structure: a thin (<0.5 m), near-surface layer ("acrotelm") in which water saturation levels vary seasonally and in which water flow and litter decay occur rapidly, and a thick (often >>1 m), underlying layer ("catotelm") that is permanently saturated, and in which water flow and peat decay occur at rates several orders of magnitude lower than in the acrotelm (Ingram 1978). Although this two-layer structure implies a duality of process rates, both the GMH and the BGM ignore the dynamics of the acrotelm and instead assume that dynamics of the system are controlled entirely by slow processes occurring in the catotelm. Moreover, each model focuses exclusively on either hydrological or biological processes: the BGM considers only peat accumulation and ignores water storage, whereas the GMH considers only catotelm water flow and ignores peat accumulation. On this basis, both models make predictions for large-scale patterns: a concave profile of peat depth vs. peat age for the BGM, and a hemi-elliptical bog cross section for the GMH. Variants of the BGM (and to a lesser extent the GMH) have been applied to several raised bogs, as well as to other peatland systems, ranging from tropical peat swamp forests (Winston 1994) to boreal continental fens (Yu et al. 2003).

Since the 1980s, approaches to modeling natural systems have broadened from the strictly reductionist and universalist to include approaches developed specifically for hierarchical, complex systems (Levin 1998, Werner 1999, Rietkerk et al. 2004a). In the hierarchical approach, larger scale dynamics emerge through the coupling and external forcing of variables

operating at intrinsically different scales of time (Werner 1999) and space (Rietkerk et al. 2004a). In bogs, the horizontal distinction of cover types and the vertical separation of fast and slow process rates are ideally suited to the hierarchical approach. The GMH and BGM are nonhierarchical, in the sense that variables operate on a single time scale and space is one-dimensional. After >20 years, the time has come to assess critically the assumptions and limitations of the GMH and BGM, and to place models of peatland form and development within a hierarchical framework.

In this paper, we reappraise the GMH and BGM, critically examining their underlying assumptions and existing tests of their predictions. This detailed analysis reveals major theoretical weaknesses and empirical limitations that have gone unidentified for the past 20 years. We identify the key processes that link dynamics at different temporal and spatial scales and that determine responses to, and interactions with, external forcing, such as climate change. We use this analysis as a basis for building a hierarchical framework for models of peatland development. We believe the GMH and BGM were landmark advances of their time, but that the hierarchical approach to modeling will lead to a better representation of peatland development and response to external forcing.

THE BOG GROWTH MODEL

Theoretical basis and assumptions

The BGM (Clymo 1984) provided the theoretical backbone for Clymo's (1984) analysis and empirical review of peat accumulation processes. The two-layer bog structure, a thin, seasonally oxic acrotelm, underlain by a much thicker, permanently anoxic catotelm, was central to his thesis. To avoid ambiguity, we will refer to organic matter in the acrotelm as "litter," and that within the catotelm as "peat." In the BGM, peat formed by processing of litter in the acrotelm is captured for long-term storage as it becomes the top of the thickening catotelm. An important consequence of continued catotelm decay is that the rate of peat accumulation decreases as the bog develops. Under the specific assumption that catotelm decay consumes a constant proportion of all remaining organic matter (as in Clymo's original 1984 paper), the peat mass will tend toward a steady-state "limit to growth" as the rate of peat loss by decay approaches the constant rate of addition. A key prediction of the model is that the rate of peat accumulation decreases over time, resulting in a concave profile of peat depth vs. peat age.

The BGM proposed that, at the bog center, peat formed by ongoing decay and burial of plant litter in the seasonally oxic acrotelm is added at a constant rate to the catotelm, where a constant proportion of the accumulated organic matter decays anaerobically at a slow rate (Fig. 1). Each year, new litter is deposited at the bog surface, and, in the case of vascular plant roots, belowground, at a constant rate p_a (with dimensions

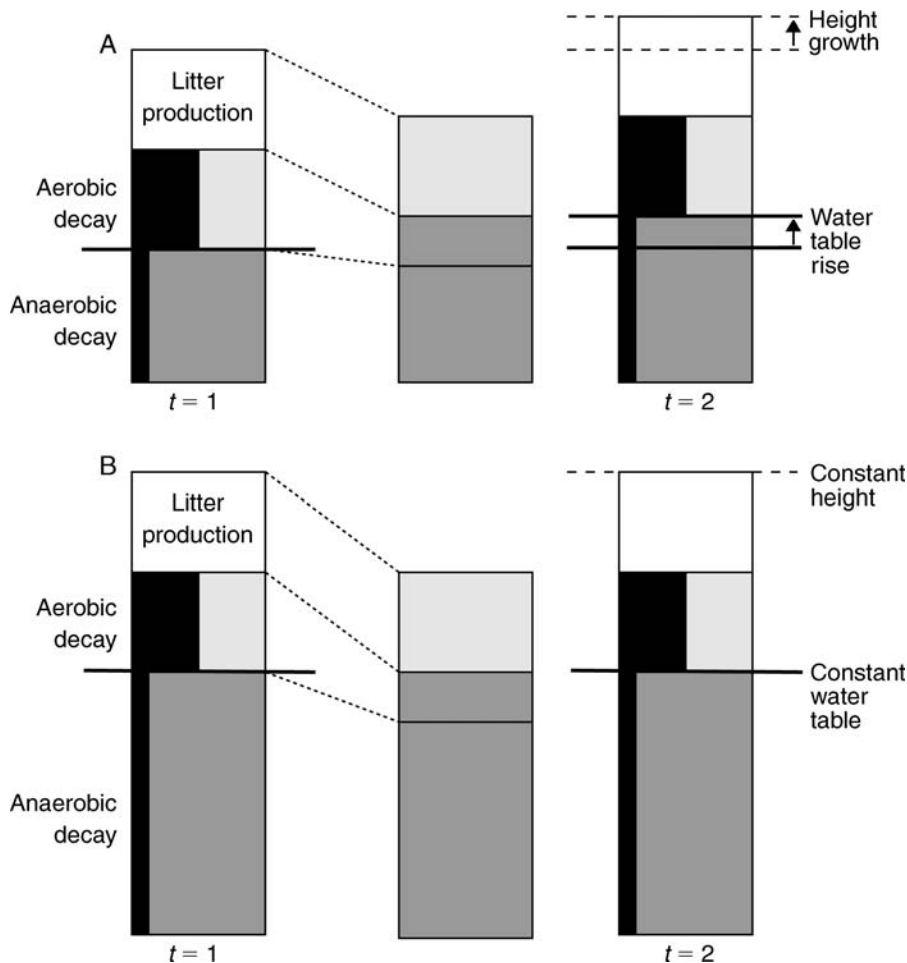


FIG. 1. Schematic diagram of Clymo's (1984) model of bog growth. The columns represent cross sections through the peat profile at observation times t_1 and t_2 . A constant amount of fresh litter (white area) is added each year. A constant proportion of all material in the acrotelm (medium gray area) is lost each year by aerobic decay (black area). Similarly, a constant (but much smaller) proportion of all material in the catotelm (dark gray area) is lost each year by anaerobic decay. The rate of water-table rise exactly matches the rate of bog growth, and the acrotelm maintains a constant thickness. (A) At an early stage of bog development, litter production exceeds all decay losses, and the bog grows in height. (B) At the steady-state, litter production equals decay losses, and the bog maintains a constant height.

mass per area per time), while a constant proportion, α_a (per time), of all litter in the acrotelm, M_a (mass per area) is lost by mostly aerobic decay. Considering the acrotelm on its own, the rate of change in mass of organic matter, dM_a/dt , is given by

$$\frac{dM_a}{dt} = p_a - \alpha_a M_a. \quad (1)$$

A generic form of this equation was introduced first by Jenny et al. (1949) and has been applied widely to both organic and mineral soils. Integrating Eq. 1, the amount of litter accumulated in the acrotelm after time, t_a [time], is given by M_a [mass per area]:

$$M_a = \frac{p_a}{\alpha_a} [1 - \exp(-\alpha_a t_a)]. \quad (2)$$

According to Eq. 2, litter accumulation in the acrotelm

proceeds rapidly at first, but gradually slows and approaches an asymptotic limit of p_a/α_a . For a bog to continue growing, the acrotelm must never get very close to this asymptotic limit. Instead, litter at the base of the acrotelm must become part of the catotelm, where, as peat, it now undergoes very slow (anaerobic) decay. Hence, the rate of change in acrotelm mass (Eq. 1) also depends on the rate at which litter is transferred from the base of the acrotelm to the top of the catotelm, p_c (mass per area per time):

$$\frac{dM_a}{dt} = p_a - \alpha_a M_a - p_c. \quad (3)$$

Clymo (1984) assumed that, under a stable climate, the acrotelm would maintain a "fairly constant depth and mass," and that it would transfer modified litter to the catotelm "at a characteristic depth and after a

TABLE 1. Analytical models of peat accumulation.

Model no.	Proportion of original mass remaining	Rate of peat bog growth	Analytical solution	Predictions
1	$m_t/m_0 = \exp(-\alpha_c t)$	$dM_c/dt = p_c - \alpha_c M_c$	$M_c = p_c/\alpha_c(1 - \exp(-\alpha_c t_c))$	height asymptotic to p_c/α_c ; depth-age profile concave
2	$m_t/m_0 = 1/(1 + \alpha_c t)$	$dM_c/dt = p_c - \alpha_c(m_t/m_0)M_c$	$M_c = p_c/\alpha_c \ln(1 + \alpha_c t_c)$	height logarithmic with t_c (no limit); depth-age profile concave
3	$m_t/m_0 = 1/\sqrt{(1 + 2\alpha_c t)}$	$dM_c/dt = p_c - \alpha_c(m_t/m_0)^2 M_c$	$M_c = p_c/\alpha_c(\sqrt{(1 + 2\alpha_c t_c)} - 1)$	height parabolic with t_c (no limit); depth-age profile concave
4	$h_t/h_0 = \exp(-\alpha_c t)$	$dH_L/dt = r_i$ for $t_c \leq H_i/r_i$ $dH_L/dt = H_i r_i / \sqrt{2H_i r_i t_c - H_i^2}$ for $H_i/r_i < t_c \leq t_{\max}$ $dH_L/dt = 0$ for $t_c > t_{\max}$	$H_L = r_i t_c$ for $t_c \leq H_i/r_i$ $H_L = \sqrt{2H_i r_i t_c - H_i^2}$ for $H_i/r_i < t_c \leq t_{\max}$ $H_L = r_m/\alpha_c$ for $t_c > t_{\max}$	height square-root function of t_c , with fixed limit; depth-age profile concave
5	$m_t/m_0 = \exp(-\alpha_c t)$	$dM_c/dt = p_c \exp(-\beta t_c) - \alpha_c M_c$	$M_c = p_c/(\alpha_c - \beta)(\exp(-\beta t_c) - \exp(-\alpha_c t_c))$	height variable function of t_c ; depth-age profile linear, or convex, depending on parameter values

Notes: For all models: m_0 , original mass of one peat cohort; m_t , mass of cohort remaining after time t has elapsed; M_c , cumulative mass in catotelm at bog center at time t_c ; α_c , catotelm decay rate coefficient; p_c , rate of peat addition to catotelm. For model 4: h_0 , original thickness of one peat cohort; h_t , thickness of cohort remaining at time t ; H_L , height of catotelm at bog center; r_i , initial rate of catotelm height growth; H_i , height of the initial layer of peat that accumulates at rate r_i ; r_m , rate of catotelm height growth at t_{\max} , time at which the catotelm reaches maximum height. Model 5: β , peat addition rate modifier.

Sources for the models are: model 1, Clymo (1984); models 2 and 3, Clymo (1992), Clymo et al. (1998); model 4, Winston (1994); model 5, Yu et al. (2003).

characteristic time" (Clymo 1984:617). On peatlands, small topographic features ("microforms") occur along a gradient of water table depth, ranging from hummocks (peat surface ~50 cm above the water table) to lawns, to hollows, to pools (sediment surface always below the free water surface). Although Clymo (1984) briefly reviewed empirical evidence showing that p_a varies 3–4 fold among microform types, he assumed "for illustrative purposes . . . that the vegetation is unchanged and that productivity is constant from year to year" (Clymo 1984:617). These statements imply that p_a and α_a are considered constant. Eq. 3 was set equal to zero, giving constant p_c at the steady-state acrotelm mass, $M_a = M_a^*$:

$$p_c = p_a - \alpha_a M_a^* \quad (4)$$

Clymo (1984) assumed further that a constant, very small proportion, α_c (per time), of all peat in the catotelm, M_c (mass per area), is lost by anaerobic decay. Hence, the rate of peat accumulation in the catotelm is analogous to Eq. 1:

$$\frac{dM_c}{dt} = p_c - \alpha_c M_c \quad (5)$$

and, integrating,

$$M_c = \frac{p_c}{\alpha_c} [1 - \exp(-\alpha_c t_c)] \quad (6)$$

where t_c (time) is the time since formation of the catotelm (t_c is generally much greater than t_a , so t_c

approximates the time since formation of the entire peat deposit). Hence, the catotelm grows rapidly at first, but gradually approaches an asymptotic limit, p_c/α_c . This "limit to peat bog growth" inspired the title of the original paper.

To summarize, the explicit assumptions leading to Eq. 6 and the asymptotic limit to bog growth are:

1) Catotelm decay is nonzero, and is a constant proportion of all material in the catotelm (i.e., $\alpha_c = \text{constant} > 0$).

2) Acrotelm depth, mass, vegetation, and process rates are in a steady state, so that peat is transferred from the acrotelm to the catotelm at a constant rate (i.e., $p_a - \alpha_a M_a^* = p_c = \text{constant}$). The catotelm is not in a steady state, but approaches an asymptotic limit of p_c/α_c .

Since publication of the original model, a number of modifications have been proposed (Table 1). Clymo (1992) allowed α_c to decrease with proportion of original mass remaining. If catotelm decay allows persistence of even a small amount of refractory material, *bog growth will not have a biological limit*, but the rate of peat accumulation nevertheless will decrease over time (Clymo 1992). Winston (1994) assumed that, until the biological limit to bog growth is reached, the rate of peat accumulation is controlled by rise of the water table and lateral expansion of the peat deposit. In effect, peat accumulation is controlled by hydrological constraints imposed by bog size and shape. Yu and co-workers (Yu

et al. 2003) allowed the rate of peat addition from acrotelm to catotelm to decrease over time according to a negative exponential function, chosen for mathematical convenience to allow analytical solution. They developed this model for application to fens, with the expectation that rate of peat addition to the catotelm would decrease as the groundwater mound developed and the peatland surface became progressively more isolated from mineral-influenced water. In their model, the rate of peat accumulation in the catotelm may increase or decrease over time depending on parameter values.

Although Clymo (1984) made no explicit assumptions about hydrological processes, his definition of the acrotelm–catotelm boundary is based on water table position. As a consequence, a highly constrained relationship between peat growth and water storage change is required for the assumption of a steady-state acrotelm mass and constant rate of peat addition to the catotelm, p_c , to be valid. The mechanism for acrotelm to catotelm transfer was described verbally rather than mathematically, and the rationale underlying the assumption of constant p_c was somewhat unclear. To explain the implications of this assumption, we describe in detail the mechanism of peat transfer from acrotelm to catotelm.

A cohort of litter that lies near the base of the acrotelm and has undergone aerobic decay for many years eventually loses its structural integrity and collapses under the mass of overlying material. At the point of structural collapse, the rapid decrease in total pore volume and average pore size impedes water flow, so that the water table rarely falls below this point. The position of the boundary between acrotelm and catotelm is difficult to define operationally, but in theory it is defined by the mean depth of the minimum (summer) water table. As long as water storage change is positive, the water table slowly rises over successive years, so that litter at the base of the acrotelm becomes part of the catotelm, now as peat.

Clymo (1984) defined p_c only in terms of litter production and decay, but clearly it is also a function of hydrological processes. Since the acrotelm–catotelm boundary is defined by water table position, a fairly constant acrotelm depth and mass implies that the rate of water table rise must equal the rate of height growth of the catotelm (Fig. 1). At any stage of development, the volumetric addition of new peat from the base of the acrotelm must compensate exactly for the volumetric loss of catotelm peat by anaerobic decay and the rate of water table rise. Otherwise, the acrotelm would increase or decrease in depth and mass and M_a would no longer be in a steady state. At the limit to growth, the rates of water table rise and height growth of the catotelm are both zero. Hence, the rate of water table rise, dH/dt (length per time), can be expressed as a function of both height growth of the catotelm,

$$\frac{dH}{dt} = \frac{1}{\rho} (p_c - \alpha_c M_c) \quad (7a)$$

and water storage in the catotelm,

$$\frac{dH}{dt} = \frac{1}{f_d} (P - E - q_s) \quad (7b)$$

where ρ is the mean dry bulk density of catotelm peat [mass per volume]. The rate of water-table rise depends on the magnitude of the water budget excess (i.e., precipitation, P , minus evapotranspiration, E , and net subsurface flow losses, q_s – [all length per time]) and drainable porosity, f_d [dimensionless]. Note that net rainfall ($P - E$) and catotelm process rates (p_c , α_c) are assumed to be constant. By substitution and rearrangement of Eqs. 7a and 7b, we can express q_s as a function of M_c :

$$q_s = \left(P - E - \frac{f_d}{\rho} p_c \right) + \left(\frac{f_d}{\rho} \alpha_c \right) M_c. \quad (7c)$$

Eq. 7c states that subsurface flow losses, q_s , increase linearly with bog size (M_c), at a rate determined by peat properties (ρ , f_d) and the catotelm decay coefficient (α_c). Hence, the inevitable consequence of a fairly constant acrotelm depth, mass, and constant p_c is that subsurface drainage must be controlled by vertical growth of the peat deposit. Eqs. 7a to 7c yield a further assumption that is *implicit* to the BGM:

3) Subsurface flow losses are controlled by growth of the catotelm (i.e., q_s increases linearly with M_c).

We will consider the mechanistic basis and implications of this implicit assumption after examining the GMH.

Empirical evidence

The BGM can be applied empirically by inverting Eq. 6 so that time corresponds to peat age, and then using curve-fitting techniques to fit the inverted model to a profile of peat depth vs. dendrocalibrated radiocarbon age, giving estimates for the model parameters. This approach was introduced by Clymo in his 1984 paper, and subsequently has been adopted as a means of testing models of peat accumulation and estimating past rates of peat accumulation and carbon sequestration (e.g., Clymo et al. 1998). For positive p_c and α_c , the original BGM predicts a concave relationship between peat depth (increasing downward on the y -axis) and peat age (increasing rightward on the x -axis). Of the 20 or so profiles tested, a majority show some suggestion of the predicted curvature, while others show either no curvature or convex curvature (Clymo 1984, 1991). But depth–age profiles that conform to the predictions of the BGM can be generated by many of the model variants listed in Table 1 (see also Clymo 1992). Given that random variation and errors on radiocarbon dates (~200 yr) will always lead to uncertainty in parameter estimates, a convincing choice between different models of peat accumulation cannot be made solely on the basis of fitting models to profiles of age and depth: “We really need models that predict more complex behavior, or

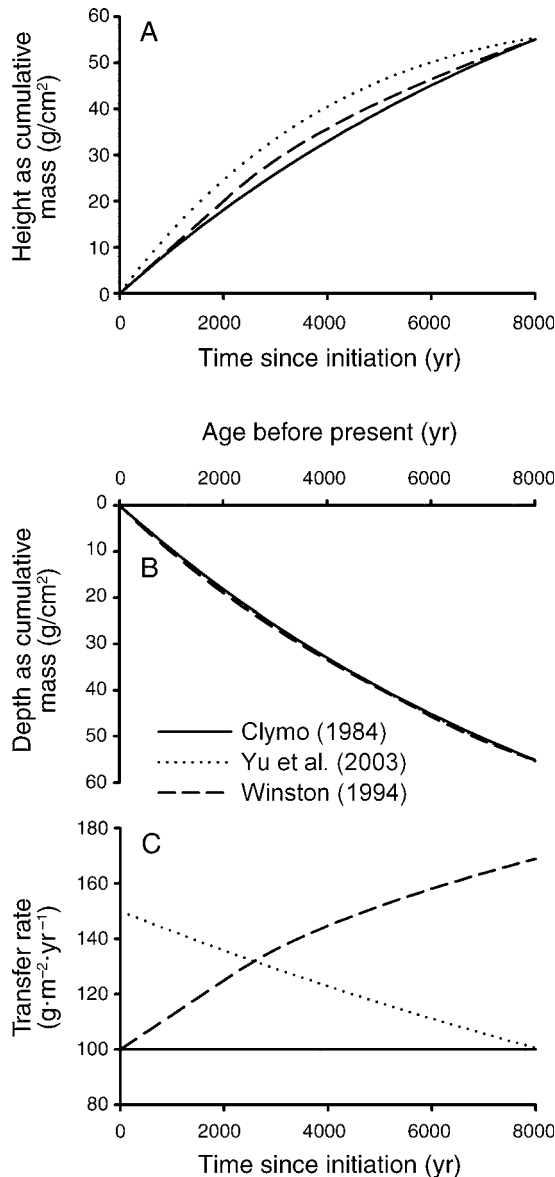


FIG. 2. Predictions of three models of peat accumulation: (A) Change in bog height (as cumulative mass) with increasing time since initiation. (B) Profiles of peat depth (as cumulative mass) vs. peat age at time of sampling. (C) Change in rate of peat transfer to catotelm with increasing time since initiation. In the models of Clymo (1984) and Yu et al. (2003), bog growth is controlled by peat accumulation. In Winston's (1994) model, bog growth is controlled by development of the groundwater mound (Table 1). Parameters were selected to give the same bog height at 8000 years and similar depth-age profiles. For Clymo (1984), peat addition rate $p_c = 100 \text{ g}\cdot\text{cm}^{-2}\cdot\text{yr}^{-1}$, and decay coefficient $\alpha_c = 1 \times 10^{-4} \text{ yr}^{-1}$. For Yu et al. (2003), $p_c = 150 \text{ g}\cdot\text{cm}^{-2}\cdot\text{yr}^{-1}$, peat addition rate modifier $\beta = 5 \times 10^{-5} \text{ yr}^{-1}$, and $\alpha_c = 1.5 \times 10^{-4} \text{ yr}^{-1}$. For Winston (1994), initial rate of bog height growth $r_i = 1.0 \text{ mm/yr}$, bog height for growth at the initial rate $H_i = 2.2 \text{ m}$, and $\alpha_c = 1.25 \times 10^{-4} \text{ yr}^{-1}$; a constant dry bulk density of 0.1 g/cm^3 is assumed.

predict the behavior of more variables" (Clymo 1992:133).

The BGM assumption that decay continues in the catotelm (i.e., α_c is nonzero) can be tested directly by examining the process of anaerobic decay. Methane concentration generally increases with peat depth below the water table (Clymo and Pearce 1995), and a variety of methane-producing microorganisms (Archaea) occur deep in the catotelm (Kotsyurbenko et al. 2004). Although the patterns are suggestive, the presence of Archaea, and a depth-related increase in methane concentration, are insufficient evidence of anaerobic decay of old peat. Much methane seems to be produced one to two decimeters below the water table, and is derived in part from recent substrates exuded or sloughed from living plant roots (Whiting and Chanton 1993, Joabsson et al. 1999, Christensen et al. 2003). Carbon isotopic evidence suggests that a proportion of deep-peat methane is derived from recently fixed organic matter, possibly transported down-profile as dissolved organic carbon, but that old peat is also utilized (Aravena et al. 1993, Chanton et al. 1995, Chasar et al. 2000). On balance, the evidence supports the assumption that old peat is consumed by anaerobic decay, i.e., that α_c is nonzero, but there is insufficient evidence to support one choice of decay rule over another (Bauer 2004). Although fossil C/N quotients have been used as indicators of catotelm decay losses (Kuhry and Vitt 1996), these quotients may reflect acrotelm, rather than catotelm, decay processes. In future, a combination of laboratory incubation experiments (Updegraff et al. 1995) and chemical analyses (Bourdon et al. 2000) of peat profiles may help to identify the correct decay rule.

Clymo (1992) demonstrated that model variants using different decay rules cannot be distinguished for empirical depth-age profiles, because the differences in curvature are too subtle to differentiate, and more than one model can be fitted to the same data set with similar statistical confidence. A similar problem occurs in trying to differentiate between models that assume constant or variable rates of peat transfer to the catotelm. To illustrate this problem, Fig. 2 contrasts the predictions of Clymo's original (1984) model with two others that allow the transfer rate at the bog center to vary (Winston 1994, Yu et al. 2003). Parameter values were selected to give the same bog height at 8000 years, and to give similar depth-age profiles, so that the models cannot be distinguished by the usual approach of nonlinear function minimization (Fig. 2B). Rates of peat accumulation differ among the models (Fig. 2A), and rates of peat transfer differ even in trend (Fig. 2C). The changes in rate of peat transfer simulated by the models of Yu et al. (2003) and Winston (1994) could be the result of changes in litter production (p_a), litter decay rate (α_a), or acrotelm thickness (M_a). Other studies have shown that changes in plant community composition can produce the expected concave pattern on depth-age

profiles (Kilian et al. 2000, Froelking et al. 2001, Bauer 2004), even though the basic assumptions of constant litter production and decay are clearly violated.

Systematic changes in p_c should be evident in the peat archive through changes in plant species composition and degree of humification, suggesting that the second BGM assumption can be tested by inferring changes in peat formation rate from stratigraphic sequences. Different microform types are dominated by distinct assemblages of plant species and differ markedly in rates of litter production and decay. The net rate of peat formation (i.e., the difference between litter production and decay losses, $p_a - \alpha_a M_a$) shows a humpbacked pattern in response to water table depth, with lowest peat formation rates occurring in open-water pools, and high hummocks and highest rates occurring in intermediate microforms such as lawns and low hummocks (Belyea and Clymo 2001). This pattern is reflected also in rates of net ecosystem exchange of carbon gases, with lawns acting as the strongest sinks for atmospheric carbon (Waddington and Roulet 1996, Alm et al. 1997), and pools showing large annual losses of carbon to the atmosphere (Hamilton et al. 1994, Waddington and Roulet 2000). For a constant acrotelm depth and mass, the peat formation rate is equal to the rate of peat addition to the catotelm, p_c (Eq. 4). Hence, stratigraphic sequences of plant macrofossils can indicate constancy or variability of peat addition.

Large peat exposures on a bog in England showed expansion and contraction of hollow-lawn and lawn-hummock margins on time scales of 10s to 100s of years (Barber 1981), suggesting that p_c must also have varied throughout the development of this peatland. On the central plain of many raised bogs, open-water pools have formed secondarily on terrestrial peat (Glaser and Janssens 1986, Foster et al. 1988), indicating a systematic decrease in p_c . Some peat profiles show systematic changes in botanical composition, and a degree of humification consistent with a progressive increase in acrotelm thickness and cumulative decay (Belyea and Malmer 2004), again suggesting a systematic decrease in p_c . In summary, stratigraphic evidence from several sites has shown that microform composition changes during peatland development, in some cases suggesting a systematic change in peat formation rate that refutes the BGM assumption of constant p_c .

The final assumption implicit in the BGM, that subsurface flow losses increase linearly with catotelm height, cannot be tested without considering hydrological processes explicitly. In his 1984 paper, Clymo considered the implications of spatial and temporal variations in hydrological conditions by constraining bog shape according to the GMH. On its own, the BGM makes no predictions about bog form. The rate of peat addition to the catotelm at the bog center, p_c , is assumed to be constant, but away from the center p_c varies systematically in both space and time. The functional explanation for systematic changes in p_c away from the

bog center is that gradual changes in surface gradient and drainage occur during development of a flat central plain (plateau), leading to a gradual shift in acrotelm characteristics that control p_c . Hence, Clymo (1984) posited that *bog growth is controlled ultimately in a vertical direction (but only at the bog center) by biological controls and in a horizontal direction by hydrological controls*. Despite implicitly linking peatland development to bog form and hydrology, the two-dimensional BGM (i.e., bog shape constrained by the GMH) does not incorporate hydrological processes explicitly, nor does it allow for any feedback between fast processes occurring in the acrotelm and slow processes occurring in the catotelm. We will address these issues in more detail after reviewing the underlying theory and assumptions of the GMH.

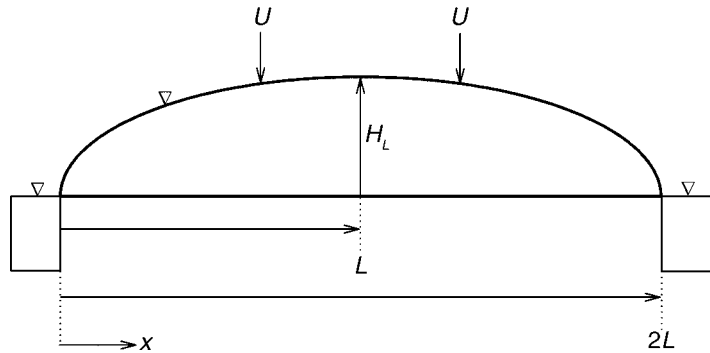
THE GROUNDWATER MOUND HYPOTHESIS

Theoretical basis and assumptions

The GMH (Childs and Youngs 1961, Ingram 1982) is usually attributed to Ingram (1982), who reproduced a simple steady-state equation from the groundwater literature and showed how it can be used to model bog shape and size. In essence, the equation predicts that the surface of a raised bog will be hemi-elliptical when viewed in section. Interestingly, Ingram's hypothesis appears to have been suggested over 20 years earlier by Childs and Youngs (1961). Ingram did not refer to this paper, but instead to a later textbook by Childs (1969) in which groundwater mounds are discussed, but not in relation to the size and shape of bogs. Since Ingram (1982) and Childs and Youngs (1961) seem to have arrived independently at the same hypothesis, we think that attribution for the GMH should be shared accordingly.

The GMH proposes that raised bogs support a mound of subsurface water under greater than atmospheric pressure, the upper boundary of which is the water table, which lies at all times within a few decimeters of the bog surface. The shape and size of the groundwater mound depend, in part, on the hydraulic properties of the peat within the bog, but the groundwater mound, in turn, controls the size and shape of the raised bog. In an *equilibrium bog* (after Childs and Youngs 1961), which we take to mean a bog that is neither growing nor shrinking in its gross dimensions of height and horizontal extent over greater than decadal timescales, decay of peat is controlled principally by the position of the water table. If the water table is curved, the surface of the peat will be curved, and this correspondence explains the shape of the equilibrium bog. Ingram said little more than this when expounding his hypothesis, either in his 1982 paper or in subsequent work (e.g., Ingram 1987). Thus, the GMH says nothing about how a bog reaches an equilibrium size and shape. Later in this paper, we explore the problem of bog development, considering the assumptions of both the GMH and the BGM.

FIG. 3. The equilibrium water table in an idealized body of peat between two rivers and overlying poorly permeable mineral sediment. The inverted triangles denote the water surfaces in the peat body and in the rivers. Bog height at the mid-point distance, $x = L$, is given by H_L ; recharge to the water table within the peat body is given by U [with dimensions length per time]. The shape of the bog is determined by U and the hydraulic conductivity of the peat, K , such that $U/K = H_L^2/L^2$. Note that x continues to increase to the right of the mid-point distance, L .



How an equilibrium bog maintains its height and an elliptical shape in cross section can be considered in the idealized case of a body of peat on a flat plain of relatively impermeable mineral sediment between two parallel streams or rivers (Fig. 3). Such a scenario is probably not common in nature, although some glacial outwash plains with anastomosing or bifurcating river channels come close (for other examples where parallel rivers occur on low-gradient, poorly permeable plains [Glaser et al. 2004]). In this scenario, the peatland is much longer than the width between the rivers and nearly all subsurface water flow is perpendicular to the rivers. The peat presents a resistance to the subsurface flow of water. In nondrought years, net rainfall ($P - E$) flows through both the acrotelm and the catotelm, and some may flow across the bog surface. According to the GMH, peatland height and shape are controlled by conditions only in a *drought* year. The GMH assumes that (1) all net rainfall delivered to the bog in a drought year flows through the catotelm, (2) this delivery of net rainfall is steady, or time-invariant, through the year, and (3) the hydraulic conductivity (K) of the catotelm is uniform in space.

Groundwater flow in shallow aquifers such as peat deposits is commonly assumed to be described by an empirical law with a physical basis discovered by Darcy (hence the name Darcy's law [cf. Freeze and Cherry 1979]). For a cross section of porous medium, Darcy's law is

$$q_x = -K \frac{\partial H_h}{\partial x} \quad q_z = -K \frac{\partial H_h}{\partial z} \quad (8)$$

where q is the rate of water discharge per unit area of porous medium (with dimensions of length per time), H_h is the hydraulic head (length—energy per unit mass of water), and K is a proportionality constant known as the hydraulic conductivity, and is the value of q under a hydraulic head gradient of unity (length per time); x refers to horizontal distance (length); and z to vertical distance (length). Effectively, the law states that hydraulic head gradients can be expected to develop both horizontally and vertically within a cross section of a porous medium. In many groundwater flow situations, such as shallow floodplain soils or peatlands overlying

poorly permeable subsoils, hydraulic head gradients are much greater in the horizontal than in the vertical direction (i.e., $|\partial H_h/\partial x| \gg |\partial H_h/\partial z|$). In such situations, it is often assumed that the vertical gradient can be ignored and that the horizontal gradient can be approximated by the gradient of the water table. This assumption is known as the Dupuit-Forchheimer (D-F) approximation (cf. Freeze and Cherry 1979). Since the drought water table corresponds to the top of the catotelm (see *The bog growth model: Theoretical basis and assumptions*), we will denote height of the water table by H (length) and the water table gradient by dH/dx . With the D-F approximation, the two-dimensional problem stated in Eq. 8 is replaced with a one-dimensional description of groundwater flow:

$$q = -K \frac{dH}{dx}. \quad (9)$$

Now, q will vary according to position on the peatland. If we consider the peatland in Fig. 3, and assume all net rainfall enters the peat and reaches the water table (i.e., there is no overland flow), all net rainfall to the left of the midpoint between the streams enters the peat and seeps to the left-hand stream, and all net rainfall to the right of the midpoint enters the right-hand stream. In this situation, the amount of net rainfall passing through a unit width of peat below the water table [$H(x)$] in the positive x direction (Fig. 3) is given by $U(x - L)$, where U denotes net rainfall or recharge (length per time), and $2L$ is the distance between the two streams (length). Thus, $q = U(x - L)/H$, which, when combined with Eq. 9, gives

$$\frac{U(L - x)}{H} = K \frac{dH}{dx}. \quad (10)$$

Separating variables and integrating over the limits $x = 0$, $H = 0$ and $x = x$, $H = H$ yields

$$\int_{H=0}^{H=H} H dH = \frac{U}{K} \int_{x=0}^{x=x} (L - x) dx$$

or

$$\frac{U}{K} = \frac{H^2}{2Lx - x^2} \quad 0 \leq x \leq 2L. \quad (11)$$

At the bog center, $H = H_L$ at $x = L$, giving $H_L^2/L^2 = U/K$. Away from the bog center, bog height is given by $H = (H_L^2 - (L - x)^2(U/K))^{1/2}$.

Eq. 11 is a steady-state equation, that is, the water table is assumed invariant in time ($dH/dt = 0$), as is the recharge, U . Eq. 11 describes the water table as a hemi-ellipse, with horizontal extent controlled by the position of the rivers. For increasing U/K , H_L and dH/dx also increase.

The key idea underpinning the GMH is that decay of organic matter proceeds much more slowly below the water table than above it, so that the peatland surface tends to follow the shape of the water table. Although, strictly speaking, the water table is a pressure surface (it is where the water in the soil is at atmospheric pressure), conditions above it are usually much less limiting in oxygen than below it, and aerobic decay in peatlands proceeds much more rapidly than anaerobic decay. A thin tension-saturated zone or capillary fringe (cf. Gillham 1984) that would allow anaerobic decay to occur above the water table may occur in highly decomposed litter with small pores. In such cases, the top of the tension-saturated zone may be a more suitable dividing line between aerobic and anaerobic conditions.

Recognizing that the water table fluctuates with climate within and between years, Ingram (1982, p. 301) suggested that the surface of the bog follows the position of the water table for “the driest period through which the mire (*i.e., bog*) survives without irreversible desiccation” (italicized text added). This presumably means periods of drought where the peat does not become so dry that it cracks or becomes hydrophobic (Ingram 1983). The peatland surface might increase in elevation during a run of wet years when mean water tables are relatively high, only to be brought back down in a dry year through aerobic decay of litter lying above the drought water table. Whether enough decay could occur in one drought year to consume all the “excess” litter that had accumulated in 10 to 30 normal years is a question open to debate. The position of the drought water table also defines the acrotelm–catotelm boundary. Hence, Eq. 11 must use a value of U appropriate for recharge to the catotelm during a drought year, and a value of K appropriate for acrotelm peat. For clarity, henceforth we will specify these parameters as U_c and K_c .

Ingram’s definition of U_c in his 1982 paper and subsequent publications was ambiguous and inconsistent. In his 1982 paper, he defined U_c both as a cumulative discharge from the bog [*i.e., $L(P - E)$* with implied dimensions of area per time] and as net rainfall [*$(P - E)$* with dimensions of length per time]. In the former definition, he noted on p. 301 (and annotated his Fig. 2 accordingly) that U_c is “the lateral discharge by seepage towards the lagg (*marginal*) streams” (italicized text added). Elsewhere, including in his calculations, it is clear that he actually intended U_c to mean net rainfall. In his 1987 paper (p. 292), he defined U_c as “the flux

density with which water enters the catotelm,” which seems to account for discharge of water through the acrotelm (*i.e., $U_c = P - E - q_{s,a}$* , where $q_{s,a}$ is discharge of water through the acrotelm per unit surface area of the peatland). However, in his use of U_c in his 1987 paper it is clear Ingram again intended U_c to mean net rainfall, *i.e.,* he assumed implicitly that no water flows through the acrotelm in a drought year ($q_{s,a} = 0$). The inconsistency of these definitions and applications of U_c has generated confusion, and, we believe, misguided applications of the GMH.

To summarize, the assumptions of the GMH are:

- 1) The hydraulic conductivity of catotelm peat, K_c , is invariant with depth in the catotelm and position on the bog (*i.e., $K_c = \text{constant}$*).
- 2) The vertical hydraulic gradient can be ignored, and the horizontal hydraulic gradient can be approximated by the water table gradient (*i.e., $\partial H_b/\partial x \approx dH/dx$*).
- 3) During a dry year, all net precipitation, $P - E$, flows steadily (*i.e., at a constant rate*) through the catotelm, and acrotelm discharge is zero (*i.e., $q_{s,a} = 0$*). Hence, annual climate data ($P - E$ for a drought year) can be used to estimate U_c .

A few studies have explored variants of the GMH. With slight modification, the equations can be applied to bogs that are different shapes or asymmetrical in section (*e.g., Glaser et al. 2004*). Armstrong (1995) allowed for an exponential decline in K_c with depth, and his model predicted a shallower gradient (lower dH/dx) close to the bog margin than did the original GMH. Winston (1994) modified U_c so that it described the net delivery of water to the catotelm (*i.e., $P - E - q_{s,a}$*). Unlike Ingram (1982, 1987), Winston (1994) did not assume that $q_{s,a}$ is zero in a drought year. Nevertheless, he did assume that $q_{s,a}$ was constant, so his predictions are analogous to those of Ingram (1982).

Although the GMH ignores water flow through the acrotelm, it has clear implications for the properties of the acrotelm. For a bog that has developed between two parallel rivers (Fig. 3), net rainfall ($P - E$) does not vary with geographical location on the bog. The amount of water that must flow through the catotelm to the rivers ($q_s H$), increases linearly with distance from the central axis of the bog: $U_c(x - L)$, where flow is positive in the positive x direction (see the derivation of Eq. 10). In nondrought years, flow of water through the catotelm will be more or less the same as during drought years, because Ingram defines the top of the catotelm by the lowest water table in a drought year. The amount of water that must flow through the acrotelm is given by net precipitation in a normal year ($P - E$) minus catotelm recharge during a drought year (U_c), all multiplied by horizontal distance: $(P - E - U_c)(x - L)$. Hence the amount of water that must flow through the acrotelm also increases linearly with distance from the central axis of the bog.

The acrotelm overlies the hemi-elliptical surface of the catotelm, and so the gradient driving water flow in the

acrotelm, dH/dx (where H is bog height and x is horizontal distance), increases towards the bog margin. The gradient can be calculated by differentiating Eq. 11 or substituting it into Eq. 10:

$$\frac{dH}{dx} = \frac{U_c(L-x)/K_c}{[U_c(2Lx-x^2)/K_c]^{1/2}}. \quad (12)$$

Flow through the acrotelm is given by the product of the transmissivity and the hydraulic gradient, where transmissivity is the product of hydraulic conductivity and thickness of flow. Hence, acrotelm transmissivity is given by

$$T_a = \frac{(P-E-U_c)[U_c(2Lx-x^2)/K_c]^{1/2}}{U_c/K_c}. \quad (13)$$

According to Eq. 13, T_a decreases elliptically with distance from the central axis. In the acrotelm, thickness of flow is the distance between the water table and the top of the catotelm. If hydraulic conductivity of the acrotelm (K_a) is fixed, thickness of flow must decrease elliptically towards the margin. Alternatively, if thickness of flow is fixed, then K_a must decrease elliptically towards the margin. The GMH says nothing about which of these is the more likely, or whether a combination of the two occurs. Whichever is the case, Eq. 13 yields a fourth assumption implicit to the GMH:

4) Acrotelm transmissivity, T_a , decreases elliptically with distance from the central axis of the bog [i.e., $T_a \propto (2Lx-x^2)^{1/2}$].

This fourth assumption of the GMH reveals the interdependence of acrotelm and catotelm structure and function. Although Ingram's presentation of the GMH emphasized the two-layer structure of a bog, acrotelm processes were effectively ignored. Eq. 13 shows that acrotelm and catotelm properties are inextricably linked, even though the rates of certain processes in these layers are radically different. We will return to the nature and implications of such cross-scale feedback later in the paper.

Empirical evidence

The GMH applies only to an "equilibrium bog," one which maintains a constant size and shape over decadal time scales. By implication, the GMH cannot be applied to a peatland that is growing (or shrinking). Since most peat deposits in northern regions have shown monotonic increases in height throughout the Holocene (see *Bog growth and development of the groundwater mound*), this requirement raises the question of whether the GMH is applicable only in a few special cases. Unfortunately, Ingram (1982) and other researchers who have applied the model have not addressed this question. The potential problems of nonequilibrium conditions should be borne in mind in the subsequent discussion.

The first test of the GMH appears to have been by Childs and Youngs in an unpublished report (see *The groundwater mound hypothesis: Theoretical basis and*

assumptions [cf. Childs and Youngs 1961]), although the first published test was by Ingram in his 1982 paper. Ingram (1982) predicted the size and shape of a small raised bog in central eastern Scotland (Dun Moss: 56°42' N, 03°21' W) based on Eq. 11, with U_c estimated from meteorological data, K_c measured using the piezometer (or seepage tube) method, and L measured directly. Although he showed a fair correspondence between the shapes of the measured and predicted bog surfaces, the value for U_c/K_c based on meteorological data and piezometer tests was larger than that obtained based on bog morphometry. Other authors have experienced even greater problems applying the model at sites in Ireland (Kneale 1987), northwest England (Bragg 1991), and southwest Scotland (Clymo 2004). In contrast, the GMH gave sensible sizes and shapes for raised bogs in the Hudson Bay Lowlands of northern Canada (Glaser et al. 2004). The problems in applying the GMH could be due to errors in the estimation of either K_c or U_c .

Large errors are possible in the estimation of K_c using the piezometer/seepage tube method (Baird et al. 2004). The method has been explained elsewhere in the literature (Rycroft et al. 1975, Butler 1998) so it will not be explained in detail here. Briefly, a tube open at both ends is inserted into an auger hole of the same or slightly smaller diameter, and any peat clogging the inside of the tube is removed. Water flows into the tube from the peat around the lower end until the water pressure in the tube at the lower end is the same as that of the water in the peat just outside the base of the tube. The water level in the tube is raised or lowered artificially, and the rate of recovery to the equilibrium level is measured. The value of K_c is estimated based on the geometry of the instrument and on the rate of recovery. A problem with the method is that peat can smear during installation of the tube, clogging pores around the lower end and causing recovery rates to be markedly reduced. Estimates of K_c may be as much as one to two orders of magnitude lower than the true value. Errors can be reduced by the removal of smeared peat, but few wetland researchers appear to have taken this precaution (cf. Baird et al. 2004).

One reason for a lack of correspondence between the GMH and reality may be the use of erroneous K_c data in Eq. 11. Moreover, K_c values obtained from piezometer tests, even when reliable and accurate at the small scale, may underestimate larger scale K_c values, and such underestimates may explain the mismatch between Eq. 11 and data. For example, water may flow very rapidly through preferential conduits, such as open-water pools. At scales exceeding 10s of meters, such features could not be considered separately, and some authors have suggested that the averaged flow through pools and peat at these scales may be described by an equivalent K_c that is much larger than the K_c of catotelm peat proper (Kneale 1987, Bromley et al. 2004). However, it is far from clear how K_c integrates over larger scales, or whether it is reasonable to use an equivalent K_c to

describe the hydraulic properties of peatlands with pools. Hydraulic conductivity is, by definition, a property of a porous medium, and, strictly speaking, cannot be used to describe flow through surface water bodies. A pragmatic approach to the problem is, perhaps, to accept that an equivalent K_c is appropriate and to scale K_c based on pool area (Ivanov 1981; Belyea, *in press*).

Estimates of U_c are also subject to large errors, in estimation of both net rainfall and the partitioning of water flow between acrotelm and catotelm. In both maritime and continental climates, evapotranspiration is low during the winter months, and rainfall is delivered to the peatland surface in discrete and irregular events, even in a drought year. Hence, net rainfall, $P - E$, is not constant through the seasonal cycle, and the assumption of steady-state flow through the catotelm during a drought year is fundamentally flawed. The controls on evapotranspiration are complicated and poorly resolved (Lafleur et al. 2005), and involve internal factors (e.g., water table depth, vegetation) as well as climate. As a result, even an annual value of $P - E$ is subject to error. Moreover, not all of the net rainfall infiltrating into a bog will flow through the catotelm. Rainfall delivery and runoff response in bogs can show large intra-annual variation, even in drought years (e.g., Evans et al. 1999, Fraser et al. 2001). During periods of high rainfall or snowmelt, the water table rises close to the peatland surface and subsurface flow occurs not only through the catotelm, but also through the acrotelm, contravening the third assumption of the GMH. Hence, annual meteorological data for a drought year cannot be used to estimate directly the amount of water discharged through the catotelm, and the values of U_c used to test Ingram's model (Ingram 1982, Kneale 1987, Bragg 1991, Clymo 2004, Glaser et al. 2004) are fundamentally biased. The inability to estimate U_c from climate data creates substantial problems for application of the GMH to field data.

Previous studies have shown that the first assumption of the GMH is not met in practice. Ingram (1982) clearly recognized that K_c was variable, and the implicit interpretation of the assumption could be rephrased as: the variable K_c of a raised bog can be described effectively by a single K_c value. In essence, Ingram's (1982) use of a single K_c value follows the assumption widely held in subsurface flow modeling that a single, "effective" K value can be used to represent a K "field" that shows random variability over small spatial scales (10^{-1} – 10^1 m). If the K field shows spatial structure or patterning, the use of a single, effective K , becomes less tenable. Binley and co-workers (Binley et al. 1989a, b) provide a clear demonstration of how spatial structure affects subsurface flow, together with a wider discussion of the use of effective K values in soil water and groundwater models. As noted above (*The groundwater mound hypothesis: Theoretical basis and assumptions*), Armstrong (1995) argued that K_c across a bog consis-

tently shows depth dependency; therefore, a single value of K_c is not sufficient to describe the hydraulic status of the entire bog. Using a numerical solution to Eq. 10 in which K_c was assumed to follow an exponential decline with depth, he showed that the shape of the bog is altered quite substantially from the single K_c case. Empirical evidence of a monotonic decline in K_c with depth is patchy (Baird and Gaffney 1996), although some bogs do show depth dependence in K_c . For example, a bog that had been cutover for peat harvesting contained layers of peat with K_c low enough to have a large effect on patterns and rates of water flow (Beckwith et al. 2003b). Nevertheless, a widely applicable function that can describe variation in K_c with depth remains elusive.

Catotelm peat might be expected to vary in K_c in the horizontal dimensions if the peat that forms under one type of microform differs from the peat under another type and individual microforms persist for, say, more than a hundred years. Because the distribution of microforms is nonrandom, so will be the K_c of newly formed peat. Surprisingly little work appears to have been done on the hydrophysical properties of peat under different types of microform (but see Ivanov 1981, Bragg 1982). Stratigraphic studies of peat exposures suggest that individual microforms (e.g., hummocks) can persist in the same place for hundreds or thousands of years (Barber 1981). If such strongly nonrandom patterns of peat composition translate into differences in K_c , then we can expect a single effective K_c value for an entire bog to be a poor descriptor of subsurface flow conditions (Binley et al. 1989b).

The second assumption of the GMH, that vertical flow is negligible in raised bogs, and therefore that the D-F approximation can be used for modeling flow, has been reviewed and tested numerically by Reeve et al. (2000). They showed that the amount of vertical flow depends mainly on the contrast in hydraulic conductivity between the catotelm and underlying mineral material, with bog size having a second-order effect. Vertical flow may be important in bogs overlying relatively permeable sediments, whereas horizontal flow will dominate, and the D-F approximation will be reasonable, in bogs underlain by poorly permeable sediments. Later work by the same research group (Reeve et al. 2006) has shown that vertical flow can also be driven by seasonal changes in water table position when the peat has very high values of a groundwater storage parameter, known as the storativity (cf. Freeze and Cherry 1979). The transient simulations of Reeve et al. (2006) suggest that exchanges between peat and underlying mineral sediments are possibly less important than previously thought, but also show that seasonal oscillations in vertical flow can be important in deeper peat. Reeve et al. (2006) still note, however, that vertical flow in peatland systems is promoted when relatively permeable mineral deposits underlie the peat.

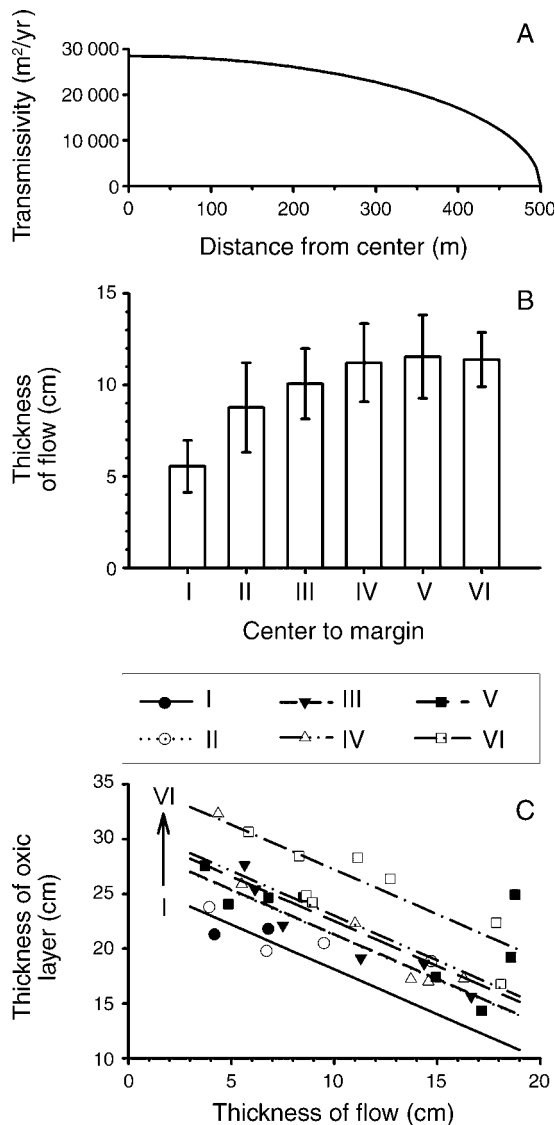


FIG. 4. (A) Spatial variation in acrotelm transmissivity predicted by the GMH. Parameter values are for Ellergower Moss, southwest Scotland: precipitation minus evapotranspiration $P - E = 1.8$ m/yr (based on climate records), bog half-length $L = 500$ m (from Ingram [1987]), hydraulic conductivity of catotelm peat $K_c = 0.5$ m/yr = 1.59×10^{-6} cm/s (a middle-range value from Clymo [2004]), recharge to catotelm $U_c = 0.0005$ m/yr (calculated from K_c and a shape-based U_c/K_c of 0.001, from Ingram [1987]). Transmissivity is the product of acrotelm hydraulic conductivity and thickness of flow. (B) Observed thickness of acrotelm flow at Ellergower Moss, southwest Scotland. Bars show the mean thickness (\pm SE) for replicate 30-m transects in six concentric rings around the bog center. Roman numerals denote relative position of rings from the bog center, where I is at the bog center and VI is at the bog margin. (C) Co-variation of acrotelm structure (i.e., thickness of permanently oxyc layer) with thickness of water flow for transects at Ellergower Moss. Roman numerals denote relative position of rings, as in (B). Lines show the results of an analysis of covariance with ring ($F_{5,27} = 7.9$, $P < 0.0001$) and thickness of flow ($F_{1,27} = 92.0$, $P < 0.0001$) as fixed effects. Note that thickness of the oxyc layer covaries with thickness of flow but increases with distance from the bog center.

Although few direct measurements of K are available for sediments underlying peatlands, stratigraphic records suggest the presence of both poorly permeable (e.g., bedrock, clay) and highly permeable (e.g., sand, silt) deposits. Ellergower Moss, a raised bog in southwest Scotland used to test the GMH, is underlain by silty sand deposits with a K that is an order of magnitude greater than the K of the lower catotelm (Clymo 2004). In a bog-fen complex at the Lost River Peatland in northern Minnesota, measurements of hydraulic head and porewater chemistry suggested that vertical flow was important (Siegel and Glaser 1987). A systematic survey of the contrast in hydraulic conductivity between catotelm peat and underlying mineral substrate is required at many more sites to assess whether vertical flow is a nontrivial component of peatland hydrology.

The final assumption implicit in the GMH is that acrotelm transmissivity, T_a , decreases elliptically with distance from the central axis of the bog (Fig. 4A). We are not aware of any studies that have measured transmissivity along transects from bog center to margin, although two studies provide partial evidence. Potential acrotelm capacity, τ_{ap} [L], was defined by van der Schaaf and Streefkerk (2003) as transmissivity per specific acrotelm discharge ($q_{s,a}$) and estimated as a function of the upstream contributing area (A_u), flow path width (w), and surface gradient, (I):

$$\tau_{ap} = \frac{T_a}{q_{s,a}} = \frac{A_u}{wI}. \quad (14)$$

At a site in Ireland, the topographic estimate of τ_{ap} decreased nonlinearly from bog center to margin, but it is unclear whether the decrease was elliptical, as predicted by the GMH. Belyea (*unpublished data*) estimated annual maximum and minimum water table depth indirectly, using a redox indicator (Belyea 1999) at multiple stations along 30-m transects distributed across Ellergower Moss. If the base of the acrotelm can be approximated by minimum water table depth, then the range (maximum minus minimum) can be used as an estimate of thickness of flow through the acrotelm. This estimate of flow thickness increased nonlinearly from bog center to margin (Fig. 4B). For acrotelm transmissivity to conform to the assumptions of the GMH at this site (Fig. 4A), acrotelm hydraulic conductivity must decrease from center to margin. The thickness of the part of the acrotelm lying above the highest water table in the permanently oxyc layer was negatively correlated with flow thickness, but it was generally thinner for transects at the bog center than for transects at the bog margin (Fig. 4C).

This pattern in acrotelm structure suggests a corresponding pattern in acrotelm hydraulic characteristics; since hydraulic conductivity tends to decrease with increasing depth in the acrotelm (Ivanov 1981), an increasingly thick oxyc layer suggests a decrease in hydraulic conductivity with distance from the bog's

central axis. The question remains as to whether this decrease in K_a would have been strong enough to offset the increase in flow thickness, leading to an elliptical decrease in T_a . Neither Belyea's (*unpublished data*), nor van der Schaaf and Streefkerk's (2003) studies provide unambiguous evidence for or against the fourth assumption of the GMH. Direct measurement of both acrotelm flow thickness and hydraulic conductivity may be required.

BOG GROWTH AND DEVELOPMENT OF THE GROUNDWATER MOUND

So far, we have considered bog growth in a vertical direction (the one-dimensional BGM) and the size and shape of an equilibrium groundwater mound (the GMH) separately. The BGM (Eq. 6) is a dynamic model for peat growth at one location on the bog. The only hydrological process implicitly considered is water table rise, and that is controlled completely by peat accumulation (Fig. 1). The GMH (Eq. 11) is a static model for height of the water table across the bog. The only biological process implicitly considered is peat accumulation, and that is controlled completely by water table elevation.

Both models effectively assume that acrotelm processes are completely determined by catotelm processes. In the GMH, the properties of the acrotelm (see implicit assumption 4 in *The groundwater mound hypothesis: Theoretical basis and assumptions*) are controlled entirely by the shape of the catotelm. In the BGM, the rate at which peat at the bog center is formed in the acrotelm and added to the catotelm is constant and the rate of water table rise is controlled by growth of the catotelm (see assumption 2 and implicit assumption 3 in *The bog growth model: Theoretical basis and assumptions*).

Growth in catotelm height implies gradual change in the size and possibly the shape of the groundwater mound. In the following sections, we will refer frequently to U_c/K_c , a dimensionless quantity related to bog size and shape ($U_c/K_c = H_L^2/L^2$) that is a measure of "catotelm excess," i.e., the relative excess of water delivery to the catotelm over specific discharge through that layer. In essence, U_c/K_c co-varies with the bog shape, and hydraulic gradient, required to balance the catotelm water budget. At any stage of development, we calculate U_c/K_c , assuming that catotelm flow is steady. Note from the preceding section that U_c is not strictly a climatic variable, but also depends on the partitioning of subsurface discharge between the acrotelm (high hydraulic conductivity, K_a) and the catotelm (low hydraulic conductivity, K_c). Note also that hydrophysical characteristics of catotelm peat are largely determined by processing in the acrotelm. For example, cumulative acrotelm decay increases with height of the peatland surface above the water table (Belyea and Clymo 2001), and so newly formed peat is likely to increase in degree of humification and decrease in K_c (Boelter 1969, Ingram 1983) for microforms increasing in depth to

water table. Hence, U_c/K_c is partially determined by acrotelm properties.

A simple analysis of the GMH will demonstrate the implications of autogenic development of the groundwater mound on acrotelm properties. If the bog is still growing, the catotelm water budget cannot be in equilibrium, as required by the GMH. To look at changes during bog development, we ignore the increase in water storage associated with height growth, because it will be very small compared with any other term in the water budget. Then, at the bog center ($x = L$), Eq. 13 gives

$$T_{a,L} = (P - E - U_c) \sqrt{\frac{K_c}{U_c}} L = (P - E - U_c) \frac{K_c}{U_c} H_L. \quad (15)$$

Eq. 15 states that, under a steady climate, either acrotelm transmissivity at the bog center, $T_{a,L}$, or catotelm excess, U_c/K_c , must change as the bog grows in height. The choice depends on whether the bog changes shape, H_L/L . Except in one special case, *bog growth must involve systematic change in acrotelm properties*.

One of the explicit assumptions of the BGM is that, at the bog center, newly formed peat is added to the catotelm at a constant rate throughout the bog's development (i.e., $p_{c,L}$ is constant). This assumption implies that acrotelm depth to water table, vegetation, chemical/physical properties, and litter residence time in the oxic layer all remain constant. It also has implications for catotelm recharge, U_c , and hydraulic conductivity, K_c . Although there are no explicit implications for K_c averaged over the whole catotelm, the hydrophysical properties of newly formed peat (litter at the base of the acrotelm that becomes the top of the catotelm) must be constant as a consequence of the invariance in acrotelm processing of litter. Hence, K_c must either be constant or vary solely as a result of systematic change in peat hydrophysical properties during slow decay and compaction in the catotelm. Under the assumption of a steady climate, the acrotelm receives a constant amount of net precipitation (rainfall and snowmelt, allowing for interannual variations) throughout peatland development. With the constraints of constant acrotelm properties and constant water supply, the BGM implies that U_c must be constant. According to the GMH, these constraints on U_c and K_c should also constrain bog shape.

Clymo (1984) reinforced his contention that bog height at the center is limited by biological (p_c/α_c), rather than hydrological, variables by linking the BGM to the GMH. Two scenarios were presented for bog growth in the length of a parallel-sided valley. In one, the bog was unconfined, growing in height and expanding along the length of the valley. In the other, the bog was confined, growing in height only. According to Eq. 15, either acrotelm transmissivity at the bog center, $T_{a,L}$, or U_c/K_c , or both, must change as the bog grows in height.

For the unconfined scenario, U_c/K_c was fixed at a constant value, implying a constant K_c throughout peatland development. Lateral extent, L , at each time horizon was effectively determined by height of the catotelm (see Eq. 11), and the unconfined bog must have expanded laterally from a central locus in direct proportion to its rate of height growth, so that bog shape, H_L/L , remained constant. From the first equality in Eq. 15, we see that $T_{a,L}$ must have increased, because L increased, but U_c/K_c remained constant.

For the confined scenario, the change in bog shape means that U_c/K_c must have increased as the bog grew in height, although only a fixed value was given. Since U_c and the hydrophysical properties of newly formed peat are assumed constant, this scenario implies that confined height growth must have been associated with a progressive decrease in K_c , solely as a result of decay and compaction of catotelm peat. From the first equality in Eq. 15, we see that $T_{a,L}$ must have decreased, because U_c/K_c increased but L remained constant.

An increase or decrease in acrotelm transmissivity, $T_{a,L}$, implies a change in the physical structure (K_a) or hydrological function (thickness of flow) of the acrotelm. For example, $T_{a,L}$ would increase if the proportional cover of seasonally flooded microforms, such as hollows and pools, increased, or if the water table rose higher within existing lawns and hummocks. Conversely, $T_{a,L}$ would decrease if the proportional cover of hummocks increased, or if the water table dropped lower in existing lawns and hollows. As well as driving changes in vegetation, such changes in acrotelm structure would affect cumulative acrotelm decay, and hence, the rate of peat formation and addition to the catotelm, $p_{c,L}$, (Belyea and Clymo 2001).

A change in p_c at the bog center invalidates one of the key assumptions of the BGM. Hence, *both the confined and unconfined scenarios presented by Clymo (1984) lead to a logical inconsistency* that is evident only if development of the groundwater mound is considered explicitly. The only possible scenario in which $T_{a,L}$, and, by implication, p_c , can remain constant throughout peatland development is for unconfined growth with K_c decreasing in proportion to $1/H_L$.

Subsequent researchers have followed Clymo's (1984) lead in linking the GMH to models of peat growth. Almquist-Jacobson and Foster (1995) simply substituted Clymo's (1984) biological limit to bog growth ($H_{\max} = p_c/\alpha_c$) into Ingram's (1982) GMH, so that bog radius at maximum height was constrained by U_c and K_c . The logical inconsistency of constant $p_{c,L}$ for all but one highly constrained scenario of peatland development applies equally to this integrated model. Winston (1994) argued that lateral expansion would continue after the bog reached a biological limit to further height growth, leading to development of a flat bog plain with a hydraulic gradient near zero. The rationale was that the hydrological and ecological processes controlling lateral expansion on to adjacent mineral soil may be dependent

on bog shape, but are independent of processes governing rate of height growth.

At a single site, patterns and rates of bog height growth depend on the history of lateral expansion, because autogenically driven changes in hydrological conditions and peat growth are related to changes in bog shape and size. Stratigraphic evidence suggests that bog size and shape change in a variety of ways, depending on local factors. At some sites, the bog reaches its physiographic limits early in development by rapid lateral expansion from a single locus (Svensson 1988, Ikonen 1993), or by coalescence of multiple loci of initiation (Heinselman 1970). At other sites, the bog initiates at a central locus and continues to expand outward at a steadily decreasing rate (Foster et al. 1988, Foster and Wright 1990). At still other sites, patterns and rates of lateral expansion are highly contingent on local topographic barriers (Korhola 1994, Anderson et al. 2003). In summary, the available evidence suggests that height growth and lateral expansion are not tightly coupled, although they may be related in the absence of topographic barriers. As a consequence, it is highly unlikely that the BGM requirement for height growth control of L and K_c will ever be met in practice.

There has been little study of the mechanisms of bog expansion on to marginal fen and mineral soil. On an area basis, paludification (peat initiation directly on mineral substrate) is a much more important process of peat initiation than is terrestrialization (lake-infilling; Sjörs 1983). Peat can begin to form on mineral soil only if waterlogging occurs due to a change in external factors (e.g., climatic change, isostatic land uplift; Hulme [1994] or internal processes of soil development (Ugolini and Mann 1979). The formation of placic horizons (sesquioxide pans) that impede vertical drainage may be encouraged by lateral inputs of bog groundwater with low pH, low redox potential, and high dissolved organic matter content (Lapen and Wang 1999). Even so, peat initiation on mineral soil and bog expansion will be limited by local topographic factors, such as slope, convergence of flow paths, and contributing area (Graniero and Price 1999). Further studies on the hydrological (Lapen et al. 2005) and ecological mechanisms driving lateral expansion are urgently needed to allow development of three-dimensional models.

Analytical models of bog growth can provide a valuable tool for quantifying regional variation in process rates across multiple sites (e.g., Clymo et al. 1998), but an appropriate model must be used in order to obtain accurate results. Of the peat accumulation models with analytical solutions (Table 1), only the model of Yu et al. (2003) can account for autogenic changes in $p_{c,L}$ without making stringent assumptions about changes in bog shape, and we recommend it as the analytical model of choice. Within a single climatic region, local factors will constrain rates and patterns of lateral expansion. As a result, the time-dependent

modification of $p_{c,L}$ is likely to vary from one site to another. In any one region, therefore, a plot of peat depth vs. basal age, with each datum corresponding to one site, is likely to show a large amount of scatter in the data, attributable to the effects of local factors on peatland development. The most robust approach to estimating regional parameters may be to fit the model of Yu et al. (2003) to the upper and lower limits of the data using quantile regression (Belyea, *in press*), rather than using traditional regression techniques to find the best fit central tendency. Sites defining the outer limits to the scatter of points represent the extremes in patterns of development, and so the upper and lower parameter estimates will provide a more comprehensive description of peat accumulation for that region than will a single set based on a central response which ignores the effects of local factors.

*Linking hydrology to autogenic models of
peatland development*

We will investigate the hydrological and ecological implications of groundwater mound development using five conceptual models (Fig. 5) derived from the BGM and the GMH. We use the BGM (Eq. 6) to calculate bog height at the center, H_L , at different times, and specify either a constant or increasing lateral extent, L . The GMH (Eq. 11) is then solved, using H_L/L to obtain U_c/K_c and the shape of the bog in cross section. Eq. 15 is solved to obtain $T_{a,L}$ using H_L , L , U_c/K_c , plus an assumed value for $(P - E - U_c)$. All caveats relating to the BGM and GMH still apply; we use these models only to illustrate the consequences of different patterns of shape change through time. For the biological effect, we use the BGM “limit” only as a convenience; the important point is that the rate of height growth decreases as the bog develops.

The five conceptual models of peatland development (Fig. 5) differ in the mode of peatland initiation and the relationship between rates of height growth and lateral expansion. The bog grows in height until it reaches either a hydrological limit (12.65 m; Fig. 5A, B), or a biological limit (8 m; Fig. 5C, D, E), to further height growth (Fig. 5F). In all cases, lateral expansion (Fig. 5G) is limited ultimately at 400 m from the bog center by physiographic constraints, such as two stream channels. The bog may initiate simultaneously across the whole interfluvial plain, or several small bogs may coalesce early in development to form a single peat mass (Fig. 5A, C). Alternatively, the bog may initiate at a central locus and gradually expand outward, either at a constant rate (Fig. 5B, D) or in pace with height growth (Fig. 5E). If an expanding bog reaches a biological limit to height growth, lateral expansion may either cease (253 m; Fig. 5E) or continue until the physiographic constraints are reached (400 m; Fig. 5D). These five models are idealized representations, but probably cover the range of possibilities that occur in nature.

The temporal development of bog size and shape differs among models, and each scenario makes a different prediction for temporal change in catotelm excess, U_c/K_c (Fig. 5H; Eq. 11) and acrotelm transmissivity at the bog center, $T_{a,L}$ (Fig. 5I; Eq. 15). If the bog initiates simultaneously across the interfluvial plain (models A and C), L is fixed but U_c/K_c increases and $T_{a,L}$ decreases as long as the bog continues to grow in height. In two of the models with gradual expansion from a central locus (models B and D), L increases and $T_{a,L}$ increases. If the rate of lateral expansion outstrips height growth (model D), a flat plain develops near the bog center and U_c/K_c decreases (Fig. 5H). Only in the model where lateral expansion and K_c are controlled by height growth (model E) can $T_{a,L}$ remain constant (Fig. 5I).

These five conceptual models show how the trajectory of ecosystem development is controlled by starting conditions, external constraints, and internal processes. From our review of the literature (see *Bog growth and development of the groundwater mound*), it is clear that both confined and unconfined bog growth occur in nature, and that patterns and rates of lateral expansion are strongly influenced by local factors. Mathematical models of bog growth should be able to accommodate this full range of possible trajectories of peatland development.

Hydrological limitation of height growth (models A and C) implies that U_c/K_c eventually reaches an upper limit (Fig. 5H). Mechanistically, this limit may represent a physical constraint on K_c combined with a climatic constraint on U_c . The upper limit to U_c is reached if all net precipitation, $P - E$, flows through the catotelm. Similarly, highly humified peat may reach some structural limit to further compression, putting a lower limit on K_c . An increase or decrease in U_c/K_c may result from a decrease or increase in K_c , or an increase or decrease in U_c , or both. Under a steady climate, K_c could decrease with increasing peatland age (i.e., with cumulative catotelm decay) or increase with change in the physical properties of newly formed peat, such as less cumulative decay or a shift in botanical composition, implying a shift in acrotelm properties. Under a steady climate, U_c could change through a shift in either the rate of evapotranspiration, E , or the partitioning of water flow between acrotelm and catotelm. Again, both sorts of change imply a shift in acrotelm properties.

Because $T_{a,L}$ is the product of acrotelm hydraulic conductivity, K_a , and thickness of flow, a systematic change in $T_{a,L}$ requires a systematic change either in physical properties of the acrotelm, or in seasonal drawdown of the water table, or both. Hence, any change in $T_{a,L}$, and most changes in U_c/K_c , involve a shift in acrotelm properties. Both the rate of peat formation, $p_{c,L}$, and the physical characteristics (ρ , K_c , f_d) of newly formed peat are likely to be affected by these changes. Hence, bog growth causes changes in hydrological behavior, which affect processes of peat for-

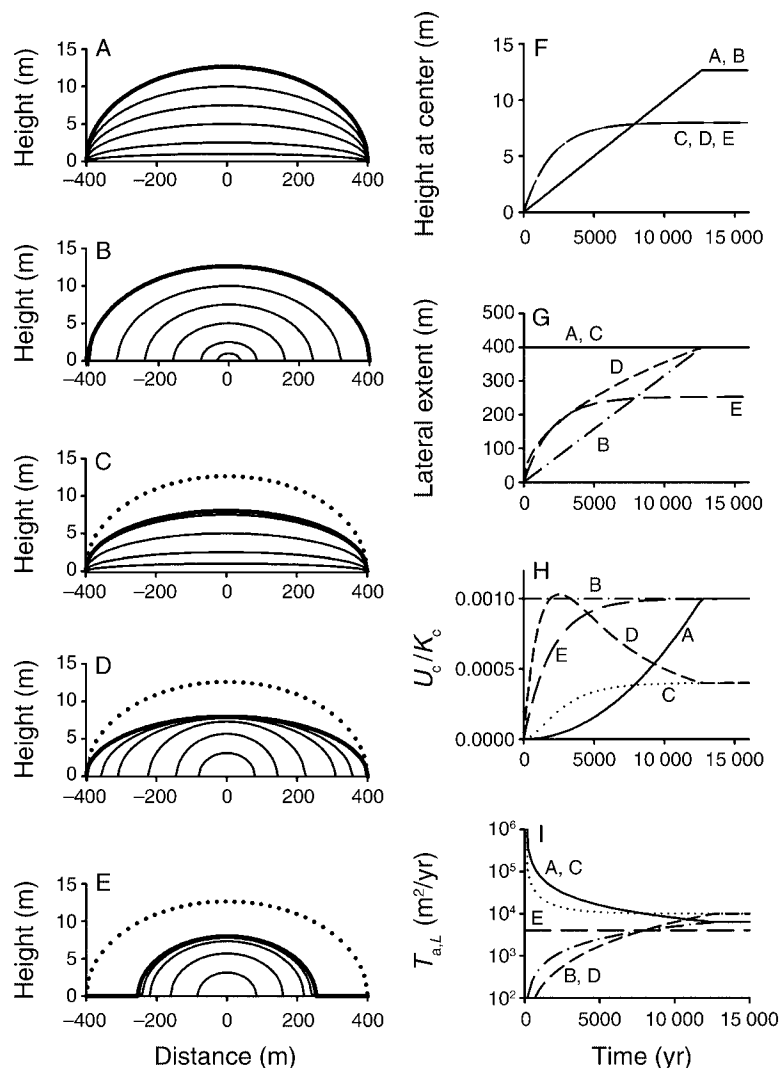


FIG. 5. (A–E) Five models of peatland development showing bog profiles at 1000, 2500, 5000, 7500, 10000, and 12650 years after initiation. The dotted profile in models C–E is the same as the final profile in models A and B. (F) Growth in height over time. In models A and B, the bog grows in height at a constant rate until it reaches a maximum height of 12.65 m, whereas in models C–E, the bog grows in height at a decreasing rate toward an asymptotic maximum of 8 m. (G) Growth in lateral extent over time. In models A and C, the bog initiates simultaneously across the entire interfluvial plain; in models B, D, and E, the bog initiates at a central locus and subsequently expands. Model E is a special case in which the bog grows in lateral extent at a rate determined by height growth. (H) Change in U_c/K_c over time. In model B, U_c/K_c is maintained at a constant value of 0.001. In model A, U_c/K_c increases to 0.001, the hydrological maximum for a height of 12.65 m. In models C and E, U_c/K_c increases to 0.0004, the hydrological maximum for a height of 8 m. In model D, U_c/K_c decreases nonlinearly to 0.0004 as the bog continues to expand laterally while ceasing to grow in height. (I) Change in $T_{a,L}$ over time: $T_{a,L}$ either increases (models B and D) or decreases (models A and C) toward a central value, except in the special case (model E).

mation. Bog development inevitably involves feedback mechanisms operating across temporal and spatial scales.

Developmental changes at a site in Sweden (Svensson 1988, Malmer et al. 1997, Malmer and Wallén 1999, Belyea and Malmer 2004) are consistent with mechanisms of cross-scale feedback. The pattern of bog growth at Store Mosse follows model C. The bog reached its maximum lateral extent 5000 yrs ago, and since then has increased in height at a steadily decreasing rate within each of three distinct vegetation stages. A

hydrological parameter analogous to $T_{a,L}$ was calculated based on reconstructions of bog height by applying the model of Yu et al. (2003) separately to depth–age profiles for three distinct vegetation stages, and climate forcing using independent lake-level records (Belyea and Malmer 2004). Transmissivity showed a general, non-linear decrease over time, consistent with the prediction for model C in Fig. 5I. But climate forcing altered this internally driven trajectory of development. Periods of increasing climate wetness were associated with increases in transmissivity, and abrupt switches in

vegetation and surface structure, as well as rapid, nonlinear increases in carbon sequestration rates between vegetation stages (Belyea and Malmer 2004). The most dramatic switch occurred about 1000 yrs ago, after which the peatland surface diverged into a system of ridges and wet hollows. The within-stage and between-stage changes at this site demonstrate that fast (acrotelm) and slow (catotelm) processes are inextricably linked, and that climate forcing may interact with internal processes to produce nonlinear behavior in peatland structure and carbon cycling.

Spatiotemporal dynamics and self-organization

The main limitation of the BGM and most other analytical models of peatland development is that they fail to account for the cross-scale coupling of hydrological and ecological processes. Both the BGM and GMH assume that catotelm properties are effectively homogeneous, and that acrotelm properties are determined only by horizontal position on the bog surface. By linking the BGM and GMH for a range of peatland development scenarios (Fig. 5), we have shown how large-scale boundary conditions can force acrotelm characteristics to change in a particular direction. We might think of this interaction as a form of top-down control, in which larger scale features (e.g., bog size and shape) constrain processes operating at a smaller scale (e.g., acrotelm transmissivity, peat formation rate). Although linking hydrological and ecological processes has provided new insight on how peatland structure develops, this approach still is unable to deal with feedbacks that operate across temporal and spatial scales. For example, the changes between stages at Store Mosse (Belyea and Malmer 2004) could be modeled analytically only by treating each vegetation stage separately. Such rapid, nonlinear changes in peatland structure and function involve a self-reinforcing interaction between top-down and bottom-up control, such that a change in hydrological boundary conditions drives changes in acrotelm characteristics, which influence rates of bog growth, which, in turn, affect hydrological boundary conditions. The limitations of the analytical approach arise from ignoring the cyclical interaction between top-down and bottom-up control.

In reviewing empirical evidence for the BGM and the GMH, we noted that peatland microforms differ in peat formation rate, and, possibly, hydrophysical characteristics. Spatial variations in the distribution of microform types across the peatland surface, therefore, may lead to spatial heterogeneity in rates of peat accumulation and water flow, with consequences for the trajectory of peatland development. For example, complexes of open-water pools and ridges often develop secondarily on unpatterned bogs (Glaser and Janssens 1986, Foster et al. 1988, Belyea and Lancaster 2002). Because pools transmit water rapidly by overland flow, we might expect $T_{a,L}$ to increase as new pools initiate and existing

ones expand in size (see *The groundwater mound hypothesis: Empirical evidence*).

Concurrently, because pools generally show net loss of carbon to the atmosphere (Waddington and Roulet 1996), we might expect bog height growth in the area covered by the pool complex to slow down or stop (Glaser and Janssens 1986). If the bog margin continued to expand laterally by paludification, the pattern of development would resemble the model in Fig. 5D, with progressive outward expansion of the pool complex on a flat central plain, and a corresponding increase in $T_{a,L}$. Detailed studies of bogs in Sweden and Newfoundland support the view that the distribution and development of pool complexes is linked to such systematic changes in large-scale bog structure (Foster et al. 1988, Foster and Wright 1990). This hierarchical structuring of peatland physiographic features suggests a process of self-organization, in which larger scale spatial patterns emerge from the dynamics of smaller scale features (Turing 1952, Lejeune et al. 1999).

We noted previously that K and the storage properties of newly formed (catotelm) peat are dependent on the type of litter deposited and the degree to which it is modified by acrotelm decay (see *The groundwater mound hypothesis: Empirical evidence*), factors that are dependent on microform type and acrotelm characteristics. Once peat of a certain hydraulic conductivity (K) has formed, its properties contribute to future behavior of the bog, serving as a form of “ecological memory” that may affect peatland development over time scales much longer than the original forcing. For example, horizontal layers of highly humified peat, thought to have formed during dry phases with high rates of acrotelm decay, are common and widespread in many peatlands (Dickinson 1975, Aaby 1976, Baker et al. 1999). Such highly humified layers are likely to have low K (Boelter 1969), and the presence of low K horizons can alter the bulk flow properties of catotelm peat (Beckwith et al. 2003a). Vertical “curtains” of low K peat, on the other hand, may form as a result of the persistence of particular patterns of microform distribution. On sloping peatlands, for example, hummocks may coalesce to form along contour ridges that alternate with bands of hollows or pools (e.g., Sjörs 1983). If the peat formed below a ridge is of low K and the ridge remains in the same place for hundreds of years, the effect on lateral water flow might be expected to be greater than if the hummocks were arranged randomly. The ridge presents a single, contiguous barrier to flow, whereas the random arrangement may allow “short circuiting” of flow through intervening areas of higher K peat. One of the few hydrological studies conducted at this scale (Lapen et al. 2005) suggests that rates and patterns of bog lateral expansion can be influenced by vertical “curtains” of low K peat that have formed at an earlier stage of development. Hence, reversible changes in acrotelm properties and the spatial arrangement of microforms

TABLE 2. Peatlands as complex adaptive systems (CAS), and requirements for modeling.

Generic feature of CAS	Expression in peatlands	Modeling requirement
Spatial heterogeneity Selective evolution acts on component parts of the system, which maintain differences in functional properties.	The peatland surface is composed of small features (microforms) that differ in hydrophysical and ecological properties; these properties become embedded in newly formed peat.	The system should be disaggregated horizontally into columns and vertically into cohorts, so that each cell (i.e., cohort/column combination) exhibits particular hydrophysical and ecological properties.
Localized flows Component parts interact by localized flows of energy, information, and resources, and the outcome of these interactions determines the path of system development.	Adjacent microforms and litter/peat layers interact through flows of water, nutrients, and information (i.e., hydrophysical properties); the peatland responds to change through shifts in the distribution and abundance of different microform types.	Processes (e.g., peat accumulation) occurring within a cell should be linked to local water and nutrient budgets, including flows between cells; process rates should be dependent on the hydrophysical and ecological properties associated with each cell.
Self-organizing structure The hierarchical structure of the system emerges from local interactions between component parts, and the patterns that emerge constrain further development of the system.	Microforms of different types are aggregated into distinct microtopes, and these in turn are aggregated to form sequential zones across a mesotope; peatland size and shape constrain processes operating at lower levels.	Vertical structures and horizontal structures larger than the microform should be allowed to emerge from localized interactions that couple fast and slow processes.
Nonlinearity Chance events can be amplified by positive feedback, leading to rapid change in system properties and dependence on past history.	Hydrological conditions at the peatland surface change with development of the groundwater mound and in response to external forcing; this change in surface conditions affects microform composition and rates of peat accumulation.	External forcing should be represented explicitly in an open model structure; hydrological and ecological processes should be coupled to one another and to the properties associated with each cell.

Note: The generic features of CAS are adapted from Levin (1998).

may lead to irreversible changes in catotelm structure and function.

Our analysis has revealed the importance of cross-scale feedback in peatland dynamics, with fast and slow processes of water flow and storage interacting with peat-forming processes to produce complex structure and behavior. Peatland development is driven by small-scale processes of peat accumulation, constrained by larger scale hydrological conditions that continuously change in response to internal and external factors. In a modeling approach that recognizes these cross-scale feedbacks, growth of the peat deposit and development of the groundwater mound would affect processes operating at smaller spatial and shorter temporal scales, so that larger scale structures and dynamics emerge from relatively simple rules operating at a lower level. In addition, past dynamics of small-scale features would be preserved in the “ecological memory” of hydrophysical properties. Now, we outline one possible approach to modeling cross-spatial and cross-temporal feedback in peatland development.

CROSS-SCALE FEEDBACK IN PEATLAND DEVELOPMENT

Four distinctive features of peatlands identified in our analysis are characteristic of “complex adaptive sys-

tems,” or CAS (Levin 1998): spatial heterogeneity, localized flows, self-organizing structure, and nonlinearity (Table 2). Microforms, the elemental component parts of the system, differ in functional properties, which become embedded as information associated with successive vertical layers as peat accumulates. Because of these differences in functional properties, water and nutrients flow unequally between adjacent microforms and litter/peat layers. These unequal flows favor the persistence and expansion of some microform types and the contraction of others, leading to the emergence of self-organized structures at the scale of microtopes (uniform areas of distinctive vegetation and physical structure, $\sim 10^{-1}$ – 10^2 m in scale) and mesotopes (hydrologically distinct peatland units, $\sim 10^2$ – 10^3 m in scale). In turn, these larger scale structures set the boundary conditions for processes occurring at the scale of the microform.

These cross-scale feedbacks (Fig. 6) can lead to rapid change in microform composition, triggered by chance events whose effects become amplified and are dependent on developmental history. Hence, fast processes occurring near the bog surface are constrained by slower processes of height growth and lateral expansion of the peat deposit. But the system also has an “ecological

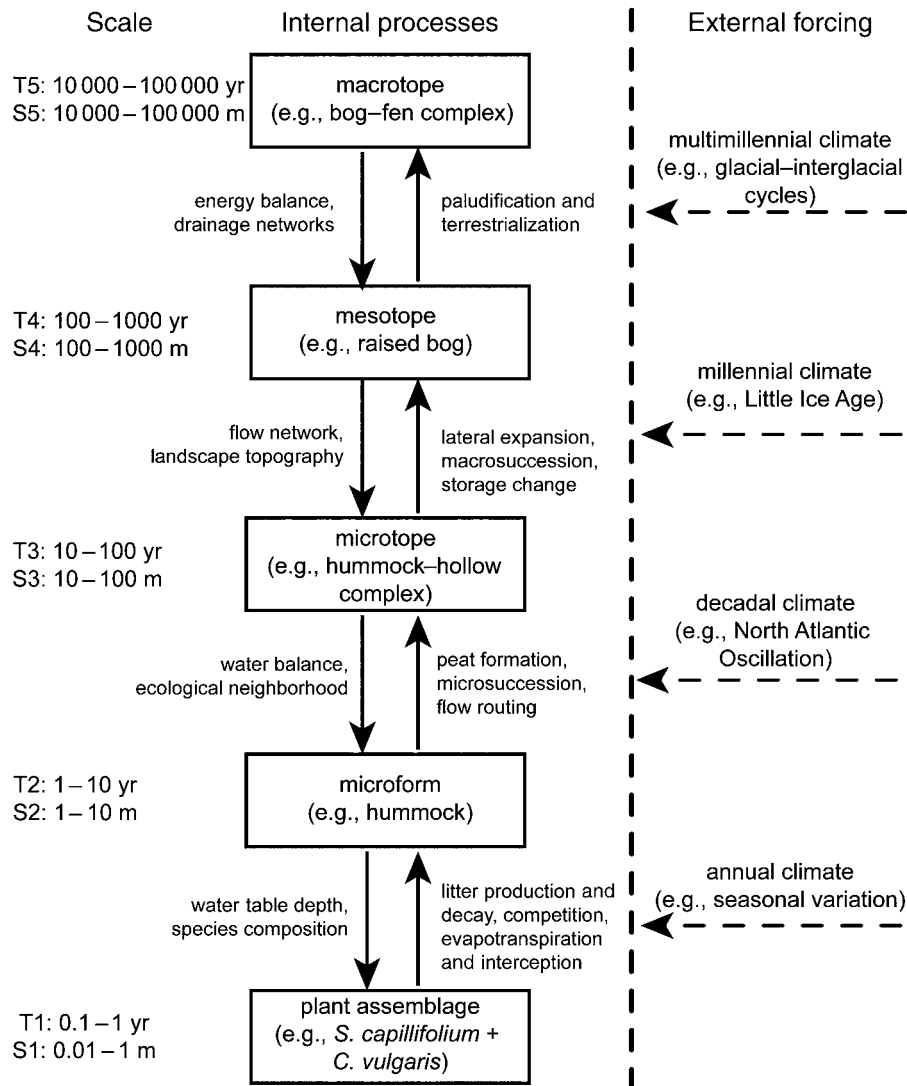


FIG. 6. Peatlands as hierarchical complex systems. State, flux, and forcing variables are arranged in order of increasing temporal (T_n) and spatial (S_n) scale. Boxes identify features at various scales of observation: solid arrows entering from the higher levels denote slowly changing boundary conditions, solid arrows entering from the lower level denote internal driving variables, and broken arrows show climatic forcing at particular temporal scales. The dashed vertical line represents the boundary of the peatland system.

memory,” in that catotelm properties depend in part on the history of microform dynamics. As the peatland develops, fast processes at the surface may become tied more tightly to slow processes, reducing the system’s capacity for adaptive response.

Understanding the dynamics at any one level in the hierarchy (Fig. 6) requires knowledge of processes operating at least one level above and one below (Allen and Starr 1982): the lower level provides the internal stimulus for change, while the upper level defines the constraints, or boundary conditions, under which the intermediate level operates. The temporal scale of external forcing must also be matched to the scale of response. As an illustration, consider the dynamics of

one type of microform. A hummock produces peat at a rate determined by litter production and decay, and these process rates are in turn constrained by the height of the hummock, which changes according to the imbalance between peat formation (bottom-up, driven by the plant assemblage) and water table rise (top-down, constrained by the water balance of the hummock–hollow complex [Belyea and Clymo 2001]). A change in external forcing, such as increased nitrogen deposition, may lead to increased dominance of vascular plants and lower rates of peat formation (Berendse et al. 2001), which should eventually result in hummock contraction. Conversely, a period of drier climate may lead to a decrease in the rate of water table rise, which should

result in expansion of hummocks on to former lawns (Barber 1981). To understand the dynamics of a hummock, both bottom-up and top-down linkages must be taken into account.

The minimum requirements for modeling peatlands as CAS can be mapped directly on to the four fundamental properties (Table 2). Effective models must be spatially explicit, allowing larger scale structures to emerge from localized interactions between smaller scale units. External constraints and forcing should be represented explicitly, with the possibility for historical effects to become embedded in the physical structure of the system. Positive feedback loops must operate across spatial and temporal scales (Fig. 6), allowing nonlinear behavior to arise. Only by incorporating all of these properties will it be possible to model the response of peatlands to internal developmental processes and external forcing.

Feedback effects and external forcing can be incorporated more explicitly and easily into numerical dynamic simulation models than into analytical models. Many numerical models have been developed that simulate bog development or peat accumulation in one dimension only (vertical), without incorporating hydrological processes at all, or only in a highly simplified way (Logofet and Alexandrov 1983/1984, Froking et al. 2001, Chimner et al. 2002, Pastor et al. 2002, Nungesser 2003, Bauer 2004). The only one-dimensional model of peatland development to focus on feedback between hydrological processes and peat accumulation is that of Hilbert et al. (2000). Their systems approach, based on nonlinear interactions between peat growth and water table depth, predicts complex behavior with the possibility for rapid development toward alternative stable states. Even if hydrological and ecological processes are coupled, the one-dimensional approach has two serious limitations. First, one-dimensional models have a limited ability to deal with changes in boundary conditions, such as bog shape. In the model of Hilbert et al. (2000), for example, drainage was simply a linear function of bog height, corresponding to the model in Fig. 5C. Other scenarios for change in bog form would be difficult to implement. Second, one-dimensional models ignore the effects of spatial structuring of hydraulic properties (e.g., hummocks of low K peat, open-water pools), which may affect water flow at larger scales. A group of low K hummocks arranged in a linear ridge along the contour, for example, would impede drainage more effectively than the same group of hummocks distributed at random.

To account for bog shape and spatial variation in hydraulic properties, models of peatland development must operate in both horizontal and vertical dimensions. The earliest two-dimensional model incorporating both water flow and peat accumulation is that of Wildi (1978), which simulated bog and fen development for different topographic situations. Although this model captured the effects of bog form (constraints at the

mesotope scale), the effects of different arrangements of microforms (constraints at the microtope scale) were ignored. Models that simulate ecosystem development in two horizontal dimensions represent a further advance and are highly appealing, because they allow hydrological and ecological processes to be coupled across spatial and temporal scales. In spatially explicit models of peatland surface patterning (Swanson and Grigal 1988, Rietkerk et al. 2004b), larger scale features develop by self-organization of smaller scale features through localized interactions. Microforms (e.g., hummocks and pools) affect patterns of water and nutrient flow, which in turn influence the dynamics of the microforms. The earliest example for peatlands (Swanson and Grigal 1988) simulated development of the two-dimensional arrangement of hummocks and flarks (wet hollows) stochastically, based on the idea that microform types differ in transmissivity and in their probability of occurrence at different water table depths ("water ponding mechanism" [Rietkerk et al. 2004b]). Water exchanges to and from a microform are affected by the local neighborhood, so that water table depth, and the probability of transition between hummocks and flarks, is controlled by microform patterning. Water will tend to pond upslope from hummocks, leading to an alternating sequence of hummocks and flarks arranged linearly across the slope.

A more recent model (Rietkerk et al. 2004b) was based on an alternative mechanism, whereby spatial variations in transpiration rates controlled by vascular plant biomass drive local flows of water and nutrients ("nutrient accumulation mechanism" [Rietkerk et al. 2004b]). Nutrients flow preferentially to areas with high biomass, and the enhanced nutrient availability further promotes growth of vascular plants.

Both models incorporate short-range positive feedback and long-range negative feedback, the two critical requirements for self-organization of spatial patterns (Turing 1952, Lejeune et al. 1999). These cross-scale feedbacks allow the system to change nonlinearly. Depending on boundary conditions, initially random arrangements of microforms can spontaneously self-organize to form distinct patterns. These spatially explicit models were developed to illustrate how specific mechanisms can lead to microform patterning, and so both models have limitations that preclude their direct application to peatland development. In both models (Swanson and Grigal 1988, Rietkerk et al. 2004b), topographic boundary conditions (i.e., surface gradient) were fixed, and changes resulting from peatland height growth and lateral expansion (i.e., macrosuccession) were not considered. Swanson and Grigal's model did not include water inputs from precipitation, and so could not simulate the effects of different or changing climates.

Neither model considered how transitions between microform types (i.e., microsuccession) may lead to vertical and horizontal variations in the hydraulic

properties of deeper peat. In Swanson and Grigal's (1988) model, peat transmissivity was determined entirely by microform type, whereas in the model of Rietkerk et al. (2004b), a single value of hydraulic conductivity was used for the entire peatland. In reality, we might expect the hydraulic and water storage properties of newly formed peat to change with succession of different microform types, because of differences in litter composition and degree of physical alteration during aerobic decay. Such effects of "ecological memory" could be incorporated in a vertical dimension quite easily by linking the properties of a cohort of peat to litter type and state of decay (Bauer 2004). To our knowledge, this approach has not yet been applied to peat hydraulic properties.

Many of the CAS modeling requirements (Table 2) have already been implemented for peatland systems, although not all in one package. The general model structure of Rietkerk et al. (2004b) could be extended easily to include a range of functional types of vegetation and to a third (vertical) dimension by discretization of annual cohorts of litter/peat. Each cohort/column combination ("cell") could be assigned particular properties, based initially on the microform type that deposited the litter, and, subsequently, on physical and chemical changes induced by decay (Bauer 2004). Hydrophysical and ecological properties would affect rates of water and nutrient flow between adjacent cells. Rates of evapotranspiration, nutrient uptake, litter production, and litter/peat decay within cells would also be affected by these properties, as well as by the elevation difference between the water table and the peatland surface. With the formation of new cohorts of litter/peat, the whole system could grow in height and lateral extent, gradually changing the boundary conditions at the mesotope scale. Although such a model would produce complex behavior, it would not necessarily be any more complex in structure, or demanding of parameterization, than many other numerical models, because process descriptions are made at the same scale as field measurements, i.e., the microform.

AN AGENDA FOR FUTURE RESEARCH

Over the past 20 years or more, the BGM and GMH have inspired much progress in peatland ecology and hydrology, both as simple aids for conceptualizing the behavior of peatland systems, and, in the case of the BGM, as a tool for estimating process rates, such as carbon sequestration, from readily available data. The simplicity of these models can be considered a strength, but simplicity must be balanced with accuracy. To be useful instead of misleading, a model of peatland development, or morphometry, must be logically consistent and must incorporate interactions between ecological and hydrological processes.

We have shown the limitations of the BGM and GMH, and demonstrated that the conceptualization of peatlands as CAS emerges logically from the important

cross-scale linkages in space and time between relatively rapid near-surface processes and slower processes deeper in the peat deposit. We have suggested how new models that take proper account of these cross-scale linkages might be developed in a way that retains as much simplicity as possible. The most obvious approach is to add a third dimension to a two-dimensional model, such as that of Rietkerk et al. (2004b). Development of such models will require an improved understanding of peatlands, and further empirical research is urgently needed in four particular areas.

1) Hydrophysical properties of microforms. Surprisingly little research has focused on quantifying differences in evapotranspiration resistance, transmissivity, or storage properties among microform types. Yet, these differences are fundamental to the hydrological functioning of peatlands.

2) Litter decay and the vertical development of peat properties. Although much effort has gone into quantifying gaseous emissions, and somewhat less into understanding processes of mass loss, almost no research describes how litter breakdown affects the physical properties of peat, such as dry bulk density, hydraulic conductivity, and drainable porosity. Linking the physical modification of peat to processes of decay is critical to understanding how spatial and temporal variability in these properties arises.

3) Microform persistence and transition. Other than in a few paleoecological and long-term monitoring studies, the spatiotemporal dynamics of peatland plant assemblages and microforms have been almost completely ignored. Predicting microform persistence and transition requires an improved understanding of how the underlying ecological processes, such as plant competition for space (Rydin 1993) and peat formation (Belyea and Clymo 2001), interact with hydrological processes.

4) Mechanisms of bog lateral expansion. The processes by which bogs expand on to marginal fen or mineral soil are poorly understood. Bog lateral extent, however, is one of the key boundary conditions constraining the dynamics of peatland systems.

Peatland dynamics have the potential for strong effects on the global carbon cycle and climate system, at time scales ranging from decades (Gedney et al. 2004, Shindell et al. 2004) to millennia (Gajewski et al. 2001, Kaplan 2002, Valdes et al. 2005). Predicting the effects of external forcing on peatland carbon cycles requires models that can simulate the full complexity of peatland response. Modeling peatland distribution is not enough. We must be able to predict changes in surface structure, including the areal coverage of features with high methane emission, such as open-water pools (Hamilton et al. 1994, Waddington and Roulet 2000). We believe that CAS models offer the best prospects for meeting this challenge.

ACKNOWLEDGMENTS

We are grateful to R. S. Clymo, Nigel Roulet, and an anonymous referee for comments on an earlier version of the manuscript. L. R. Belyea is supported by an Advanced

Fellowship from the U.K. Natural Environment Research Council (award NER/J/S/2001/00799).

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