5. DO HOLLOWS CONTROL THE RATE OF PEAT BOG GROWTH?

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HOW DOES PEAT ACCUMULATE?

How does a peat bog grow in thickness? We take an ombrotrophic bog as an example to focus our discussion.

Plant matter is added by photosynthesis in the living part of the plants at the bog surface, at a rate that can be measured as net primary productivity (NPP), both at the surface and, of equal or greater importance (Wallén 1986; Wallén 1987), in rhizomes and roots below it. The bog-moss, *Sphagnum*, is important in such bogs and, together with the below-ground structures of vascular plants, forms a porous mass through which air circulates and surplus water drains readily. Light penetrates only a few centimetres into this carpet. In the dark below, aerobic decay, mainly fungal, dominates. Eventually the main plant structures collapse. The much reduced spaces between structural elements have very much reduced hydraulic conductivity, and surplus water therefore runs off sideways.

The peat below is waterlogged. Bacteria in the top few cm of this waterlogged peat consume oxygen faster than it can diffuse down from above, and thus create anoxic conditions. Anaerobic decay which results is about a thousand-fold slower than was aerobic decay above the water level.

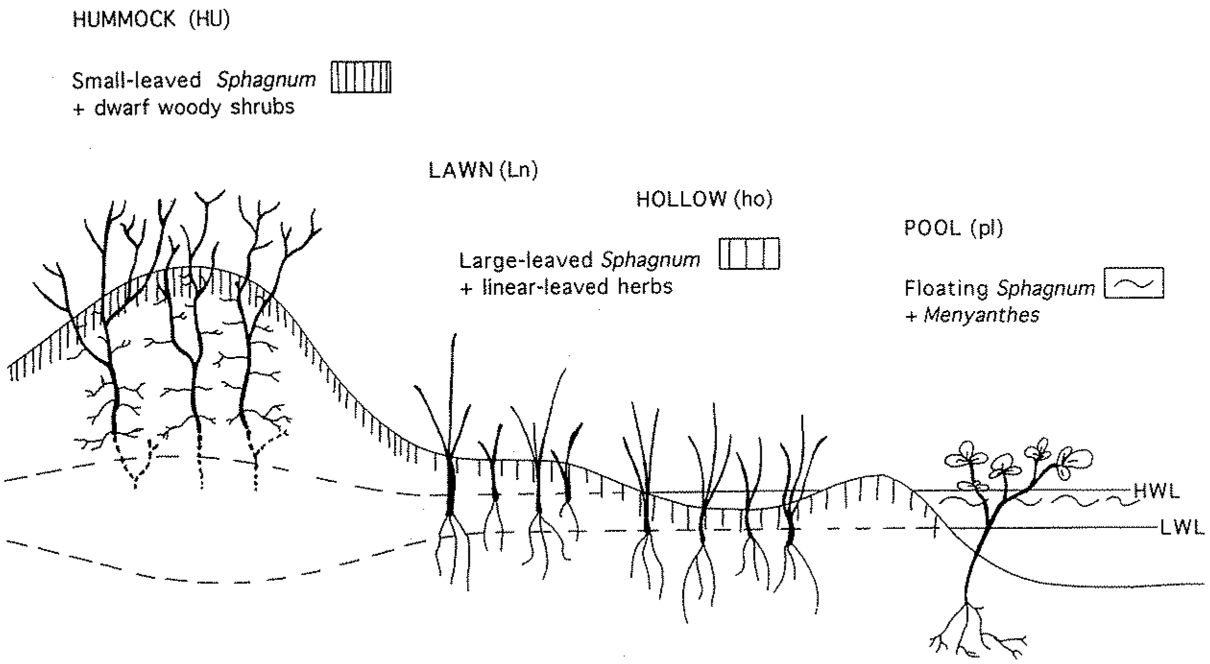
During summer drought, water is able to drain down very slowly perhaps 50 cm into the peat. There is thus a layer that is anoxic in winter but becomes oxic during drought. The oxic and seasonally anoxic layers together are the acrotelm; the permanently anoxic layer below - the peat proper - is the catotelm (Ingram 1978). Fuller accounts of this two-layer structure are given in Clymo (1984) and in Clymo & Pearce (1995).

The same play is repeated endlessly over decades and centuries while the actors constantly change. New matter is added to the acrotelm; older matter is lost from the acrotelm by aerobic decay; even older partially decayed structures collapse; and, 20-200 years after the structures were first formed, the water level rises to submerge what is left of them in the catotelm. *So long as hydrological conditions remain the same, the acrotelm remains about the same thickness*, growing at the top and passing surviving matter on to the catotelm at an approximately constant rate.

The *rate that matter is submerged by the catotelm, RSC*, is central to our argument. It is the rate at which the site of peat accumulation, the catotelm, increases in thickness and also, by implication, the rate at which the water level mound increases in thickness. It has physical dimensions $M\ L^{-2}\ T^{-1}$, and its units might be $g\ m^{-2}\ yr^{-1}$ or perhaps $mol\ m^{-2}\ yr^{-1}$. In Clymo (1984), RSC is denoted dx_c/dt_c; in Clymo, Turunen & Tolonen (1998), it is denoted dM/dt.

The acrotelm is the creator and processor of the plant matter that is the precursor of peat. *Net primary productivity, NPP*, is the rate at which plant mass is added to the acrotelm. Mass is lost at a rate that is the *cumulative rate of loss by decay of the plant matter in the acrotelm, CRD_A*. The *local rate of burial, LRB*, is the rate at which the acrotelm at a particular place on the bog produces peat: LRB = NPP - CRD_A. In the steady state, all of this material is transferred to the catotelm, and RSC is the difference between LRB and the *cumulative rate of loss by decay, CRD_C*, of peat in the catotelm: RSC = LRB - CRD_C. The rate at which water level rises is linked closely to RSC, and both are processes that operate on a regional scale. Note that 'regional' in this context implies the assemblage of microforms within a radius of, say, 25 m. The acrotelm at one place on a peat bog may have low NPP, but be thin with consequent low CRD_A; another may have high NPP but lose more mass by decay because it has a thicker acrotelm, with consequently higher CRD_A. Nevertheless, the LRB and the RSC may be the same at these two places.

FIGURE 1. Characteristics of microforms on ombrotrophic peat bog (based on Malmer *et al.* (1994)). LWL, HWL are low (summer) and high (winter) water level, respectively.



BOG MICROFORMS

An uneven microtopography is characteristic of the surface of many northern mires (Fig. 1). The associated microhabitats and vegetation, together defining a microform, differ. In what follows we give examples from western Europe; other species are found in other areas.

At one extreme are hummocks rising 30 - 60 cm above the mean water level, and 1 - 20 m across. Their vascular plant vegetation is typically dwarf ericaceous shrubs (*Erica tetralix*, *Calluna vulgaris* and several others) set in a matrix of small-leaved relatively tough-stemmed bog-mosses (*Sphagnum capillifolium*, *S. fuscum*). The small imbricate leaves of these bog-mosses and their well-developed pendant branches that clasp the stem form a capillary network that is able to maintain sufficient water at the moss apex to allow it to continue growing even when the apex is 30 cm above the water level (Hayward & Clymo 1982). In the light shade of the ericaceous shrubs the mosses grow up around the woody stems of the dwarf shrubs, which form a tough perennial scaffold. These woody stems in turn are stimulated by the resulting humid atmosphere to produce new roots direct from the stems. This in turn rejuvenates the shrub and stimulates its growth (Forrest & Smith 1975), while the matrix of fine roots and overgrown stems reduces compaction of the peat (Malmer, Svensson & Wallén 1994). The NPP of this combined and potentially immortal system is greater than pure stands of either of its components separately.

Hollows are quite different. The water level is just below their surface in summer, and above it in winter. Dwarf shrubs are unable to grow here because their roots cannot survive in waterlogged peat. Indeed, the '*Calluna* (lower) limit' is often conspicuous on hummocks. Instead, the vascular plant vegetation of hollows comprises linear-leaved species (*Eriophorum angustifolium*, *Rhynchospora alba* and several others) in a matrix of large-leaved soft and brittle-stemmed bog-mosses (*Sphagnum cuspidatum*, *S. papillosum*). These bog-mosses have larger spaces between the leaves and less well-developed pendant branches than the hummock species. They are unable to maintain sufficient water for growth at their apices if these are more than a few centimetres above water level (Hayward &

Clymo 1982). The linear-leaved vascular plants have no arboreal perennial structure, and provide only a temporary scaffold, which the mosses are unable to take advantage of in any case because of their poor water-raising abilities.

This functional difference between hummocks and hollows, first reported by Malmer *et al* (1994), is crucial to our argument.

Pools, which are not synonymous with hollows, have their water level above the surface even in summer. Their vegetation comprises sparse linear-leaved species and *Menyanthes trifoliata*, with scattered but robust *Sphagnum cuspidatum*. Whilst the individual plants grow well, the NPP (on an area basis) is usually low, while CRD_A in the seasonally warm water is high and, averaged over a year, may exceed NPP.

A fourth type of microform is the lawn, which is usually flat and occurs a bit higher than the hollows, but well below hummock tops. It resembles a hollow in vegetation, structure and function. The lawn water level is close below the surface except after a very wet period.

In the wetter climates and wetter parts of ombrotrophic bogs, one gets the impression of hummocks as entities set in a matrix of hollows and pools; in drier conditions, hollows and rare pools seem to be isolated amongst hummocks.

PERSISTENCE OF MICROFORMS

Palaeoecological analyses of peat sequences in Ireland (Walker & Walker 1961), the Netherlands (Casparie 1972), Denmark (Aaby 1976), England (Barber 1981), Estonia (Ilomets 1984), and Sweden (Svensson 1988) have shown that, in those cases where evidence is sought, hummocks and hollows have been persistent features of the landscape. They have often occupied much the same position on the mire surface, spreading and shrinking, for hundreds or even thousands of years. Persistence of the same bog spatial pattern for such long periods of time requires that, despite differences in NPP and CRD_A, all microforms contribute peat to the catotelm at about the same rate. If this were not so, differences in topography and water level across the bog surface would become catastrophically large.

We therefore postulate that the processes that control microtopographic development must also control LRB and RSC. Water running off the bog surface flows preferentially through the microform of lowest surface height, and the LRB of this microform therefore determines the regional RSC. The LRB in adjacent microforms must be constrained to match this rate, and the mechanism that enforces uniformity must have strong negative feedback to stabilise it. (Acronym definitions are repeated in the Summary, and a mathematical statement is given in the Appendix.)

RATE OF SUBMERGENCE BY THE CATOTELM IN DIFFERENT MICROFORMS

What are the feedback mechanisms that enforce a single overall LRB? To answer this question, we must consider three controls on the rates of component processes (Fig. 2) that are involved in development and maintenance of the surface microtopography:

- net primary productivity, NPP;
- cumulated rate of loss by acrotelm decay, CRD_A;
- rate of submergence by the catotelm, RSC.

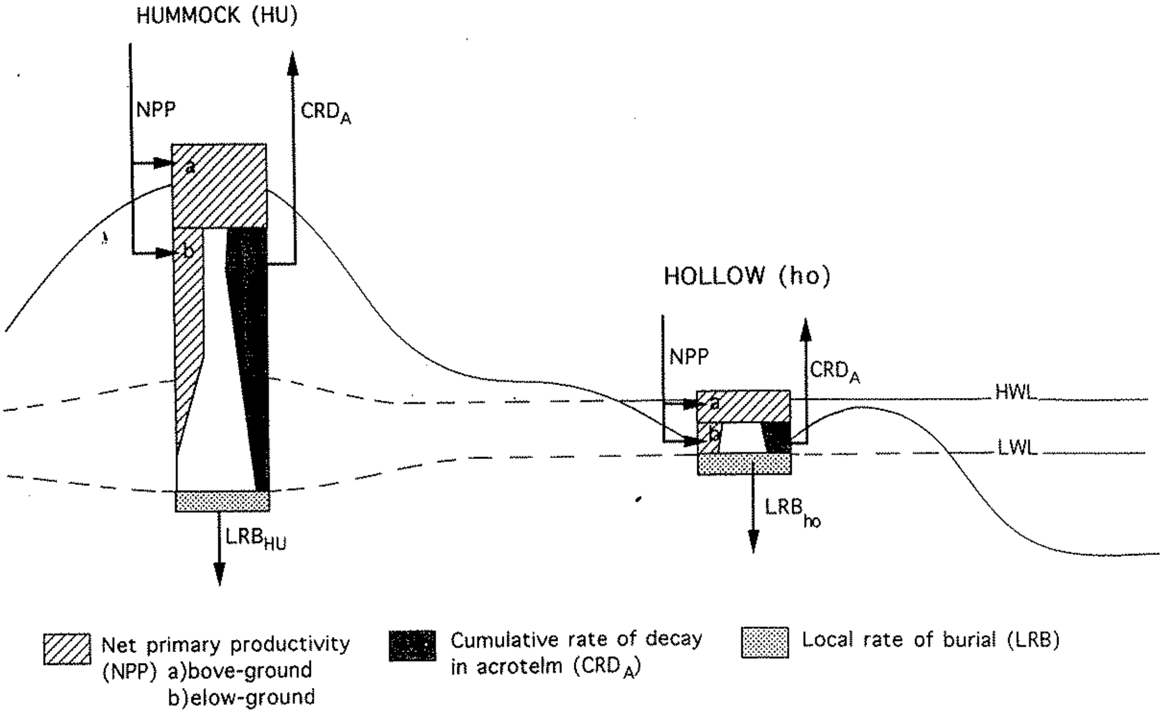
We know that the acrotelm regulates water level (Ingram & Bragg 1984; Clymo & Pearce 1995), and water level, in turn, affects both NPP of the vegetation (Wallén 1987; Wallén, Falkengren-Grerup & Malmer 1988) and CRD_A (Clymo 1965; Belyea 1996).

Our hypothesis is that the local rate of burial, LRB, and hence the rate of rise of the water level and of the RSC, must be approximately the same in most adjacent microforms of different kinds.

Both NPP (Wallén *et al.* 1988) and CRD_A (Clymo 1965; Belyea 1996) differ among microforms. A control mechanism involving production alone or decay alone is thus insufficient to account for the same LRB across microforms; the mechanism must include both. The functional relation of NPP and of CRD_A with distance above the water level (and hence acrotelm thickness) is the most obvious place to start looking for a mechanism.

How does NPP differ among microforms and in relation to the water level? In laboratory and garden experiments, the NPP of bog moss

FIGURE 2. Idealised rates of processes of peat accumulation in hummocks and hollows. Peat is added to the acrotelm through (a)bove-ground and (b)elow-ground net primary productivity (NPP), and lost at the cumulated rate of decay (CRD_A) through the entire depth of the acrotelm. The peat which survives passes into the site of accumulation (the catotelm) at the local rate of burial (LRB). Note that rates of production and acrotelm decay differ in the hummock and the hollow: $NPP_{HU} > NPP_{ho}$; $CRD_{A,HU} > CRD_{A,ho}$. But both microforms contribute peat at the same rate, LRB, to the catotelm: $LRB_{HU} = LRB_{ho}$.



species was ranked in the order hollow > lawn > hummock, with the water level having a non-significant effect on growth in mass (Clymo 1973; Hayward & Clymo 1983). In field conditions, however, the length-increment of different moss species (a surrogate for NPP) reaches a maximum at different heights above the water level, in the rank order: hummock > lawn > hollow (Wallén *et al.* 1988). Length increment of any one moss species varies considerably from year to year in response to historical and climatic factors (Backéus 1988; Wallén *et al.* 1988). We do not know if growth in mass varies to the same extent, because some of the length-increment may result from internode elongation rather than new growth. Total NPP (including above- and below-ground production of vascular plants) is generally greater in hummocks and lawns than in hollows (Wallén 1986; Wallén *et al.* 1988).

In summary, field and laboratory studies give no clear consensus on the effect of the water level on NPP of mosses alone. Total NPP, however, probably increases with density of vascular plants, and hence with height above the water level, until heights are reached where associated mosses can no longer transport water to their apices. The inferred form of these relationships is shown in Fig. 3a, which is based on, and confirmed by, unpublished measurements at Ellergower Moss in S.W. Scotland (Belyea 1995).

The factors affecting instantaneous rates of decay are complicated, but are now fairly well understood. There are four of them:

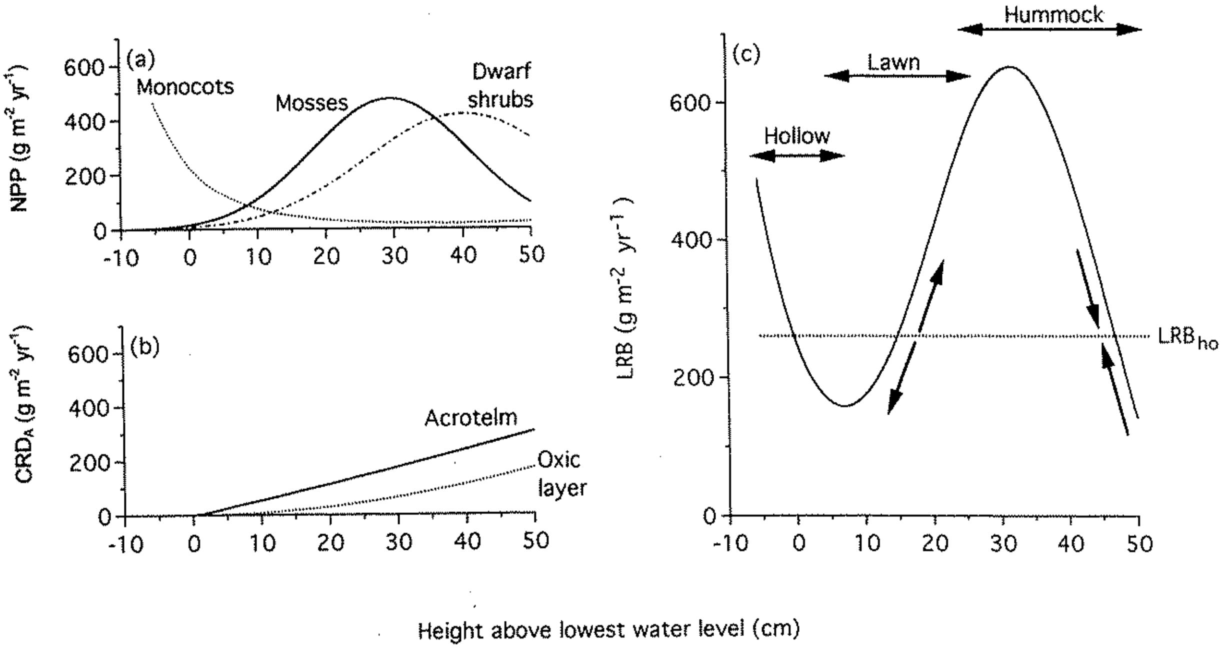
- botanical composition of the material;
- composition of the decomposer community;
- length of time the material has already been decaying;
- environmental conditions, especially oxygenation, temperature, and water potential.

Figure 3. Relationships of the water level with net primary productivity (NPP), cumulative rate of decay in the acrotelm (CRD_A) and local rate of burial (LRB). Based on unpublished measurements at Ellergower Moss, SW Scotland (Belyea 1995).

(a) Total NPP for linear-leaved plants ('Monocots'), *Sphagnum* mosses, and ericaceous dwarf shrubs. Curves are second-order polynomial regressions of ln(NPP + 1)-transformed data. Monocots: $n = 30$, $R^2 = 0.34$, S.E. of estimate = 5.6 g m^{-2} yr^{-1}, $P = 0.0040$. Mosses: $n = 24$, $R^2 = 0.72$, S.E. of estimate = 2.5 g m^{-2} yr^{-1}, $P < 0.0001$. Dwarf shrubs: n=30, $R^2 = 0.65$, S.E. of estimate = 4.0 g m^{-2} yr^{-1}, $P <$ 0.0001.

(b) CRD through the whole acrotelm and through the oxic layer only. Curves are power functions of $\log_{10}$(CRD)-transformed data. Acrotelm: $n = 24$, $R^2 = 0.79$, S.E. of estimate = 2.0 g m^{-2} yr^{-1}, $P <$ 0.0001. Oxic layer: $n = 15$, $R^2 = 0.48$, S.E. of estimate = 2.6 g m^{-2} yr^{-1}, $P = 0.0040$.

(c) LRB for hummocks, lawns and hollows. The curve is the difference between total NPP and CRD_A. The broken horizontal line is a specific LRB_{ho}. It intersects both the lawn and the hummock curve, at which point $LRB_{ho} = LRB_{ln} = LRB_{HU}$. Arrows show the direction a lawn or a hummock would move from these two balance points: the lower point is unstable, the upper is stable.



Species-specific differences in litter quality lead to different initial rates of decay in different microforms, in the rank order: hummock species < lawn species < hollow species (Johnson & Damman 1991; Belyea 1996). The more the litter has decayed, the more refractory it becomes (Hogg 1993; Belyea 1996). Effects of microform differences in composition of the decomposer community are difficult to distinguish from environmental conditions, which also differ both among microforms (Farrish & Grigal 1985; Belyea 1996) and with position relative to the water level (Belyea 1996). The combined effect of all these factors yields a complicated profile of instantaneous decay rate which differs among microforms (Belyea 1996).

Although few studies (Clymo 1965; Belyea 1996) have measured rates of decay at different depths through the acrotelm, it is well established that rates of decay are much faster in the seasonally oxic acrotelm than in the permanently anoxic catotelm. Within any particular microform, CRD_A must increase with time spent in the oxic layer and with microform height above the water level. This monotonic increase in CRD_A with height above the water level is illustrated schematically in Fig. 3b, which is also based on measurements at Ellergower Moss in S.W. Scotland (Belyea 1996).

At any distance along the line of water flow, surplus water will tend to run off via the microform of lowest surface height, i.e., via hollows rather than hummocks. Hollows are less productive than hummocks, and their litter decays more quickly than that of hummocks, at least initially. *The resulting LRB of hollows, which in effect controls the RSC, is roughly constant, because hollows are confined (Fig. 3c) to a narrow range of heights above the water level.* Hummocks, on the other hand, can tolerate, and in practice occupy (Fig. 3c), a much wider range of heights. *Hummock LRB varies in a hump-backed pattern in relation to height of the hummock surface above the water level.* The combined effect of all of these factors gives the patterns shown in Fig. 3c, which is based on Fig. 3a and 3b. It is important to recognise that the hummock graph in Fig. 3c *must* be hump-backed, though the exact position of the hump will depend on local conditions: even if NPP does not eventually diminish as the height of the hummock increases, CRD_A increases because a greater depth of material is exposed to decay, and thus $\mathrm{LRB} = \mathrm{NPP} - \mathrm{CRD}_A$ eventually decreases.

THE FEEDBACK MECHANISM

Figure 3c relates an output (LRB) to a 'causative' variable that it affects directly (height above water level); i.e. there is feedback. Hummocks have the same LRB as hollows at two (balance) points on the graph (Fig. 3c). These points are subject to different feedback mechanisms: a destabilising positive one where the graph has positive slope, and a stabilising negative one where the graph has negative slope.

The lower balance point is unstable because it invokes positive feedback. If hummock LRB is less than that of adjacent hollows then the hummock grows less rapidly than the hollows. The gap between hollow and hummock diminishes, hummock dwarf shrubs find their roots in water and die, and with them goes the hummock association between dwarf shrub and *Sphagnum*. What was once a hummock becomes functionally and environmentally a hollow, and is then invasible by plant species appropriate to hollows.

On the upper side of the lower balance point the reverse happens: LRB increases, the hummock grows further above the (still rising) water level, and this causes an even larger LRB. The hummock moves steadily up through the peak in Fig. 3c and down the other side where LRB is decreasing, but is still greater than it is in hollows. The hummock continues to grow until its top reaches the upper balance point, where LRB is the same as that in hollows, and the RSC value is determined. This upper balance point is stable: deviation above or below it produces effects that tend to return the hummock to the stable point. At heights above the stable point $\mathrm{LRB}_{HU} < \mathrm{LRB}_{ho}$, thus 'pushing' the hummock back toward the stable point. At heights below the stable point, however, $\mathrm{LRB}_{HU} > \mathrm{LRB}_{ho}$, but this also pushes the hummock back toward the stable point, though from the opposite direction.

Growth of the hummock is now restrained by the slower growth of the hollow, and their matched LRBs determine the local rate of bog growth:

$\mathrm{LRB}_{HU} = \mathrm{LRB}_{ho}$ and $\mathrm{RSC} = \mathrm{LRB} - \mathrm{CRD}_C$.

By analogy, one may imagine the hummocks as small but active dogs on leads, straining as far ahead as they can from the staid hollow that holds the leads in hand and controls the rate at which the convoy moves.

FURTHER QUESTIONS

How can the LRB be measured? At a particular time and place it may be necessary to make detailed measurements of NPP and CRD_A. A long-term average may be got from the slope (but not the chord; Clymo *et al* 1998) of a graph of cumulative mass below the surface *vs* age.

In general, one might expect that in a long-established peat bog most of the hummocks exist near the upper, stable, LRB point. What happens when the climate fluctuates from year to year? In a dry year, the LRB of the hummock will be greater than that of the hollow, and the hummock will increase in height relative to the hollows and the water level, thus moving above the stable balance point. This will generate a reduced LRB, and hence 'push' the hummock back toward the stable point. In a wet year the LRB will increase as the hummock moves back toward the peak, and this too will 'push' it back again toward the stable point, though in the opposite direction. Interannual variations, and especially a series of unusually wet or dry years, will thus always tend to push the hummock back to its original position at the stable point. The hummock-hollow complex is therefore resilient to minor changes in the water level.

What prevents a hollow with relatively low LRB from becoming a hummock with higher LRB (the part of Fig. 3c above the lower unstable balance point and below the peak)? One reason is that as the surface begins to rise the incipient hummock is pushed back down from the lower unstable balance point for the reasons explained in the previous section. A further reason is the difficulty that dwarf shrubs have in establishing in such wet conditions, and thus the inability to change from a functional hollow to a functional hummock. Some such transitions clearly have happened in the past, or there would be no hummocks now. If the water level falls just far enough for a hummock association to establish, then the positive feedback mechanisms above the lower balance point in Fig. 3c will ensure that it continues to develop. Once hummocks have established in a particular climate, the water flow through the acrotelm will become more channelled through the hollows, which have relatively high hydraulic conductivity (Ivanov 1981). Hollows would thus be kept wetter than they were, and the chances of further hummocks starting would be reduced.

An allied problem is that of the recorded expansion and contraction of hollow size in wetter and drier climatic phases. What controls this? Wallén (1988) and Malmer *et al.* (1994) suggested that the peat-forming communities at 5 - 15 cm above the water level may be sensitive to year-to-year variations in NPP, and species dominance in these parts of the bog surface may shift accordingly (Wallén *et al.* 1988). The same may be true of the dwarf-shrub/moss association (Malmer *et al.* 1994). The few empirical studies (Clymo & Reddaway 1971; Belyea & Warner 1996; Alm *et al.* 1997) which have examined RSC in different microforms have all shown at least slight differences among them. Shifts in dominance at the interface between hummocks and hollows may function as a self-regulating mechanism, providing the system with resilience to changes in hydrology (Barber 1981; Wallén *et al.* 1988). That is, hollows may expand laterally during wet periods, and hummocks may expand during dry periods, with lawns shifting position in concert. These lateral shifts would not necessarily preclude an equilibrium being maintained between established hollows and hummocks. Indeed, they may actually facilitate the persistence of bog surface pattern through periods of climatic variability. The high hydraulic conductivity of hollows would promote more rapid runoff if these microforms expanded laterally during wet periods. Conversely, the low hydraulic conductivity of hummocks would retard runoff if these microforms expanded during dry periods.

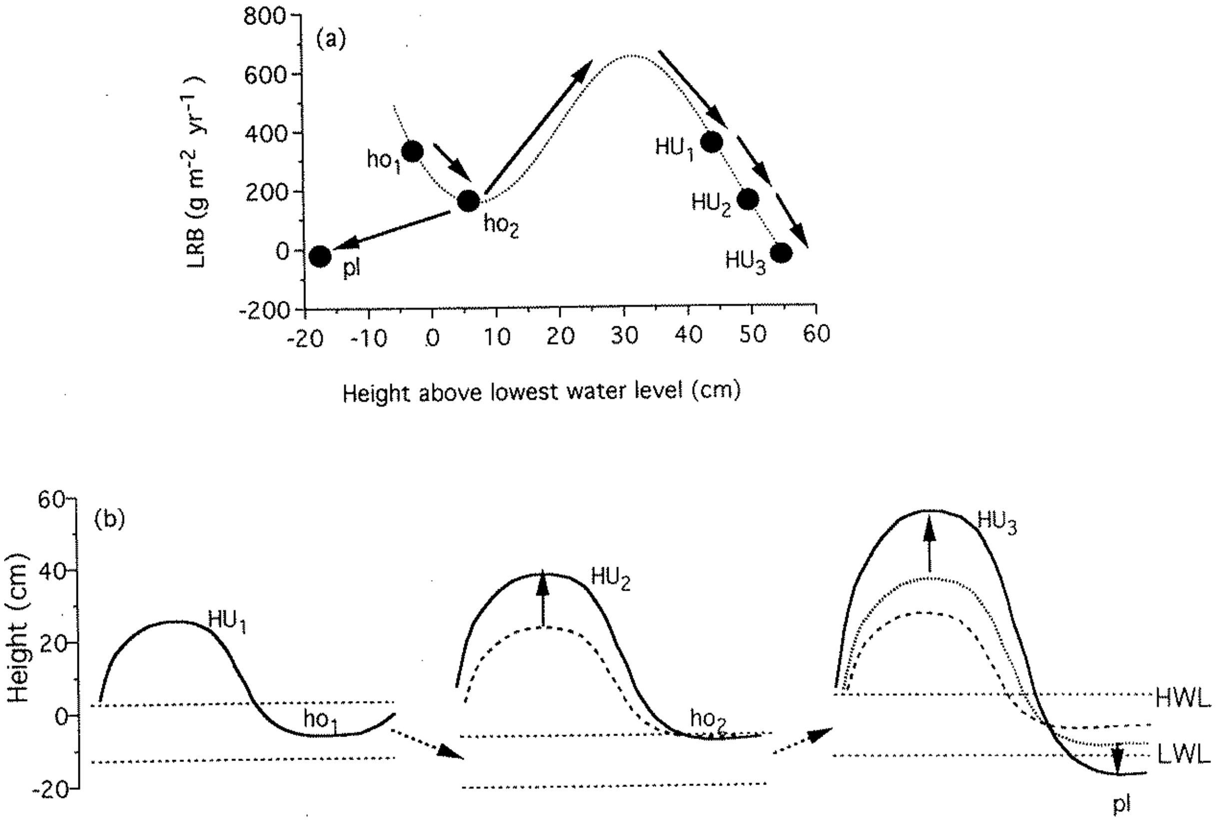
We have assumed, for simplicity, that the rate of decay in the catotelm is the same below hummocks and hollows. There is no empirical evidence on this point, but what would happen if the catotelm decay rates were not the same? In principle, a site with greater decay rate would need a larger LRB to reach the same RSC, because it is being let down, relatively, from below. However, all the other mechanisms would be unchanged. The decay rate in the catotelm is roughly a thousand-fold slower than it is in the acrotelm. To become as important as the decay rate in the acrotelm one would need a correspondingly greater depth of peat (strictly as cumulative mass) in the catotelm. For a 30-cm acrotelm that implies 300 m of peat. These calculations are very rough but they suggest that differences in decay rate in the catotelm are unlikely to affect RSC by much.

We find it difficult to account for permanent *shallow* pools, but there is a ready mechanism to account for deep ones. Pools with permanent open water differ from hollows in two important respects: they lack a continuous vegetation cover, and the peat surface is submerged throughout the year. Few studies have focused on the production ecology of bog pools, but the relatively high temperature in them (Clymo 1983) causes a high decay rate (Daulat & Clymo 1998). We can infer that peat

FIGURE 4. A scenario for transition from hollow to pool and implications for rates of peat accumulation.

(a) Schematic diagram of the relationship of water level with LRB. With a drop in water level, hollow LRB decreases (ho$_1$ to ho$_2$) and hummocks increase in height (HU$_1$ to HU$_2$), thus maintaining balance with the lower LRB$_{ho}$ imposed by the hollow. Hollow margins may be invaded by hummock mosses, contributing to hummock expansion (ho$_2$ to HU$_2$). Hollow centres, inaccessible to invaders, become permanently flooded pools with lower LRB (ho$_2$ to pl). Hummocks increase in height further to maintain balance with the lower LRB$_{pl}$ (HU$_2$ to HU$_3$).

(b) Schematic diagram of surface microtopography relative to highest (HWL) and lowest (LWL) water levels. At the left are the original hummock (HU$_1$) and hollow (ho$_1$) surfaces. In the central panel, water level drops and the hollow mosses reach their height limit (ho$_2$). The hummock increases in height (HU$_2$), thus maintaining balance with the reduced LRB$_{ho}$, and expands on to the margins of the hollow. At the right, water level rises in response to expansion of the hummocks and the hollow becomes a pool with permanently open water (pl). Variance of the microtopography increases further (HU$_3$) and this reinforces the conversion to a pool.



deposition rates must be much smaller than in surrounding hummock-hollow complexes. Any material deposited on the pool bottom quickly enters the catotelm, and is then subject to very slow rates of decay (except in the flocculant layer in the upper few cm). Despite these small losses in mass, the long-term accumulation of peat beneath pools is slower than in the surrounding telmatic peat (Foster & Wright 1990). Open-water pools on the Hudson Bay Lowlands are a net source of carbon dioxide and methane throughout the year (Hamilton *et al.* 1994). One of the implications of a mass budget that is smaller than for surrounding peat (or even negative) is that, once established, pools increase in depth (Foster &

Wright 1990).

What might cause transition from a hollow to a pool? Suppose that a change in hydrological conditions causes water level, and hence LRB, in a hollow to fall (ho_1 to ho_2 in Fig. 4a, b). Surrounding hummocks continue to increase in height, thus reducing their LRB and maintaining a balance with the hollow LRB, though at a reduced RSC (HU_1 to HU_2 in Fig. 4a, b). The hummocks expand laterally by invading the margins of the hollow (ho_2 to HU_2 in Fig. 4a, b), and may cover entirely a small hollow. The centre of a large hollow lacks a ready supply of invaders to replace the doomed hollow mosses; NPP falls close to zero but CRD_A remains high. The hollow deepens, and LRB falls even lower (ho_2 to pl in Fig. 4a, b). Variance of the surface microtopography increases as the hummocks grow further (HU_2 to HU_3 in Fig. 4a, b), and the moribund hollow deepens. Continued lateral expansion of the hummocks retards water flow and the water level rises (Fig. 4b), so that the hollow centre is submerged throughout the year. The failed hollow has become a pool: a fate from which there is little prospect of recovery.

SUMMARY

1. Hummocks and hollows can coexist for many millennia. This requires that peat be transferred from the seasonally oxic acrotelm to the rising permanently anoxic catotelm (the site of peat accumulation) at approximately equal rates below each. The *local rate of burial (LRB)* beneath a hummock or a hollow is the difference between *net primary productivity (NPP)* and *cumulative rate of loss of material by decay during passage through the acrotelm (CRD_A)*: LRB = NPP - CRD_A. In the steady state, LRB beneath all microforms is approximately equal, and determines the *rate of submergence by the catotelm (RSC)* within a radius of, say, 25 m.

2. Field measurements along a microtopographic gradient show that NPP and initial decomposability have the same pattern: highest in hollows, lower in hummocks (and lowest in open water pools). The acrotelm is shallow in hollows, and its thickness varies little, so litter passes quickly through this layer of intense aerobic decay. Hummocks, whose thickness is potentially much more variable, increase in thickness, lengthening the time that litter is exposed to aerobic decay, until the difference between their greater NPP but increasing CRD_A makes LRB the same as in adjacent hollows: $LRB_{HU} = LRB_{ho}$. This is a stable state maintained by negative feedback.

3. If LRB in a hollow falls too low, while adjacent hummocks continue to grow, then the local water level rises. The hollow becomes an open water pool in which LRB (and hence RSC) is smaller than it was previously. The pool then deepens indefinitely.

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APPENDIX

The following definitions are on a unit area basis.

Define the local rate of burial under a specific microform (LRB_m) as the local difference between net primary productivity (NPP_m) and cumulative rate of decay through the acrotelm ($CRD_{A,m}$):

$$LRB_m = NPP_m - CRD_{A,m}$$

We assume that the rate at which water level rises is the same rate at which the catotelm (of mass, X_C) thickens, and we call this the regional rate of submergence by the catotelm (RSC). 'Regional' implies the assemblage of microforms within a radius of, say, 25 m. We assume that RSC is constrained by the microform of lowest surface height. If the microform of lowest surface height is the hollow, then:

$$RSC = dX_C/dt = LRB_{ho} - CRD_C$$

where CRD_C represents regional total rate of loss by decay in the catotelm.

The acrotelm (X_A) under any specific microform, m, increases or decreases in thickness at a rate dX_A/dt:

$$dX_A/dt = NPP_m - CRD_{A,m} - (RSC + CRD_C) = LRB_m - LRB_{ho}$$

So, under any microform, a change in thickness of the acrotelm depends on the local (for the specific microform) difference between NPP_m and $CRD_{A,m}$, as well as on RSC.

For the acrotelm to stay the same thickness over time, dX_A/dt is zero and,

$$LRB_m = RSC + CRD_C = LRB_{ho}$$

PATTERNED MIRES AND MIRE POOLS

Origin and Development;
flora and fauna

PROCEEDINGS

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