PRODUCTIVITY AND DECOMPOSITION OF PEATLAND ECOSYSTEMS

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SUMMARY

(1) The surface half-metre of a peatland is complex with four distinguishable structural layers (whose physical position is relatively constant) and four functional layers (three of which move up and down with the watertable).

(2) Productivity, p, adds new matter at the surface but aerobic decay at a proportional rate, α, removes matter through the full depth of the oxygenated layer. The thickness of this layer from year to year is nearly constant at a mean thickness, m_a, measured as mass on an area basis. Collapse of the structure at the base of this layer induces waterlogging and anoxia. Material that has survived the oxygenated layer is engulfed by the anoxic layer at a rate p'.

(3) This anoxic layer is the real peat-accumulating layer, but decay continues here too though at a much lower rate α'. This applies to the whole anoxic mass and eventually, as the mass increases, the rate of loss approaches p'. Accumulation slows and eventually ceases.

(4) Methods of estimating p, α, m_a, p' and α' exist but are not satisfactory.

(5) These ideas can be applied to explain some of the consequences of management.

INTRODUCTION

In most ecosystems productivity and decomposition are approximately in balance when averaged over a period of years. When production exceeds decomposition then organic matter accumulates. Indeed this is as good a definition of peatland as any although it puts the emphasis in the wrong place. The imbalance between productivity and decay rate might, in principle, be a result of unusually high productivity or it might be a result of unusually low decay rate (or both). In most cases it seems that unusually low decay rate is the main cause of peat accumulation.

It is worth trying to sharpen these ideas by considering the processes involved in a typical precipitation-dependent peat bog. For simplicity consider a lawn or low hummock on a *Sphagnum* bog, starting at the surface and working downwards. One may recognize four layers from their structure, each with associated functional properties (Fig. 1).

(a) Surface to 2 - 5 cm down: the euphotic layer. The plants are live and photosynthetic. The light flux at the base of this layer is about 1 % of that at the surface (Clymo & Hayward 1982). The dry bulk density is about 0.01 - 0.02 g cm^{-3}. About 90 % of the volume is void and about 10 % is water-filled. The rest is gas-filled. Water moves easily through this porous structure. Temperature fluctuations are large - typically 20 - 30 °C during a summer day.

(b) From the base of the euphotic layer for 10 - 50 cm. Material here was once at the surface but has been slowly buried by the continued apical growth of the plants. Most of the original material is dead. Aerobic decay is the dominant process but the macroscopic structure is still mainly intact, the peat remains very porous, and any water not retained in capillary films moves easily between the pieces of plant material. Fungi and bacteria are the main agents of decay.

(c) A layer of collapse, perhaps 2 - 15 cm thick. Progressive decay has weakened the plant structure and the load above has increased. In early summer about 10 % of the load is generated by the plant matter that has accumulated above. but 90 % is caused by attendant capillary water. The load at 20 cm depth is likely to be about 10 g cm^{-2} (100 kg m^{-2}). Even greater loads may occur if there is a blanket of snow over unfrozen peat. As a result of this collapse the dry bulk density increases perhaps 5-fold to about 0.1 g cm^{-3}. This has crucial consequences. The space between structural elements is reduced in proportion but, because the hydraulic conductivity is related approximately to the fourth power of the distance across the flow path, the hydraulic conductivity of the peat is reduced 625-fold. The flow of water through the peat beneath is thus very slow so most of the peat remains water-saturated for most of the time. If a hole is made in such peat and left for a while then a (perched) watertable appears
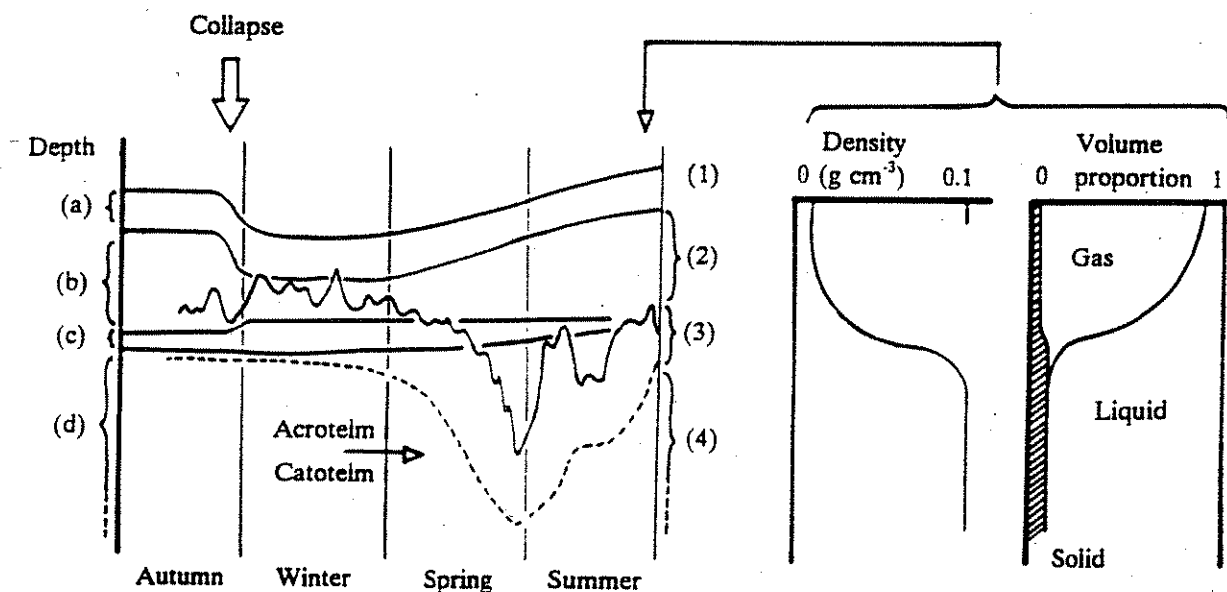

Fig. 1: Schematic representation (not to scale) of the seasonal relation of structural layers (a) to (d) and of the functional layers (1) to (4). See text for details. The irregular line at the (2)/(3) boundary represents the watertable. The broad arrow shows the point at which collapse occurs. At the right are profiles at the end of summer of dry bulk density and the proportion of space occupied by gas, liquid and solid.

in it. Some water seeps through the peat below but as long as the input from precipitation exceeds losses by downward seepage, by evapotranspiration, and by refilling of storage, then the loss by seepage is replaced and the peat remains waterlogged. Surplus water runs off laterally through the porous layers above.

(d) Lower peat, from 10 - 1000 cm thick. This is usually the thickest layer. Most of it is of relatively high bulk density (about 0.1 g cm^{-3}), of low hydraulic conductivity, and is permanently water-saturated. Microorganisms in the top of this layer use up the oxygen aerobically. It is replaced by oxygen diffusing down, but the diffusion coefficient of oxygen in water is only 10^{-4} of that in air so the rate of replacement is slow and, apparently, slower than the potential rate of aerobic consumption. The peat becomes anoxic, anaerobic metabolism (mostly in bacteria) is the new mechanism of decay, the redox potential falls, reduced organic compounds may accumulate, and H$_2$S may be produced. Another change is that the amplitude of temperature fluctuations decreases the deeper one goes. At a depth of 100 cm the daily cycle is scarcely perceptible - perhaps 1 °C. The longer yearly cycle is less strongly damped and at 4m depth is still perhaps 2 °C. From the point of view of bacteria however conditions are almost isothermal. Predicting these conditions numerically is considered by Brovka (this volume). The rate of decay is much lower than it was in the oxygen-rich layers; uniform low temperature may be part of the explanation.

The remaining plant structures may disappear leaving amorphous highly humified dark brown peat that is almost gelatinous. Some of this material may be from the original plant matter, with polymers reduced in size but essentially unchanged. Some of it may be chemically new, produced by very slow chemical reactions. A third component may be chemically new, made by microorganisms - mostly by bacteria. At present we do not know what proportion of humified peat is in these three categories.

The gelatinous peat has a negligible hydraulic conductivity but high matric forces too. Imagine a bowl of jelly from which a 1-cm diameter core has been removed down to within 1 cm of the bottom. This hole will not spontaneously fill with water by seepage, but if water is put into it the watertable will remain where it is. In practice peat is more heterogeneous than this. The existence of recurrence horizons shows that what happens, or does not happen, in zones (a)-(c) may have consequences that persist for millennia. Fig. 2 shows a schematic representation.

These structures and changes in structures thus have important consequences on attendant processes. In fact the process-zones do not coincide with the structures in such a simple way as that described. The processes are most strongly linked to the position of the watertable. In autumn there is surplus precipitation and the watertable is likely to be high in zone (b). The higher the watertable rises the higher it finds the hydraulic conductivity (Bragg 1982) and so the more easily the water can escape laterally: the system is self-limiting in all normal (and most abnormal) conditions. In summer drought, however, the watertable may sink through zone (c) and some way down - perhaps 30 cm - into zone (d). It is useful therefore to recognise four functional zones.

(1) The euphotic zone - coincident with structural zone (a) - in which almost all production occurs.

(2) An oxygen-rich zone of aerobic decay. This includes structural zone (b) and, at times of low watertable, part or all of (c) and part of (d).
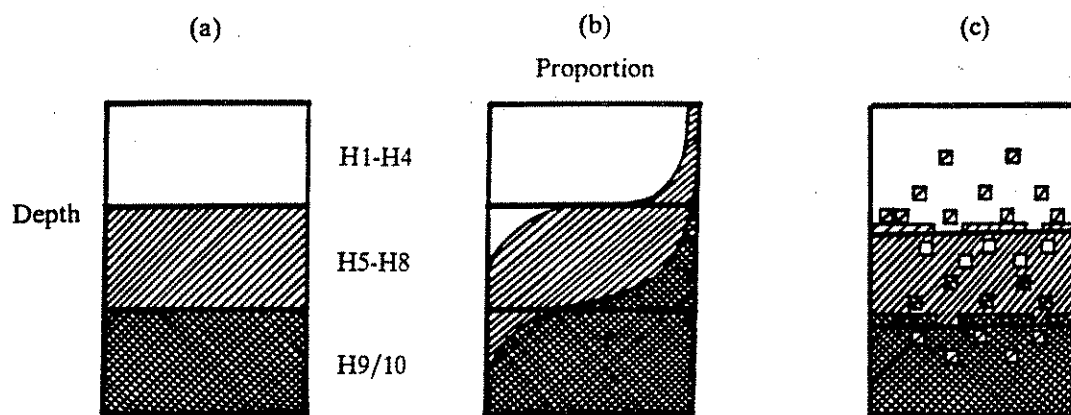
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Fig. 2: Three schematic representations of the increase of humification with depth. H1 - H10 are von Post humification values. (a) Slab. A crude representation showing only that there is layering. (b) Proportional, showing that the transitions are gradual. (c) Pictorial, showing heterogeneity of distribution as well. This modifies expectations about the effective hydraulic conductance for example.

(3) A transition zone from oxygen-rich to anoxic conditions, extending approximately from the watertable to 10 cm or so below it. Decay occurs by a mixture of aerobic and anaerobic processes. This zone is one of relatively high microbial activity. Values of pS down to 2.7 have been measured here, compared with 4.2 - 5 at greater depths and to >7 above (Claricoates *in lit.*, Clymo in press). The efflux of methane is strongly dependent on temperature (which fluctuates seasonally in this zone) and this fact argues that this zone is likely to be the main source.

(4) An anoxic zone (except for a few places where roots of vascular plants conduct oxygen deep into the peat). This comprises most of zone (d) all the time and all of it for most of the time.

These functional zones move up and down through the structural ones, which are more nearly static, in the sort of way shown schematically in Fig. 2. The term acrotelm is now commonly used for everything above the ordinary greatest depth of the (2)/(3) boundary, while catotelm is used for everything below this (Ingram 1978).

Specific cases deviate to a greater or lesser extent from this general account. For example, the 3.3 m deep peat found in a cave in Patagonia and composed of dry leaves and dung of the recently-extinct giant ground sloth (*Mylodon*) deviates greatly. So too do the 2-m deep moss-bank peats of Signy Island in the maritime Antarctic in which the lower layer of slow decay is imposed by the low temperature in permafrost. In other cases the upper layers may be unusually extensive (hummocks) or reduced (hollows) or absent (some pools). In others, such as fens, the process of collapse may be diffuse and the ability to self-regulate the

watertable may be minimal. In forested peatlands, again, the details differ: the zone of production is of much greater depth and the layers are likely to be more heterogeneous.

PRODUCTION, DECAY AND ACCUMULATION

It is necessary to consider the acrotelm and catotelm separately. Most production - the addition of newly formed organic matter - occurs in the euphotic zone at the top of the acrotelm. There are exceptions. For example, rhizomes and roots are formed and this is conveniently considered as production, though the structures are produced from a stream of soluble materials transported internally from leaves. The rate of organic matter insertion into the peat in this way may be very important. In extreme cases in sub-arctic tundra about 90% of total production first appears below ground (Wallén 1986). This is still within the acrotelm however. More awkward are those cases such as *Eriophorum* (Giles 1977) and *Rubus chamaemorus* (Stavset 1973) where roots penetrate to more than 1 m down into the catotelm. The amounts are probably small in general though.

While production is to a greater or lesser extent localised, decay is almost ubiquitous: it occurs throughout the peat mass. The more peat, the greater the amount of decay. The general principle is shown in Fig. 3.
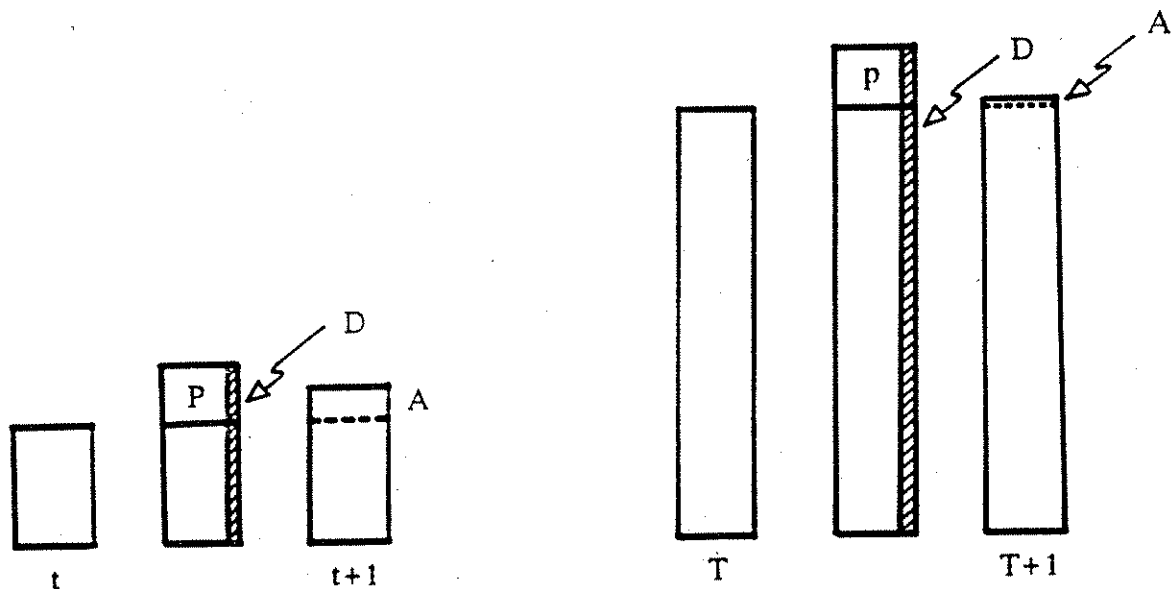

Fig. 3: The interrelations of production P, decay D and accumulation A at times t and (much later) T. The amounts P, D and A refer to one year and A = P - D. Between t and t + 1 then P >> D so A is quite large. By T however D is almost as big as P so A has become very small: there is almost no true accumulation in the system any longer even though P is just as large as ever.

Productivity remains the same, but as more peat accumulates so the total lost by decay during a given period increases, so the net accumulation rate gets steadily smaller. This may be described more specifically if the rates can be defined. For example:

$$\frac{dm}{dt} = p - \alpha m \qquad (1)$$

where m is the dry mass on an area basis, p is the productivity on an area basis, α is the proportional rate of decay, and t is time. This gives

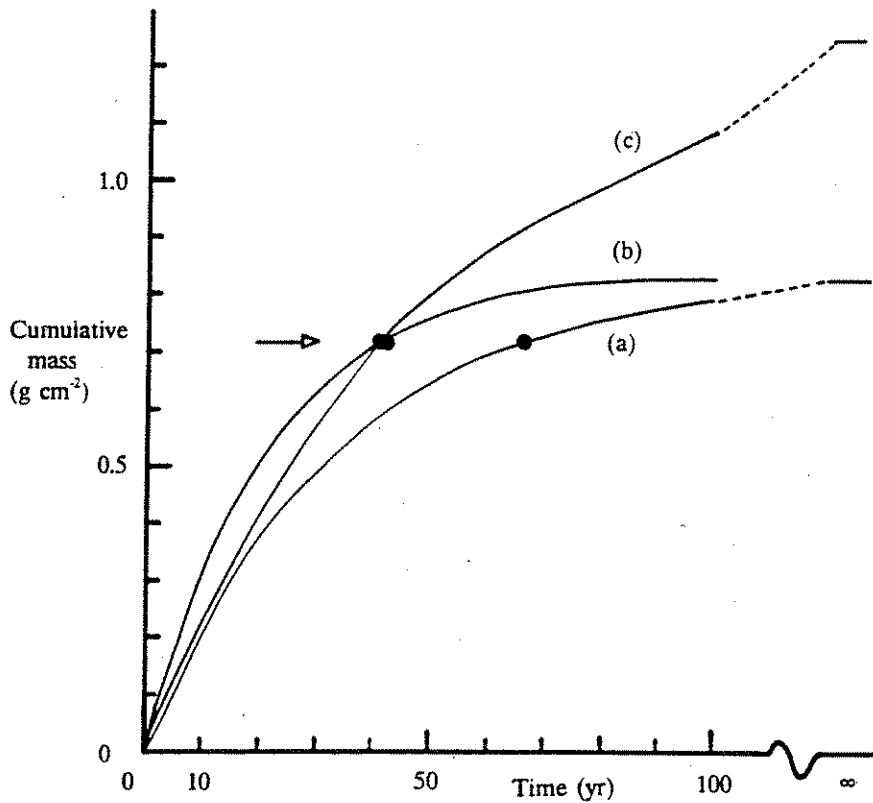$$m = \frac{p}{\alpha} (1 - e^{-\alpha t}) \qquad (2)$$

which is shown in Fig. 4.

Fig. 4: Illustrative examples of (2). The slope p', in (3), is calculated at t_a, m_a shown by the arrow.

	p (g cm^{-2} y^{-1})	α (yr^{-1})	t_a (yr)	p' (g cm^{-2} y^{-1})	p'/p
(a)	0.025	0.030	67	0.0034	0.14
(b)	0.040	0.048	42	0.0054	0.14
(c)	0.025	0.020	42	0.0106	0.42

The proportion p'/p depends on p/α, though the time taken to reach m_a depends on the specific values of p and α. Conversely, for the same t_a the value of p' and of p'/p can be very different.

It is obvious that m approaches p/α as an asymptote. In practice the acrotelm moves up past any particular piece of organic matter and when the catotelm conditions arrive the assumption in (1) of constant α is no longer true. This point is shown in Fig. 4. At the origin, where m = 0, then it follows from (1) that the slope of the curve is p. At the point where the acrotelm becomes the catotelm the slope p', which has the same physical nature as a productivity, gives the rate at which matter is leaving the acrotelm to enter the catotelm. At this point

$$\frac{dm}{dt} = p - \alpha\ m - p' = 0 \qquad\qquad (3)$$

Once established the acrotelm is thus of constant thickness, m_a. It does not accumulate peat (the catotelm is the accumulator). The acrotelm takes in matter at a rate p, and transmits it to the catotelm at a rate p'. The value of p'/p is about 0.1.

These conclusions are fairly robust. For example, it is plausible to suppose that the value of α changes systematically. In Fig. 5a are data for the antarctic moss *Chorisodontium aciphyllum* which suggest a sigmoid rather than an exponential relation between mass and time. These give the cumulative curve shown in Fig. 5b. After a century or so the curve begins to deviate substantially from that of (2), but at the time when the catotelm arrives - about 80 years in the example - the differences in m_a are rather small.
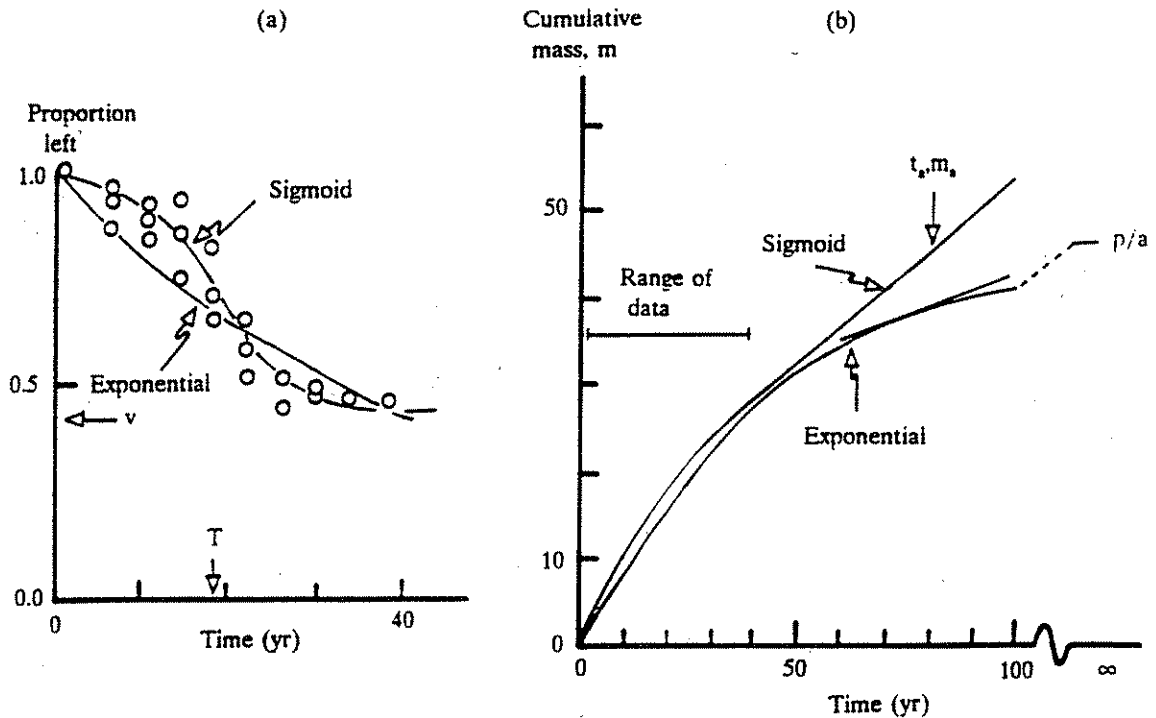

Fig. 5: (a) Decay of the antarctic moss *Chorisodontium aciphyllum* (Baker 1972). Two lines are fitted. The exponential assumes that $dm/dt = -\alpha m$ giving $m/m_0 = \exp(-\alpha t)$. The other (sigmoid) is purely descriptive: $m/m_0 = 1-\{(1-v)/(1+\exp[-r(t-T)]\}$ where v is the lower limiting value, T is the age for steepest descent, and r controls the curvature (Clymo in press). (b) Cumulative mass for the two cases. The exponential follows (2). The sigmoid: $m = p\{tv-[(1-v)/r][\ln(1+\exp[-r(t-T)])-\ln(1+\exp[rT])]\}$. The sigmoid tends toward a continuous slope of v flux units. At the acrotelm/catotelm boundary the exponential is passing on 18 % of what entered; the sigmoid 43 %.

Differences in p and α could account for the difference between hummocks and hollows, but even more important may be the depth of the acrotelm - or at least of layers down to (c) - because this controls the length of time that the plant matter is exposed to relatively rapid aerobic decay. The longer this continues the smaller the value of p' will be.

Malmer & Wallén (personal communication) have pointed out the significance of an observation recorded by Forrest & Smith (1975) and by Wallén (1980). On hummocks, dwarf shrubs with a woody persistent superstructure encourage the rapid upward growth of *Sphagnum*. This covers the shoot bases, encourages lateral roots to develop on the woody stem and thus rejuvenates the shrubs and makes them potentially immortal. It also increases the proportion of structural material (Luken *et al.* 1985), provides a framework which supports the *Sphagnum*, and ensures a deep acrotelm. In hollows, by contrast, the vascular plants are mostly non-woody and graminaceous. They provide no permanent framework for *Sphagnum*, so the acrotelm remains shallow.

In the catotelm the same sort of considerations apply. The rate of supply from the acrotelm is approximately constant at p'. The rate of decay is much smaller than in the acrotelm. By analogy with (1) we have

$$\frac{dm'}{dt'} = p' - \alpha't' \qquad (4)$$

where the ' is to indicate the catotelm. The solution is

$$m' = \frac{p'}{\alpha'}(1 - e^{-\alpha't'}) \qquad (5)$$

This indicates that m' approaches p'/α' asymptotically. The important point is that there *is* an asymptote - an upper limit to the height to which peat can accumulate - for the reasons shown pictorially in Fig. 2. At this point the surface would still be green and growing as fast as it always had done, but the overall rate of accumulation would be zero. This has important implications for those who still consider peatlands as being a sink for carbon, and at a rate approximately that of p. This particular model for the catoteim may be tested using published C-14 dates and bulk density profiles. To do this one needs to take (5) and derive the consequences for M', the cumulative mass on an area basis, below an arbitrary horizon (usually the catotelm surface) as a function of T', the age, looking back in time. Then:

$$M' = \frac{p'}{\alpha'}(1 - e^{-\alpha'T'}) \qquad (6)$$

(The formal similarity to (5) is unique to this particular equation.) About two thirds of the tests of this (Clymo 1984, Smith & Clymo 1984, Clymo in press) give the predicted concave relation, from which p' and α' can be estimated (Fig. 6).
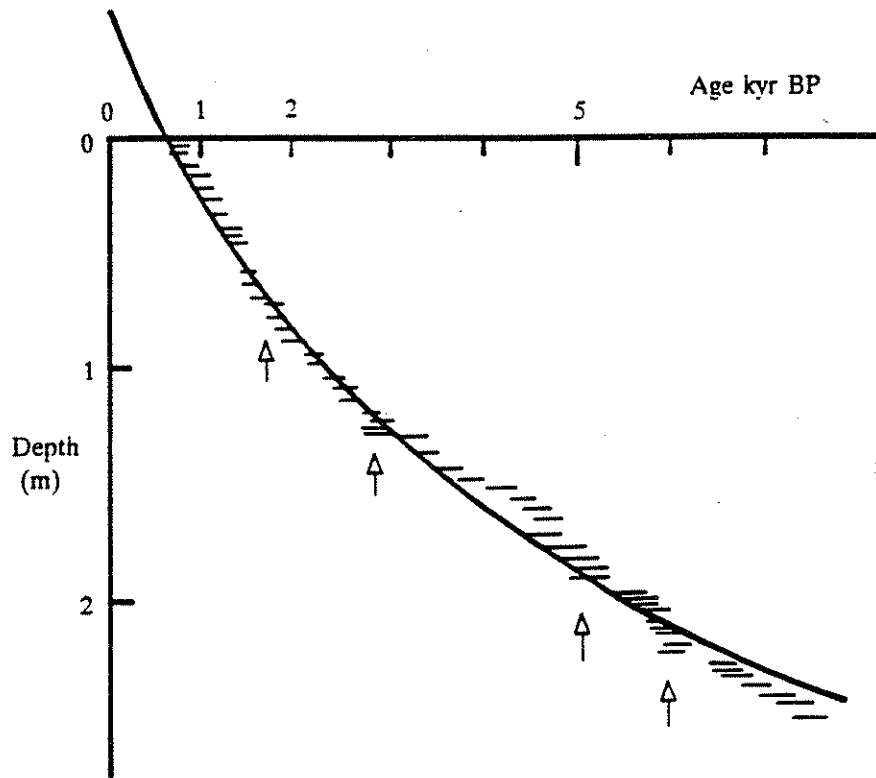
Fig. 6: Equation (6) fitted to age *vs* depth in Draved Mose, Denmark (Aaby & Tauber 1974). The dry bulk density was not recorded and has been assumed to be 0.10 g cm^{-3}. The fitted estimates are: $p' = 0.0050$ g cm^{-2} y^{-1} (50 g m^{-2} y^{-1}); $\alpha' = 0.00012$ yr^{-1}). There were temporary variations in rate (spanning perhaps 500 yr) shown by arrows but the overall fit spans 7 millennia.

The other one third of cases show no evidence of concavity. This is a puzzling result, because the concentrations of methane and carbon dioxide - the likely products of decay - increase steadily as one goes down the catotelm (Clymo 1984, Dinel *et al.* 1988, Claricoates *in lit.*) and this is consistent only with continued decay at all depths. The point is an important one: if decay really did cease altogether then there would be no maximum depth to peatlands except that set by mechanical instability.

It has become accepted practice to calculate so-called 'accumulation rates' from the age at two depths and the mass, on an area basis, between them. For recent peat the error is probably small but for older peats it can be large. For example, if $\alpha' = 0.0003$ yr^{-1} (a plausible value) then after 5500 yr only 20% of the original peat is left: calculation of the apparent 'accumulation rate' would give a value only one-fifth of the true value.

Variations in p, α and the depth of the acrotelm may account for p', as well as for surface patterns. This, combined with α' or some functional equivalent, set the asymptotic maximum depth to peat accumulation. This in turn may be combined with hydrological theory to explain the overall shape of ombrotrophic peat bogs. A start has been made (Ingram 1982, Clymo 1984) but much remains to be discovered and a discussion is beyond the scope of this article.

11

MEASUREMENTS

In the preceding analysis five parameters are critical: p, α, m_a, p' and α'. The α and α' in particular should perhaps stand for functional equivalents. It may well be that we will eventually know enough to see them as variables rather than parameters, but that day is some way off.

There are many measurements of p either for individual species or, more usefully, for whole peatland communities. Reviews or summaries are given (*i.a.*) by Heal *et al.* (1978), Brown *et al.* (1980), Sonesson (1980), Bliss *et al.* (1981) and Gore (1983). More detailed work is described (*i.a.*) by Reader & Stewart (1971, 1972), Tint (1982), Vasander (1982), Grigal *et al.* (1985) and Wallén (1986). These measurements are sufficiently accurate for it to be quite clear that the productivity of most ombrotrophic peatlands - at 200 - 900 (1900) g cm^{-2} y^{-1} - is on the low side. The accumulation of peat must thus result from particularly low rates of decay. But there are great difficulties in using these values for more exacting work. First, the precision of such measurements is rarely given (if only because ecologists do not in general know how to combine estimates of precision in different measurements - though physicists have been taught this for decades). Secondly, the bias (i.e. the extent to which the methods used give systematically too high or too low a result) is unknown or, at least, is not reported. Thirdly, the values seem to vary by a factor of 2 at least from year to year (Clymo & Reddaway 1974, Wallén *et al.* 1988, Vitt in press, Rochefort & Vitt *in lit.*). It is rare enough to see two years' measurements; three are virtually unknown. We must therefore be cautious about the accuracy of calculations based on equations such as (2): reliability to a factor of 2 - 5 may be about the best that can be achieved. To explain the differences between hummocks and hollows may need considerable improvements. More to the point, these improvements must be demonstrable: in addition to estimates of precision (standard errors or equivalent) we need indications of bias and of temporal variation over 5 - 10 years.

Much the same applies to measurements of decay rate α, (or its equivalent). Litter bags are the commonest technique. They have the great advantage that they allow experiments to be made. Some of these experiments (e.g. Heal *et al* 1978) have been continued for up to 5 years. But zones (a) - (c) may span 20 - 80 years and no litter-bag experiments have lasted that long - or are likely to because the fragments fall out of the bags before that (and research grants expire). Litter bags are of unknown bias for other reasons too. The physical and chemical conditions inside them are not demonstrably the same as those of undisturbed material. Preliminary air drying has unpredictable effects.

The most informative measurements of decay rate have been those cases (Baker 1972, Fenton 1980, Johnson 1987) in which the decay rate has been inferred after the event in undisturbed natural situations by comparing measured dry bulk density with that calculated. The technique relies on using the length of moss stems in a slice of known thickness to calculate the amount of compression and hence the dry bulk density to be expected if there had been no decay. These methods can be applied only in special circumstances: unfortunately they are not usually applicable to hollows, for example.

Decay studies in the acrotelm are also hampered by the difficulty of getting a demonstrably reliable age for undisturbed samples (Clymo 1987). The best method is probably C-14 'wiggle matching'. but this is impossibly expensive for routine use.

Measurements of m_a, the mass of dry matter on an area basis, are fairly simple. The main difficulty is in determining the depth of the oxygenated layer either at the time of sampling or by reference to the profile of some other variable such as dry bulk density. There is much to be said for collecting cores of peat with the water retained in the field state (Clymo 1988). Such cores can then be sliced into relatively thin layers - 1 cm for instance - from which calculations can be made to whatever depth seems requisite in the light of other measurements.

Measurements of p' are, at present, not really satisfactory. One way is to use values of p, a and m_a to calculate p' from (3) or some similar equation. A more direct method is to use age vs depth curves fitted to (6). An example is shown in Fig. 6. Broadly speaking the slope determines p' and the curvature a'. It is surprising to find that the range of values of p' is generally rather narrow - 0.004 to 0.008 $g \, cm^{-2} \, y^{-1}$ - though there are exceptions such as the *Poa flabellata* peat on Beauchêne Island in the south Atlantic ocean (Clymo 1984, Smith & Clymo 1984).

The parameter a' can also be estimated from age vs depth curves though not as precisely as p' because it is based on small curvatures. The range is 7×10^{-5} to $5 \times 10^{-4} \, yr^{-1}$. In principle a' can also be calculated from the rate of production of the products of decay, methane and carbon dioxide. The few measurements that have been made seem to be consistent with those from age vs depth curves (Clymo 1984).

EFFECTS OF MANAGEMENT

The porous acrotelm is well-adapted to deal with ordinary fluctuations in precipitation, but 'management' usually disrupts the complex but delicate structures just described.

Some management is almost totally destructive: peat mining on a commercial, semi-commercial (Meharg & Montgomery this volume), or even on a domestic scale is irreversible in a single lifetime. Other sorts of management are also destructive but less so than mining. An example of growing importance is liming with the intention of raising the pH and calcium concentration in runoff water for the benefit of fish in acidified streams and lakes (Mackenzie this volume). Lime, when applied as powder, kills adjacent *Sphagnum* of some species at least. Equally destructive, though an unintended consequence of human activity away from peatlands, was the emission of sulphur oxides during the combustion of fossil fuels. In the southern Pennines *Sphagnum* and other species disappeared almost completely because the plants were sensitive to low concentrations of HSO_3^- (Lee et al. 1987). Now it seems that the damaging effects of HSO_3^- may have been replaced by those of NO_3^-.

Perhaps the commonest forms of management in Britain are burning and draining. Moderate burning is repeated at intervals of 4 to 20 years to improve grazing for sheep and the gamebird

grouse. This reduces the diversity of species and the complexity of structure, but the surface remains fairly intact and can recover within 20 - 30 yr when burning and grazing cease (Rawes 1983).

Draining is nowadays usually a prelude to peat mining or to improve the growth of forest trees (e.g. Vompersky *et al.* this volume) or to allow the establishment of trees for the first time on unforested peatland. [Whether this last would have been attempted at all on the peatlands of Caithness and Sutherland if it were not for tax incentives to the extemely rich may be doubted. It is ironical that William King (1685) recommended that Irish bogs should be drained because 'they are a refuge for Torys and Thieves']. Drains in peatlands have three main effects: they change the hydraulic behaviour of the peatland; they increase the depth of the acrotelm (thus increasing the rate of aerobic decay): and they change the chemistry of the runoff water (e.g. Lishtvan *et al.* this volume, Sallantaus this volume). The consequences of increased decay in peatlands were estimated by Bramryd (1980) and by Armentano & Menges (1986) amongst others. If their calculations are correct then the global effects of the present trends in wetland drainage on atmospheric carbon dioxide may be significant. Studies of the shrinkage of peat as a consequence of drainage continued over 130 yr have been recorded by Hutchinson (1980), but it is on detailed work revealing carbon dioxide and methane fluxes over drained and undrained peatlands that the global calculations rely. For example, Silvola *et al.*(1985), Silvola (1986, 1988) found that undrained mire accumulated carbon, but drained mire became a net emitter of carbon: it changed from a modest sink to a substantial source. Global calculations can be no better than the detail on which they are based. We need far more of this detailed work.

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