

The Limits to Peat Bog Growth

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# THE LIMITS TO PEAT BOG GROWTH

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Not less than 2% of the Earth's land surface is peat-covered, so it is important to try to understand the dynamics of peat accumulation.

Peat-forming systems (mires) accumulate peat because conditions within them impede the decay of the plant material produced by their surface vegetation. This paper concerns the rate of peat production and some unexpected consequences of the processes of decay. These consequences are likely to be of interest to those concerned with mire ecology and with the history of vegetation during Flandrian times.

Most peat-forming systems consist of two layers: an upper 10–50 cm deep aerobic layer of high hydraulic conductivity, the acrotelm, in which the rate of decay is relatively high; and a thicker, usually anaerobic, lower layer, the catotelm, of low conductivity and with a much lower rate of decay.

Plant structure at the base of the acrotelm collapses as a consequence of aerobic decay, and the hydraulic conductivity consequently decreases. As long as precipitation continues the water table therefore rises to this level, thus engulfing material at the base of the acrotelm. The rate,  $p_c$ , of this input to the catotelm is exactly analogous to the rate,  $p_a$ , of input to the acrotelm i.e. of primary productivity of the vegetation.

During passage through the acrotelm the peat becomes richer in the more slowly decaying components. The depth of, and the time for transit through, the acrotelm thus control  $p_c$ . The catotelm, however, usually forms much the largest part of the peat mass.

Selective decay may continue in the catotelm. The specific composition of the peat thus becomes a progressively poorer indicator of the surface vegetation that formed it, and to a degree that is not generally realized: reconstructions of the past surface vegetation may become very inaccurate.

If  $p_c$  were constant and there were no decay in the catotelm then for the centre of a peat bog the profile of age against depth (measured as cumulative mass below the surface) would be a straight line. But if either or both these conditions is untrue then the profile would probably be concave. Most of the cases for which data exist are consistent with a concave profile and a value (constant over several thousand years) of  $p_c$  of about  $50 \text{ g m}^{-2} \text{ a}^{-1}$  and a decay rate coefficient,  $\alpha_c$ , proportional to the amount of mass remaining, of about  $10^{-4} \text{ a}^{-1}$ . This rate of input to the catotelm is about 10% of the primary productivity i.e. about 90% of the matter is lost during passage through the acrotelm. The relation seems to hold in spite of short-term fluctuations such as those represented by recurrence surfaces.

Although  $10^{-4} \text{ a}^{-1}$  seems a very slow rate, it has important consequences.

(i) The peat mass tends towards a steady state in which the rate of addition of matter at the surface,  $p_a$ , is balanced by losses at all depths: *the rate of accumulation is zero*. This depth is, for the cases examined, about 5–10 m.

(ii) The very *concept* of 'peat accumulation rate' thus needs careful consideration. To calculate it as the difference between two  $^{14}\text{C}$  dates divided by the depth between the samples from which they were measured, as is commonly done, may be seriously misleading. The error is likely to increase with age, depth and time span.

(iii) Progress in such studies can be made *only if the easily measured profile of bulk density is known*. The position of the profile in the peat bog must also be known.

There is some evidence that peat contains, or comes to contain, about 1% or less of the original mass in a highly refractory state, so that the concept of a steady state is unlikely to be correct if times much greater than about 50000 years are involved.

Three more consequences of the continued very slow decay in the catotelm may be of interest to mire ecologists.

(iv) Most of the mass that leaves the catotelm probably does so as methane gas. The concentration of methane increases with depth and may be as high as  $5 \mu\text{mol cm}^{-3}$  at 5 m depth (about 10% by volume). Diffusion alone is able to remove mass at the necessary rate and would create concentration profiles similar to those observed. The solubility of methane in water is exceeded, however, and much of the methane may in practice be lost by mass flow of bubbles to the surface.

(v) The *amplitude* of temperature fluctuations, as well as the mean temperature, may have a significant effect on the rate of peat decay, particularly in a cold climate.

(vi) If this analysis is correct then the maximum depth of peat which can accumulate in 50 000 years is determined largely by the value of the quotient  $p_c/\alpha_c$ . The usual view that the *maximum* depth is determined directly by climate operating through hydrology may be incorrect, though hydrology may have an indirect effect on the value of  $p_c$ , the rate of input to the catotelm at the bog centre. Away from the centre  $p_c$  is probably variable  $\tilde{p}_c$  and determined by hydrology. Its dependence on distance from the centre and on time is complicated:  $\tilde{p}_c/p_c$  may be more than, equal to, or less than 1.0. The age against depth profile away from the bog centre may be directly affected by hydrology, though the effect is not large except near the edge of the bog or near the base of the peat. There may, of course, be catastrophic failure – a bog-burst or ‘flow’ – before the  $p_c/\alpha_c$  limit is reached in the centre, or slower but equally destructive development of gullies and erosion.

### 1. INTRODUCTION

Estimates of the amount of peat worldwide have increased steadily and differ considerably (Bramryd 1979). The most recent (Kivinen & Pakarinen 1981) is that peat covers about 3.0% of the Earth’s land surface and that the dry mass of carbon in deep peat deposits is about 180 Gt. This may be compared with estimates of the amount of carbon of 600–700 Gt in the atmosphere, 800 Gt in live plant biomass, 700–3000 Gt in ‘humus’ including peat; and of productivity on land of 50 Gt a<sup>-1</sup> (Woodwell *et al.* 1978). About three quarters of all peatland is distributed between Canada and the U.S.S.R. About 0.7% is in the British Isles and it covers about 10% of their area. Although the basis of most of these estimates is not clear, it is beyond doubt that there is a lot of peatland, that it may have a significant effect on the Earth’s carbon budget (Bramryd 1979), and that it is important in the British Isles. In addition it is a repository of the Flandrian pollen record. Not surprisingly, therefore, there has been considerable interest in the rate at which peat accumulates and the way in which the environment affects this rate.

Some simple assumptions are commonly made about peat accumulating systems. Among these are that the rate of decay is appreciable and measurable at the surface but that in the main mass of peat it is not only unmeasurable but also, therefore, negligible. Peat accumulation rates are therefore calculated very simply from <sup>14</sup>C ages at two or more depths. It is also assumed, as a rule, that although there may be selective decay near the surface, such selection is unimportant at greater depths, and in consequence the macrofossil composition of peat from 5 m depth is no more distorted a reflection of the vegetation that formed it than is peat from 1 m depth. It is also commonly assumed that if the surface vegetation of a peat bog is ‘healthy’ and appears to be growing well, then the bog must be accumulating peat, and it may even be supposed that the rate of accumulation is directly dependent on the productivity at the surface. These assumptions are rarely questioned, and their numerical consequences are almost universally ignored, but most are, to a greater or lesser extent, untrue and some of their consequences are surprising. In particular, a very slow rate of decay is not at all the same as a negligible rate. Of crucial importance is the interaction between the 2–50 cm deep, predominantly aerobic, surface layer and the much thicker predominantly anaerobic underlying layer. The boundary between them is approximately at the mean depth of the minimum water table in summer (Ivanov 1981) but is not sharp. These two layers used to be called, respectively, ‘active’ and ‘inactive’. Wanton introduction of jargon is to be avoided, but the old terminology

has served to perpetuate the mistake that it summarized. The terms 'acrotelm' and 'catotelm' were introduced by Ingram (1978) to avoid this prejudice and are used here.

The main purpose of this article is to assess the truth of these commonly made assumptions. This requires the statement of explicit models of the processes involved in peat formation, and these, in the form of equations, may appear complex and difficult to understand. This appearance is superficial however: the ideas incorporated are simple and are explained in the text, and the mathematics is trivial. The evidence on which the models are based is considered briefly, where necessary, to justify the choice of description. The detailed results do, of course, depend on these choices, but the general consequences are largely independent of the exact choice of description. The consequences may usefully be considered as numerical – that arise from the use of particular (realistic) values in a model – and conceptual. Both types point to particular effects that are, at present, neglected by students of peatlands, and throw into relief the reasons why peat accumulates at all and the maximum depth that it can reach.

Many of the processes that cause peat to accumulate in fens are similar to those that cause it to accumulate in acid bogs, but suitable data from fens are more scarce than those from bogs, and fens are probably more complicated too. In this article, therefore, bogs are used as exemplars for all peat accumulating systems.

## 2. THE PROCESS OF PEAT FORMATION

It is useful to begin with an outline of the processes that lead to peat formation. Plant mass is added at the surface. When the plants die they begin to decay, mainly in aerobic conditions. As mass is lost, and more plant material accumulates above, so the main structural elements (for example moss stems in a *Sphagnum*-dominated bog) lose their integrity and collapse. The bulk density therefore increases (figure 1). The distance between the remaining structural elements decreases so the radius of curvature of liquid menisci in these spaces decreases, and the capillary fringe of water rises. Capillary forces in such spaces are unable to maintain or raise the water table by more than 0.5 m or so, as Granlund (1932), Wickman, (1951) and Ingram (1982) point out. There is a more plausible explanation of the maintenance and gradual raising of the water table to the observed height of several metres, however. Much of the precipitation on the bog surface must run off laterally. When the water table is above the average height, after prolonged or heavy rain, most of the water flows rapidly between the widely spaced elements of the uncollapsed plants in the acrotelm, in which the hydraulic conductivity is high. But when the water level falls to that of the collapsed plants the rate of runoff from the bog decreases markedly, because the channels for water flow are smaller and the conductivity is related to some power, greater than one and perhaps as much as four, of the channel width. The height of the water table in successive summers rises, therefore, as peat accumulates and as long as precipitation continues, to an average position close below that at which macroscopic structure has collapsed. The boundary between the acrotelm and catotelm therefore rises, in constant climatic conditions, at the same rate as that at which peat accumulates, and the boundary in such conditions is always at approximately the same average depth below the vegetated surface.

Close below the water table the peat, as it now is, becomes anaerobic because the flux of oxygen down from the air is less than the rate at which it is consumed by microorganisms: the rate of diffusion of oxygen in water is about  $10^{-4}$  that in air. The anaerobic microflora that

develop cause decay of most materials at a rate that is much lower than it was in aerobic conditions.

The transition from a high rate to a low one is not instantaneous, of course; there are probably small anaerobic pockets in the predominantly aerobic zone, and they increase in size as the water table is approached (figure 1; Clymo & Hayward 1982). However, in terms of the life of a peat mass the transition *is* sharp. It is obvious, therefore, that the time that elapses before the water table (in summer) rises and engulfs the dead plant matter is important, because it is during this time that decay is relatively rapid. From the point of view of the plant material the acrotelm is a dangerous place and the time needed for the plant material to be rescued by the rising water table, and to be incorporated in the relative safety of the catotelm, is likely to be important in determining the rate of peat accumulation.

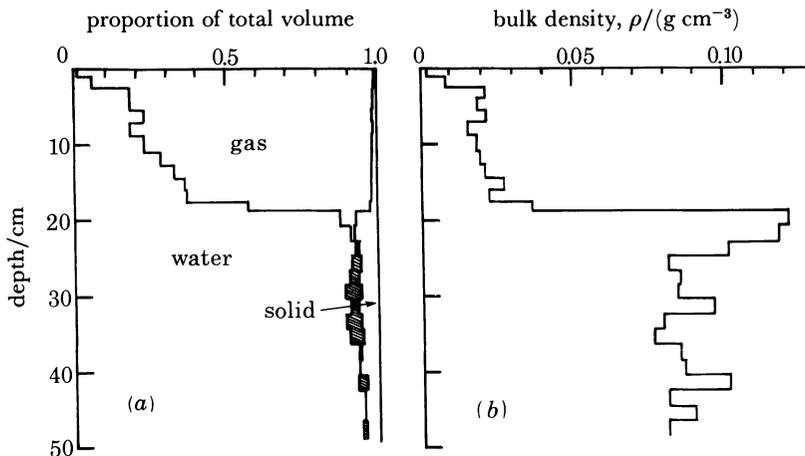


FIGURE 1. (a) Proportion of volume occupied by water, gas and solid in a core of *Sphagnum magellanicum* peat from Anghult, south Sweden (latitude  $15^{\circ} 21' E$ , longitude  $50^{\circ} 57' N$ ). (b) Bulk density in the same profile.

The core was collected with a 20 cm diameter steel tube by a method which retains the water in position (Clymo 1983). The hatched area in (a), where the sum of water and solids exceeds the total measured volume, gives a measure of the inaccuracy in measurements (mostly in total volume).

There is one very simple and obvious fact about peat-accumulating systems that is worth mentioning here, and that is developed later. Plants grow on the surface, and the process of primary production adds mass at the surface. If the layer of peat is thin then this addition exceeds the total loss by decay *at all depths* and peat accumulates. But if the peat layer is thick and if decay does continue in the catotelm – however slowly – there must inevitably come a time when the integrated loss at all depths approximately balances the gain of dry matter at the surface. A steady state is approached in which there is no further net gain and no further increase in the depth of the peat.

In what follows I consider first the processes in the acrotelm, then those in the catotelm, then the two combined.

### 3. THE ACROTELM

#### (a) Decay

The terms decay, decomposition, breakdown and humification are rather vague and have overlapping meanings. Collectively, and with varying emphasis, they include at least three processes: (i) loss of organic matter as gas or in solution, (including leaching) and by removal

by small invertebrates; (ii) loss of physical structure; and (iii) change of chemical state, including those changes mediated by microorganisms. In what follows decay is used for the first of these – loss of organic matter – though it often results in loss of structure too. Humification is used to describe the chemical changes.

Estimates of the rate of decay near the surface of peat bogs, and of the way in which it is influenced by the nature of the plant material and by external factors, are summarized by Heal & French (1974); Clymo (1978); Heal *et al.* (1978); Flanagan & Bunnell (1980); Heal *et al.* (1981) and Clymo (1983). The decay rate coefficients range from about  $0.01 \text{ a}^{-1}$  to about  $0.8 \text{ a}^{-1}$ . The causes of differences in rate, whether they are among species, among organs, among chemical constituents, or of the same material with time, are not particularly important for the present purpose. What is essential is to be able to give a quantitative description of the changes in the amount of matter left. Decay rate probably fluctuates cyclically with a period of 1 day and 1 year. These fluctuations are probably fairly regular, though there are few cases where rate has been followed in such detail or for more than 1 or 2 years. The age of the base of most peat deposits is measured in thousands of years however, so the accumulation process probably ignores these high frequency oscillations.

Two descriptions of the time-course of decay have been commonly used. Imagine a mass,  $m_0$ , of newly formed plant matter, and consider what happens to it. The first description assumes that the rate of loss of mass is directly proportional to the original mass:

$$dm'/dt = -\alpha', \quad (1)$$

where  $m$  is the mass at time  $t$ ;  $\alpha'$  (dimensions  $\text{MT}^{-1}$ ), is the decay parameter; and prime indicates this linear assumption. It follows that

$$m' = m_0 - \alpha' t \quad (2)$$

(where  $m_0$  is the original mass). This equation implies that all the plant material will have been lost after  $m_0/\alpha'$  time units, and that a graph of  $m'$  against  $t$  is a straight line. This assumption has seemed implausible to many ecologists, and most have preferred to follow Jenny *et al.* (1949) and assume that the rate of loss is directly proportional to the amount of material remaining:

$$dm/dt = -\alpha m, \quad (3)$$

where  $\alpha$  (dimension  $\text{T}^{-1}$ ) is the decay parameter. This gives

$$m = m_0 e^{-\alpha t} \quad (4)$$

and implies three things: that there is always some of the plant material left, that the half-time for decay is  $-(\ln 0.5)/\alpha = 0.693/\alpha$ , and that a graph of logarithmically scaled  $m$  against  $t$  is linear.

What evidence is there against which the accuracy of these descriptions can be tested? Most of the estimates of decay rate have been made by the litter bag method. This entails disturbance at the start of measurements and unknown consequences of whatever method is used to assess the initial dry mass. These factors each decrease both accuracy and precision to an unknown extent. The measurements have rarely been continued for longer than 5 years (e.g. Heal *et al.* 1978). One exception is the measurements made by Baker (1972) on the moss *Chorisodontium aciphyllum* growing in nearly pure stands on moss-banks on the subantarctic Signy Island. As the moss grows so the dead remains decay, and the bulk density at first decreases. Eventually,

as Fenton (1980) showed, the weakened stems become unable to support the increasing mass above and gradually collapse into a horizontal position and the bulk density then increases. At about 20–30 cm depth the remains enter the permafrost layer, which is the catotelm in this case. Baker took 1 cm sections of moss from the top 10 cm, in which the stems were still vertical, and weighed samples. If the productivity remained nearly constant then the course of decay

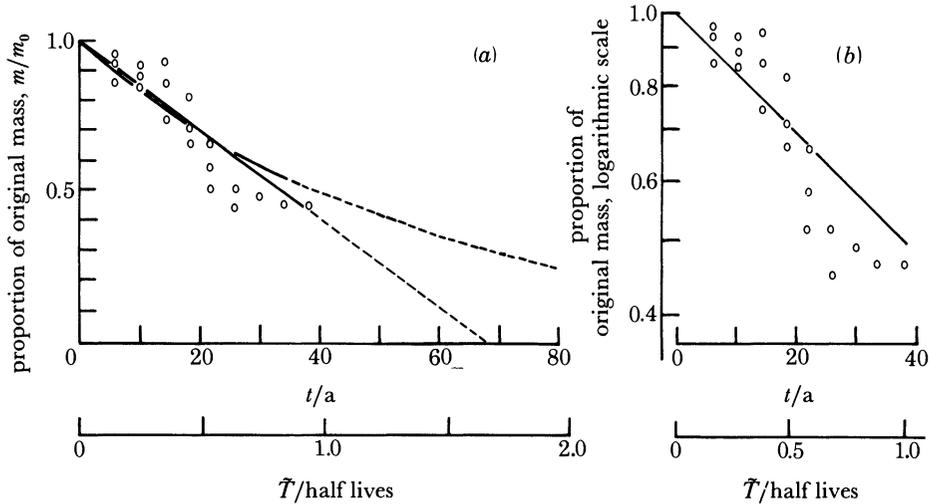


FIGURE 2. Decay of the moss *Chorisodontium aciphyllum* in the maritime Antarctic, from data of Baker (1972). Proportion of the original mass is shown on (a) linear scale and (b) logarithmic scale. The lines of best fit are constrained to pass through the point (0, 1.0). In (a), the straight line,  $\alpha'/m_0 = 0.015 \text{ a}^{-1}$ , represents the linear model (see text). The curved line in (a) and the straight line in (b), with  $\alpha = 0.017 \text{ a}^{-1}$ , represent the exponential model. The time axis is scaled in absolute units and in half-lives (for  $\alpha = 0.017 \text{ a}^{-1}$ ) for comparison with figure 3b.

could be followed with depth. That productivity *was* nearly constant is indicated by the nearly constant rate of extension growth estimated from innate markers in associated *Polytrichum alpestre* (Fenton 1980). It is then possible to convert the depth scale to a time scale. Baker (1972) estimated the rate of extension as  $3.3 \text{ mm a}^{-1}$ ; Fenton (1980) estimated  $2.4 \text{ mm a}^{-1}$ , and thought this was likely to be a small underestimate. If we assume  $2.5 \text{ mm a}^{-1}$  then Baker's measurements give the results shown in figure 2. They span about 40 years, and the method required no disturbance or pretreatment: it is unlikely that any method applied to peat will produce results of greater accuracy and precision, or covering a greater span of time. The lines of best fit according to equation 2 (figure 2a) and equation 4 (figure 2b) are shown. They are constrained to pass through the origin, as the equations imply, though it is more usual to fit a regression with intercept. The lines each account for about 0.98 of the variance, so there is no good reason to prefer one description to the other. Indeed both show systematic bias, the points seem to follow a reversed sigmoid curve, and extrapolation would be dangerous.

Litter bags entail more disturbance and are usable for a few years only, though this may be a substantial proportion of the time spent in the acrotelm. Two examples are shown in figure 3a. Decay of stems of *Calluna vulgaris* is slightly better described by the linear model than by the exponential one (when both are constrained to pass through the origin), though less than 0.25 of the mass has disappeared after 5 years, and both descriptions account for more than 85% of the variance. The reverse is true of leaves of *Rubus chamaemorus*: the linear description is poor and the exponential one is much better. The main reason why neither is particularly

satisfactory is that 0.16 of the mass disappears in the first 11 weeks – about 5% of the total time that loss was followed. If these first 11 weeks are ignored, both linear and exponential models are a much closer fit, and the exponential one particularly so, with little indication of bias. After 4 years about 0.7 of the original mass has disappeared, and by this stage of decay the remaining fragments are so small that some at least can fall out of litter bags, so the results are likely to be increasingly inaccurate.

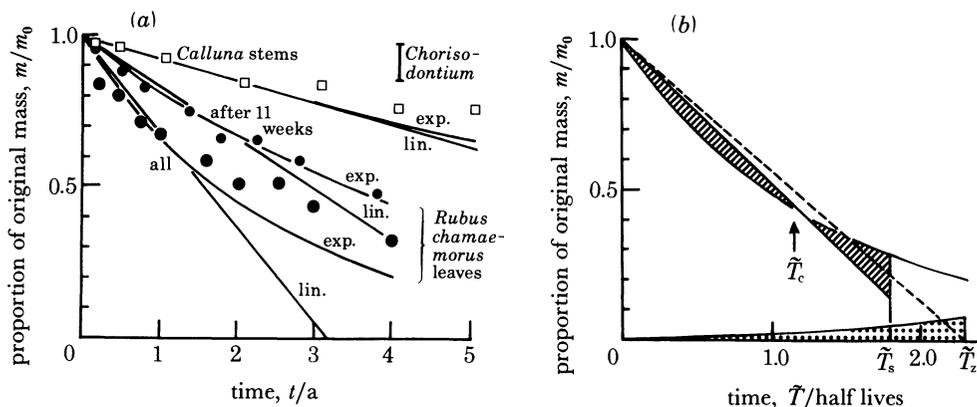


FIGURE 3. (a) Decay of stems of *Calluna vulgaris* (top), of leaves of *Rubus chamaemorus* (bottom), and of *Rubus chamaemorus* after the first 11 weeks (middle) from data of Heal *et al.* (1978). The lines are similar to those in figure 2a. The range for *Chorisdontium aciphyllum* after 4 years is shown for comparison. The decay parameter values and, in brackets, the proportion of variance accounted for are:

	$\frac{\alpha'/m_0}{a^{-1}}$	$\frac{\alpha}{a^{-1}}$
<i>Chorisdontium aciphyllum</i>	0.017 [0.98]	0.015 [0.98]
<i>Calluna vulgaris</i> stems	0.084 [0.92]	0.079 [0.87]
<i>Rubus chamaemorus</i> leaves	0.32 [0.67]	0.40 [0.93]
<i>Rubus chamaemorus</i> leaves (after 11 weeks)	0.17 [0.98]	0.20 [0.99]

(b) Comparison of linear and exponential models of decay. The time is in half-lives. The time  $\tilde{T}_s$  is chosen, and then the straight line that makes the two shaded areas equal is found (appendix). The intersection of linear and exponential lines is at  $\tilde{T}_c$ . At  $\tilde{T}_s = \tilde{T}_z$  the straight line intersects the  $m/m_0 = 0$  line. For all larger values of  $\tilde{T}_s$  some of the shaded area would be below this line, i.e. negative mass left. The slightly upward curving line bounding the stippled area shows the mean deviation between the lines as  $\tilde{T}_s$  is increased (see text and appendix).

The difficulty in distinguishing the linear and exponential descriptions depends therefore partly on the relative size of random errors and partly on the steadily increasing bias beyond about 70% loss of mass. It is useful therefore to investigate the relation between proportion of the original mass remaining and the mean deviation between linear and exponential models (equations 2 and 4). It is convenient to consider time,  $T$ , in units of half-life of the decay process. Figure 3b specifies this problem. Given a specific value  $\tilde{T}_s$ , what value must  $\alpha'$ , the linear decay parameter, take to make the shaded areas equal, and what is the mean deviation between the two lines? This problem is analysed in the appendix, and the mean deviation is graphed at the base of figure 3b. When half the original mass has gone, after one half-life, the mean deviation between the lines is 0.018; when 0.7 has gone the mean deviation is 0.04, and by the time that the straight line intersects the time axis – at  $T = 2.30$  half-lives – only 0.20 of the original mass remains (on the exponential assumption) and the mean deviation is 0.07. It seems clear that it is not only rarely possible to choose between linear and exponential

descriptions on the evidence that exists now, but also that it is unlikely that it ever will be easy to do so in field experiments.

Does the choice matter then? There are various estimates of the proportion of dry matter that is lost before it passes into the catotelm: Heal *et al.* (1975) conclude that 90% of the mass fixed during plant growth is lost in the acrotelm of an English blanket bog; Moore *et al.* (1975) give values for productivity and of rate of input to the catotelm of an Irish blanket bog, from which it seems that 94% is lost in the acrotelm; and Pakarinen (1975) suggests that 80–90% is lost in the acrotelm of a Finnish raised bog. All these values are some way beyond the 70% that is the most for which there is evidence about the time-course of decay: few results extend beyond 50% loss. The linear and exponential descriptions differ little between 0 and 50% loss, but between 50 and 90% loss they differ greatly.

There are also known to be very big differences in the rate of decay of different species, organs and chemical constituents (Clymo 1983) and the average values quoted here conceal big differences between components. For the slowly decaying components the choice of description may be less important than it is for the rapidly decaying ones, unless the rapidly decaying component disappears almost completely in any case, and this has consequences when an attempt is made to reconstruct the vegetation from which the peat has formed. The course of decay of a mixture of chemical components was considered by Minderman (1968). Curves such as those for *Rubus chamaemorus* in figure 3*a* were obtained. They give a poor fit if one assumes a single component with a single value for  $\alpha'$  or  $\alpha$ : it seems likely that the improvement in fit if the first 11 weeks of decay of *R. chamaemorus* leaves is ignored reflects the presence of a second component with a high rate of decay, or that is lost by leaching, and that makes up about 0.15 of the total mass (figure 4*a*).

In these circumstances it is perhaps surprising, and encouraging, that in so many cases the course of aerobic decay of a particular plant organ with all its chemical complexity, can be described fairly exactly to the point where about 0.4 of the original mass is left as if it were a single component following either linear or exponential kinetics. The *experimental* results do not encourage the adoption of more complicated postulates, such as the existence of a component that is totally refractory in aerobic conditions, and whose mass is approached asymptotically. But for simulation and for illustration of the sort of effects that may result with a mixture of different species in the surface vegetation we must include at least two components with different decay parameters, and, if more than 0.7 of the original mass may have disappeared, we must choose one particular model. Because the linear model predicts complete disappearance, and that seems implausible, I use the exponential model here. Although the detailed results differ, the general conclusions do not depend critically on this choice: almost any functional relation that shows a monotonic decrease in mass with time shows the same general features.

For a two-component system, the proportion,  $M/M_0$ , of the original mass,  $M_0$ , remaining (where  $M$  represents the sum of the mass of the components) is given by

$$M/M_0 = (m_{1,0} e^{-\alpha_1 t} + m_{2,0} e^{-\alpha_2 t})/M_0 \quad (5)$$

where  $m_{1,0}$  represents the mass of component 1 at zero time. Illustrative examples are shown in figure 4*a*. The first curve was chosen to give a fairly close fit to the *Rubus chamaemorus* data of figure 3*a*. In the second the rate of decay of component 1 was assumed to be reduced, though it was still five times that of component 2. After 3 years almost all of component 1 had gone.

An error in assessment of either the original mass or decay rate of component 1 ( $m_{1,0}$  or  $\alpha_1$ ) would therefore not be of much importance. In the third case, half the original material was in component 1, and the consequences of error in the values of the original mass or in the value of the decay parameter, or in both, would be much greater.

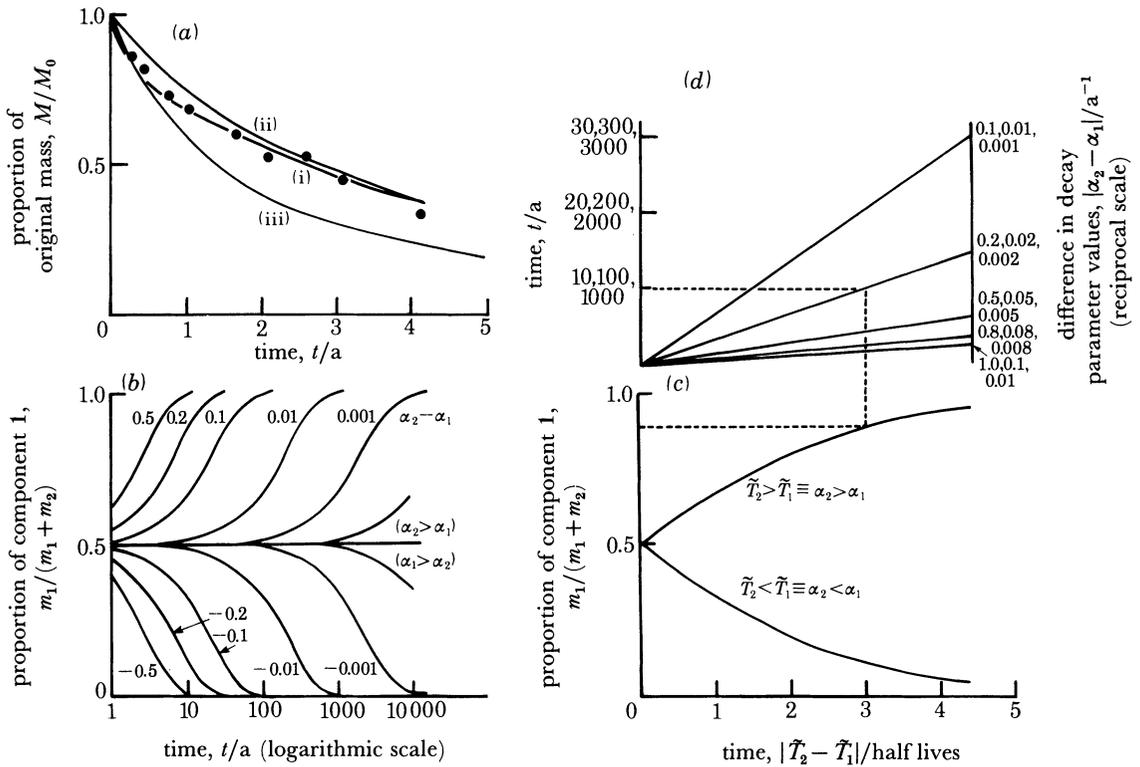


FIGURE 4. Differential decay of components in a two component mixture. (a) Time course of loss of mass. The initial proportion of the components and the decay parameter values are:

	$m_{1,0} M_0^{-1}$	$\frac{\alpha_1}{a^{-1}}$	$m_{2,0} M_0^{-1}$	$\frac{\alpha_2}{a^{-1}}$
(i)	0.15	10.0	0.85	0.20
(ii)	0.15	1.0	0.85	0.20
(iii)	0.50	1.0	0.50	0.20

The values for (i) give a fairly close fit to the *Rubus chamaemorus* data of figure 2a. The values in (ii) illustrate the effects of slower decay of component 1, and those in (iii) the additional effects of a larger proportion in component 2.

(b) The proportion of component 1, which starts (at  $t = 0$ ) as half the total mass, as a function of time for specified differences in the rate of decay,  $\alpha_2 - \alpha_1$ . The time scale is logarithmic and this transformation makes the curves sigmoid.

(c) The general relation (lower graph, see appendix) as in (b) but time scaled in units of the difference in half-life for the two components. Specific values of  $t$  and  $\alpha$  may be applied by starting on the upper graph (d) and following a line similar to that dotted for  $t = 10$  a,  $\alpha = 0.2$  a<sup>-1</sup>. The same result is obtained for any mutually reciprocal pairs of  $t$  and  $\alpha$ , for example  $t = 100$  a,  $\alpha = 0.02$  a<sup>-1</sup> and  $t = 1000$  a,  $\alpha = 0.002$  a<sup>-1</sup>.

In the general case where, for simplicity, each component is half the original mass, it can be shown (appendix) that the proportion at any time which component 1 forms of the total is given by

$$\frac{m_1}{(m_1 + m_2)} = \frac{1}{1 + e^{-\phi(T_2 - T_1)}}, \tag{6}$$

where  $T_1$  and  $T_2$  are the time expressed in half-lives of the two components and  $\phi = -\ln(\frac{1}{2})$ . This general case is shown in the graphs of figure 4c. The upper graph, (d) allows specific values for  $t$  and  $\alpha_2 - \alpha_1$ , to be chosen. Some of these specific cases are illustrated in figure 4b. The

time scale there is logarithmic, which makes the curves sigmoid. It is also the case (appendix) that by the time that the first component has come to form 0.8 of the total the product  $(\alpha_2 - \alpha_1)t \simeq 1.4$ . For peat which originally contained equal amounts of both components and where the difference in decay parameter values is, say,  $0.1 \text{ a}^{-1}$ , then after 14 years the ratio of the components will no longer be 1:1 but 4:1. After 28 years the ratio will be 16:1. The ratio increases as the *square* of the time (appendix, equation A 8).

The time before peat is engulfed by the rising catotelm is thus important not only because it controls the proportion of mass lost, but also because it has a big effect on selection between components. The length of this critical time in natural conditions is perhaps 10–100 years, and from figure 4*b* it can be seen that the components most affected by a small change in this time – those with a steep part of the graph in this range of time – are those with  $\alpha \simeq 0.01$ – $0.20$ . At Moor House, on north Pennine blanket bog at about 550 m altitude, this range includes most of the species in the surface vegetation except for *Rubus chamaemorus* and shoots of *Calluna vulgaris* (Clymo 1983, figure 4.24) that decay more rapidly and most of which probably do not survive, in recognizable form, their stay in the acrotelm.

(*b*) *Productivity on the surface*

As with decay, it is reasonable to ignore short term (daily, yearly) fluctuations. Longer term drifts probably occur and may be important. There are very few detailed measurements except on the subantarctic moss banks where Fenton (1980) showed that the mean rate of extension growth changed little in the top 30 cm, representing 100–150 years. Extension growth is not the same as dry matter production of course, and these data have already been assumed to indicate a constant rate of annual production so that the course of decay could be examined. Similar measurements can be made in favourable cases, on *Sphagnum capillifolium* and *S. fuscum* using innate markers (Malmer 1962; Clymo 1970; Pakarinen & Tolonen 1977; El-Daoushy *et al.* 1982), but again all that can be shown is that the rate of extension growth is approximately constant over a few tens to hundreds of years. There is strong evidence in the record of microscopic remains of plants in peat, however biased that record may be, that large parts of the surface of a particular peat bog have at some times been wetter than they have at others (e.g. Walker & Walker 1961; Casparie 1969; Barber 1981; Smart 1982). One estimate of productivity of adjacent pools, lawns and hummocks on the same *Sphagnum*-dominated bog gave values of 490, 380 and 240  $\text{g m}^{-2} \text{ a}^{-1}$  respectively (Clymo & Reddaway 1971) and independent estimates of productivity of a series of *Calluna*–*Eriophorum* dominated bogs in the same region gave values of 490–870  $\text{g m}^{-2} \text{ a}^{-1}$ . The median was 590  $\text{g m}^{-2}$  (Smith & Forrest 1978). In this single area there is thus a three to four fold range of productivity in different types of vegetation. For illustrative purposes however, I assume that the vegetation is unchanged and that productivity is constant from year to year. Any error in this latter assumption will become obvious later on.

(*c*) *A model for the acrotelm*

A general model for the acrotelm is one in which the rate of accumulation of dry matter per unit area,  $x$ , at any instant is determined by the rate of addition – productivity (per unit area) – and the integrated rate of loss per unit area at all heights,  $z$ , in the peat. For illustration I here assume a very simple specific model with a constant rate,  $p_a$ , of addition of plant dry mass at the surface, and decay at a rate proportional to the amount of mass at any time:

$$dx/dt = p_a - \alpha_a x \quad (7)$$

This model was used by Jenny *et al.* (1949), and has been assumed to hold for peat-forming systems innumerable times since. It has also been assumed to hold for mineral soils rich in organic matter (Maltby & Crabtree 1976). The solution is

$$x = \frac{p_a}{\alpha_a} (1 - e^{-\alpha_a t}) \quad (8)$$

TABLE 1. STEADY STATE,  $p/\alpha$ , DEPTH OF PEAT EXPRESSED IN TWO WAYS: AS CUMULATIVE MASS PER UNIT AREA,  $x$  ( $\text{g cm}^{-2}$ ); AND AS DEPTH,  $z$  (cm), ASSUMING THAT THE PEAT HAS BULK DENSITY,  $\rho$ , OF  $0.05 \text{ g cm}^{-3}$

(The peat is assumed to accumulate according to the equation  $dx/dt = p - \alpha x$  i.e. that  $x = p\alpha^{-1} (1 - e^{-\alpha t})$ . Improbable combinations of  $p$  and  $\alpha$  are omitted; appropriateness to the acrotelm and catotelm are shown by subscripts and and c respectively.)

$\frac{p}{\text{g cm}^{-2} \text{ a}^{-1}}$	$\frac{\alpha}{\text{a}^{-1}}$							
	0.1		0.01		0.001		0.0001	
	$\frac{x}{\text{g cm}^{-2}}$	$\frac{z}{\text{cm}}$	$\frac{x}{\text{g cm}^{-2}}$	$\frac{z}{\text{cm}}$	$\frac{x}{\text{g cm}^{-2}}$	$\frac{z}{\text{cm}}$	$\frac{x}{\text{g cm}^{-2}}$	$\frac{z}{\text{cm}}$
0.1	$1_a$	$20_a$	$10_a$	$200_a$	—	—	—	—
0.01	$0.1_a$	$2_a$	$1_a$	$20_{ac}$	$10_c$	$200_c$	$100_c$	$2000_c$
0.001	—	—	$0.1_c$	$2_c$	$1_c$	$20_c$	$10_c$	$200_c$

and is shown in figure 5. At first the mass of peat accumulated increases rapidly. But the greater the mass that has accumulated the greater the rate of loss from the whole mass, and because  $p_a$  is constant so the rate of accumulation,  $dx/dt$ , declines. Eventually, when  $x$  is large enough,  $p_a$  is just balanced by  $\alpha_a x$  and the rate of accumulation is zero even though  $p_a$  has not changed. The bog surface may appear to be green and healthy, the plants may be growing fast, and *yet the overall rate of peat accumulation is zero*. The bog as a whole is not growing. Formally, as  $t \rightarrow \infty$ ,  $dx/dt \rightarrow 0$  and  $x \rightarrow p_a/\alpha_a$ . Table 1 shows values of this steady state depth. (The symbols  $p$  and  $\alpha$  are not subscripted there because some are appropriate to the acrotelm and some to the catotelm.) Figure 5 illustrates cases with the same asymptotic (steady state) value of  $x$  but different values, appropriate for the acrotelm, of  $p_a$  and  $\alpha_a$ . One of these is based on the values for the blanket bog at Moor House:  $p_a \simeq 450 \text{ g m}^{-2} \text{ a}^{-1}$  and a median value of  $\alpha_a = 0.15$ .

The collapse of plant structure and the consequent raising of the water-table (or the existence of permafrost below a seasonally unfrozen layer) may prevent the acrotelm reaching the asymptotic limit. The acrotelm has a particular depth, less than this limit, that may be equated with a particular accumulated mass. The specific value of this mass depends on the nature of the plants and on the water supply, among other factors. The essential characteristic of a peat-accumulating system is that *the acrotelm does not manage to get very close to the asymptotic mass,  $p_a/\alpha_a$* . But it may nevertheless, in a generally stable (though not of course constant) climate, reach a steady state in which there is a balance between on the one hand the rate of addition,  $p_a$ , and on the other hand the rate of loss by decay and *by submergence by the rising catotelm*. From the point of view of the catotelm this rate of input from the bottom of the acrotelm is the exact analogue of the productivity at the surface of the acrotelm, and it seems appropriate therefore to represent this by  $p_c$ . Formally,

$$dx_a/dt = 0 = p_a - \alpha_a x_a - p_c. \quad (9)$$

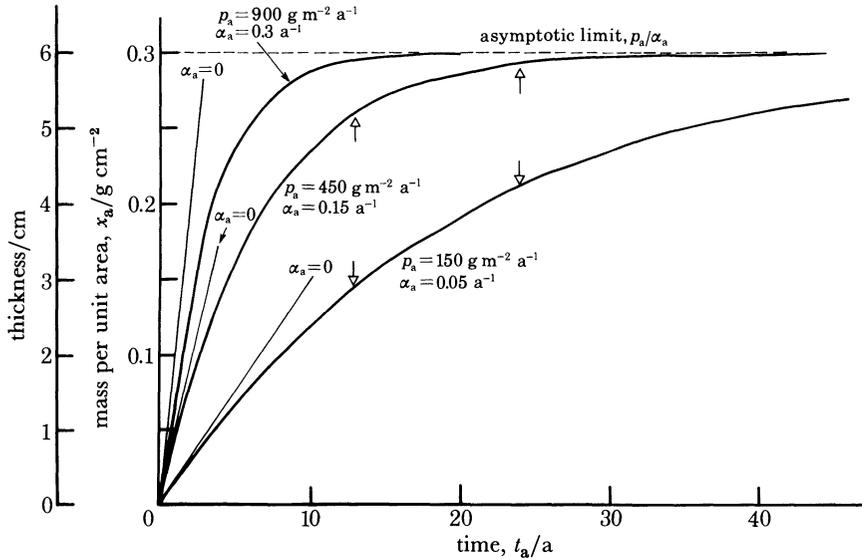


FIGURE 5. Accumulation of mass to the same asymptotic limit for three combinations of productivity,  $p$ , and decay parameter,  $\alpha$ . The straight lines show the result if there were no decay i.e.  $\alpha = 0$ . The values of  $p$  and  $\alpha$  span the likely range for peat bogs. The depth scale is calculated on the assumption that the bulk density,  $\rho$ , is  $0.05 \text{ g cm}^{-3}$  (figures 1 and 12 and Clymo 1983). Arrows indicate example values referred to in the text.

The problem of peat accumulation may now be seen from a different point of view. There is an acrotelm, of fairly constant depth and mass. It generates new plant matter and modifies the amount selectively, both in species-composition and in chemistry, and then passes the modified mass on at a characteristic depth and after a characteristic time to the catotelm. The acrotelm acts as a distorter of the input to the catotelm. A numerical example illustrates these points. Suppose that the bog surface vegetation has two components that have  $p_a = 450$  and  $150 \text{ g m}^{-2} \text{ a}^{-1}$ , and  $\alpha_a = 0.15$  and  $0.05 \text{ a}^{-1}$  respectively. These are two of the cases shown in figure 5, and may be imagined as *Eriophorum vaginatum* shoots and *Sphagnum papillosum* respectively. The asymptotic value is that of the sum of the components:  $6000 \text{ g m}^{-2}$  or about 12 cm depth if the bulk density,  $\rho$ , is  $0.05 \text{ g cm}^{-3}$ . Suppose the acrotelm is actually only 10 cm deep ( $5000 \text{ g m}^{-2}$ ). The point at which the sum of the components has this value (figure 5, right arrows) is reached after 24 years, and this is the average time that plant matter spends in the acrotelm. By that time (equation 6) the mass of the three fold more productive component is only 0.58 (rather than the initial 0.75) of the total acrotelm mass, and the rate of transfer to the catotelm,  $p_c$ , is  $12 \text{ g m}^{-2} \text{ a}^{-1}$  compared with  $45 \text{ g m}^{-2} \text{ a}^{-1}$  from the originally less productive component. For the two components together  $p_c = 57 \text{ g m}^{-2} \text{ a}^{-1}$ , and is about 0.10 of the original combined  $p_a$ . An increase or decrease of 2 cm in the depth of the water-table (i.e. of the acrotelm) has a very marked effect on the values resulting from these calculations. If the depth is increased by 2 cm  $p_c$  becomes equal to 0: there is no catotelm. If the depth is decreased by 2 cm (figure 5, left arrows) the time for passage through the acrotelm becomes 13 years; the more productive component is 0.64 of the total mass in the acrotelm; the component values of  $p_c$  are 64 and  $78 \text{ g m}^{-2} \text{ a}^{-1}$ —a total about 2.5 times that in the first example and about 0.24 of  $p_a$ . These matters may be stated formally. Equation 9 is easily rearranged to give the time,  $t_A$  that plant matter spends passing through the acrotelm. Let the mass in the acrotelm (per unit area) be  $x_A$  and the depth be  $z_A$ , defined by  $z_A = x_A/\rho_a$ ,

where  $\rho_a$  is the mean bulk density of dry matter in the acrotelm – about  $0.05 \text{ g cm}^{-3}$  (Clymo 1983). Then

$$t_A = -\ln(\alpha_a x_A/p_a - 1)/\alpha_a. \quad (10)$$

At the steady-state, when  $dx_a/dt = 0$  (equation 9) then the rate of input to the catotelm is given by

$$p_c = p_a e^{-\alpha_a t_A} \quad (11)$$

#### 4. THE CATOTELM

##### (a) A model for the catotelm

Direct measurements of the values of ‘productivity’,  $p_c$  in the catotelm, or of the way in which rate of decay changes with time, do not exist. Indeed many commentators assume either explicitly, or implicitly when they use  $^{14}\text{C}$  ages to calculate ‘peat accumulation rates’ that there is no decay. Indirect methods must be used therefore: one may assume that particular processes are occurring, calculate what would be expected, and then compare measured values with calculated ones.

The simplest assumption is that processes in the catotelm are similar to, but much slower than, those in the acrotelm. Formally

$$dx_c/dt_c = p_c - \alpha_c x_c \quad (12)$$

and therefore,

$$x_c = \frac{p_c}{\alpha_c} (1 - e^{-\alpha_c t_c}) \quad (13)$$

where the subscript c refers to the catotelm and time runs from that when the catotelm began to form i.e.  $t_c = t - t_A$ . Figure 6 illustrates the accumulation of peat in constant conditions. The vertical position in terms of mass,  $x_c$ , of peat newly formed at a particular time  $\hat{t}$  when there was  $x_{c,\hat{t}}$  of peat, is calculated from

$$x_c = x_{c,\hat{t}} e^{-\alpha_c(t-\hat{t})}. \quad (14)$$

The older the peat mass, the faster a newly incorporated piece of peat sinks down, because mass is being lost by decay of all the accumulated peat below, and the larger the accumulated mass the greater the speed of descent, tending towards  $p_c$  as the asymptotic mass is approached after a long time. It is not easy to determine whether a particular peat mass has come close to the asymptotic limit, and fortunately it is unnecessary to do so. The time in the catotelm,  $t_Q$ , needed for a proportion  $Q$  of the asymptotic mass to have accumulated is

$$t_Q = -\ln(1 - Q)/\alpha_c. \quad (15)$$

For  $Q = 0.86$ ,  $t_Q = 2/\alpha_c$ . So for  $\alpha_c = 0.0005 \text{ a}^{-1}$ , as in figure 6,  $t_{0.86} = 4000$  years. This calculation may be used in reverse: if the peat has been accumulating for 4000 years and is thought to be near its asymptotic limit, then the value of  $\alpha_c$  must be at least as large as  $0.0005 \text{ a}^{-1}$ . This is a very small value *but it is not negligible*: if it were half this value the asymptotic limit  $p_c/\alpha_c$ , and the value of  $t_Q$  would both be doubled. Conclusions about  $t_Q$  depend on  $\alpha_c$  but not on  $p_c$ : decay is the only variable. The right end of figure 6, which represents a profile of a 5000 year old peat bog, shows that the age–depth relationship *is not linear*. The only way to make it so is to set  $\alpha_c = 0$ , or to involve a particular temporal change in  $p_c$  that exactly counters the effects of decay. It would be useful to be able to calculate the expected profile

of age against depth at any time as a function of  $p_c$  and  $\alpha_c$ , because there are many examples of  $^{14}\text{C}$ -dated peat profiles and these are potentially useful to test the catotelm model proposed here. This relation can be obtained (appendix) and is

$$X_c = \frac{p_c}{\alpha_c} (1 - e^{-\alpha_c T_c}) \tag{16}$$

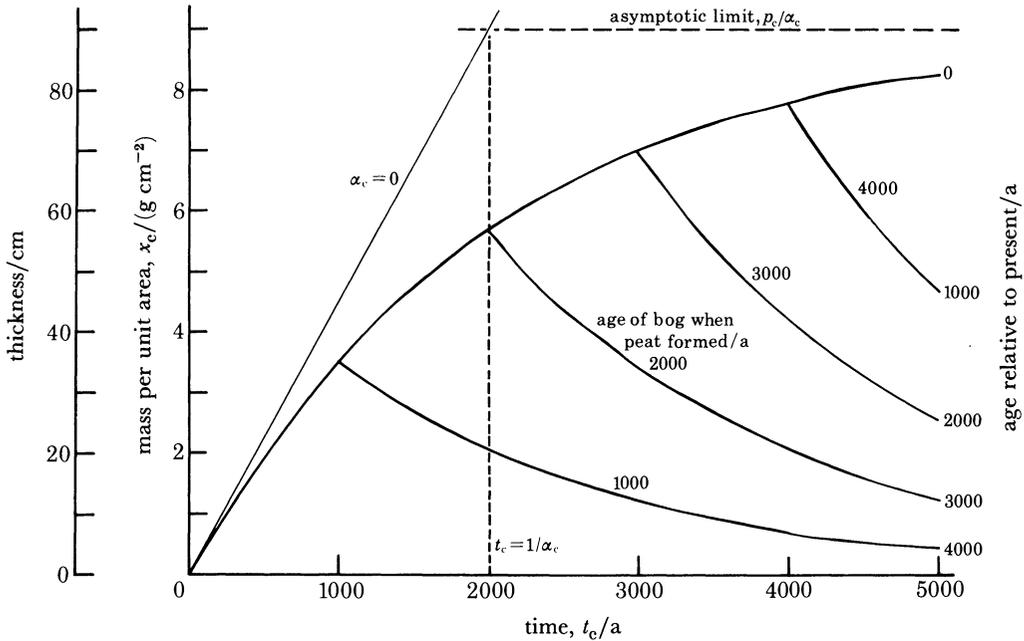


FIGURE 6. Accumulation of mass in the catotelm. Input to the catotelm,  $p_c$ , is  $45 \text{ g m}^{-2} \text{ a}^{-1}$  (one tenth of  $p_a$  in figure 5, centre curve). The decay parameter,  $\alpha_c$ , is  $0.0005 \text{ a}^{-1}$  ( $3/1000$  of  $\alpha_a$  in figure 5, centre curve). The depth scale is on the assumption that bulk density,  $\rho$ , is  $0.10 \text{ g cm}^{-3}$ . Subsidiary lines show the vertical position of peat which entered the catotelm at 1000 year intervals. The increasing rate of descent is because as time passes there is an increasing mass of peat below the top, and with a fixed value of  $\alpha_c$  the total rate of loss is greater. The straight line is for  $\alpha = 0$ ; at the place where it intersects the horizontal asymptote  $x_c = p_c/\alpha_c$ , then  $t_c = 1/\alpha_c$ .

where  $X_c$  and  $T_c$ , corresponding to  $x_c$  and  $t_c$ , are the mass and age of peat *below* an arbitrary datum in the catotelm. The structure of this equation is the same as that of equation 13 for mass accumulated after a given time, but time has in effect been redefined to run backwards, thus giving age. This result is not as obvious as it seems, but it is important because it shows that there is no need to know exactly when peat formation began, or to assume that  $p_c$  and  $\alpha_c$  have always been constant: all that is necessary is that they shall have been constant over the (arbitrary) time under consideration. Nor is it necessary to know where the present surface of the catotelm is: the arbitrary datum may be taken at any depth, and other values of mass and age expressed relative to that depth. The minimum information needed to calculate the values of  $p_c$  and  $\alpha_c$  is the age at three depths, and the mass of peat between any two of these levels (appendix). This procedure is likely to be unsatisfactory unless the samples are far apart, because of random errors in sampling the peat and in estimating the age. But if the samples are far apart one remains uncertain of what was happening in between them. There could be a hiatus, as, for example, there seems to be in the Red Sike Moss and Weelhead profiles in Teesdale (Turner *et al.* 1973). It is better to have a series of samples and to fit equation 16 by a minimization technique (appendix). This gives not only an estimate of the values of  $p_c$  and

$\alpha_c$ , but also a test of the assumption that they have been constant over a long time and that the rate of decay is a constant proportion of what is left, i.e. that equation 16 is followed. For a satisfactory test one needs several  $^{14}\text{C}$  ages, known stratigraphy, and a measured profile of bulk density, so that  $X_c$  may be calculated. In only a few cases have all three been described for the same profile: *too rarely has the profile of bulk density been recorded although it is easily measured*. All that is necessary is to take a complete set of samples of known volume, dry them and weigh them. For reasons discussed later it is also necessary that the profile be taken near the centre or highest part of the bog.

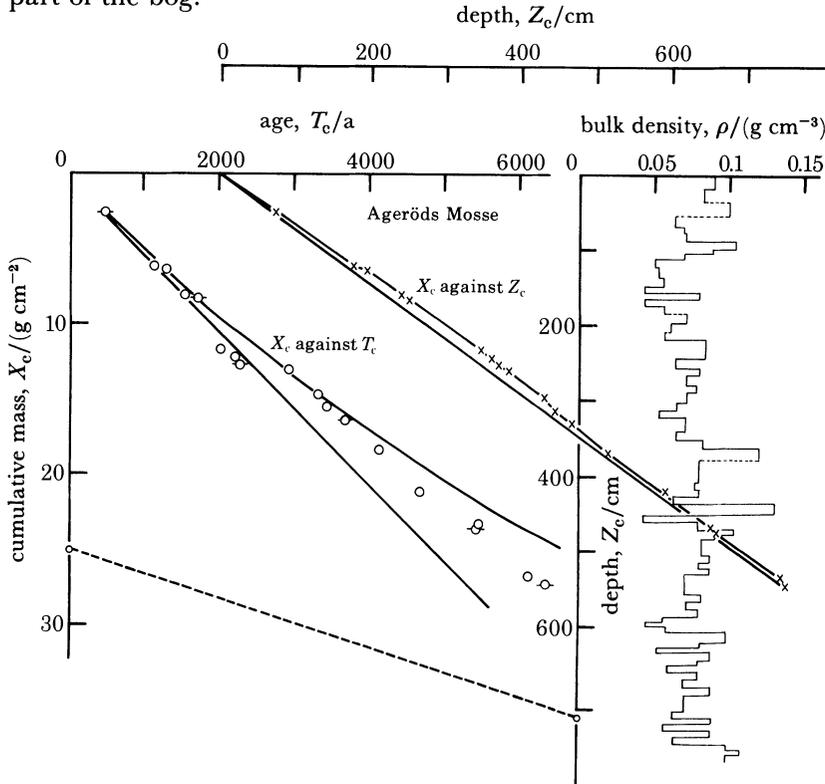


FIGURE 7. Profile, for Ageröds Mosse, south Sweden, of corrected  $^{14}\text{C}$  age against depth as cumulative mass below the surface. The diverging lines are 95% confidence limits on equation 16 using the parameter estimates in table 2. Representative points have the  $^{14}\text{C}$  counting error shown as a horizontal bar. The histogram is of bulk density against depth as distance and the diagonal line of crosses shows the relation between depth as distance and as cumulative mass; the diagonal line allows non-linearity in this relation to be assessed: it represents bulk density of  $0.069 \text{ g cm}^{-3}$ . The dashed line at the bottom links corresponding points on the two depth scales. Data of Nilsson (1964 and unpublished).

The five cases where all four requirements are met are the south Swedish Ageröds Mosse (Nilsson 1964 and personal communication), and four Finnish bogs: Laaviosuo (Tolonen 1979); Kaurastensuo and Munasuo (Tolonen 1977); and Varrassuo (Tolonen 1966, 1979; Donner *et al.* 1978). In other cases the  $^{14}\text{C}$  age and stratigraphic profiles but not that of bulk density are known. The discussion that follows is restricted to the bog peat, i.e. that in which *Sphagnum* is an important identifiable constituent. The  $^{14}\text{C}$  age is not the same as the true age for a variety of reasons, summarized by Harkness (1979). In the analyses that follow the  $^{14}\text{C}$  age has been 'corrected' to dendrochronological age by using either the original author's own corrections or, if there are none, those of Clark (1975). No allowance is made for isotopic fractionation because, in most cases, no measurements were made. The error resulting from

this omission is probably unimportant. For the work described here the choice of calibration curve is not important either because the curves in common use are fairly similar (Clark 1975), and all enhance the concavity of depth against age curves. The representative error bars shown are those given by the authors: most are probably  $\pm$  one standard error in the counting. Clark (1975) points out that they underestimate the real error.

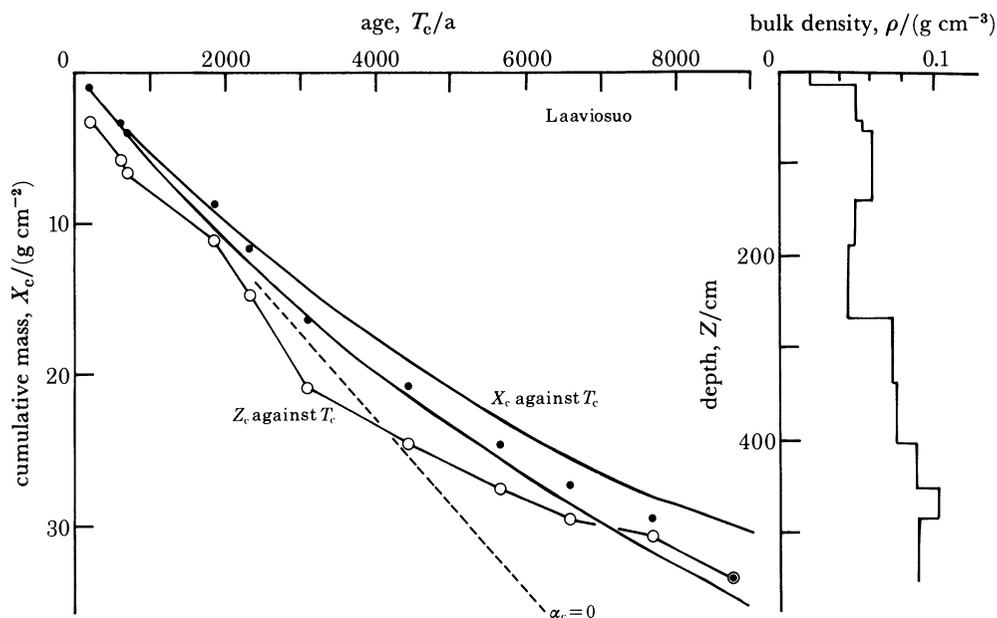


FIGURE 8. Profile for the catotelm of the peat bog Laaviosuo, south Finland, of corrected  $^{14}\text{C}$  age against depth as cumulative mass (filled circles, left axis) and depth as distance (open circles, right axis) below the surface. The diverging curved lines are 95% confidence limits on equation 16 using the parameter estimates in table 2. The histogram is of bulk density against depth as distance. The depth-as-distance axis is scaled so that the lowest measured points on both depth scales coincide, so that the smaller concavity of the curve on the depth-as-cumulative-mass axis can be seen. The broken diagonal line is that which would have resulted with the same value of  $p_c$  but no decay ( $\alpha_c = 0$ ). The asymptotic steady state ( $p_c/\alpha_c$ ) is  $52 \text{ g cm}^{-3}$ , corresponding to a depth of about 730 cm if the bulk density were  $0.1 \text{ g cm}^{-3}$  below 530 cm depth. Data of Tolonen (1979; table 1 and figure 7). No indication of counting errors is given there.

The most detailed of the profiles is that from Ageröds Mosse (figure 7). Bog peat began to accumulate about 6300 years ago. The bulk density fluctuates rather erratically about a mean value of  $0.07 \text{ g cm}^{-3}$ . The age against depth (both as distance, which is not shown, and as cumulative mass) relation is approximately straight except for a section between about 3000–1700 years ago which may indicate a phase of slower growth followed by an almost exactly compensating phase of more rapid growth. The stratigraphy of this section does not differ in a unique way from that in the rest of the profile. The lower 95% confidence limit is almost straight (it cannot become convex), the upper is markedly concave, but there is little reason for rejecting the hypothesis that there has been no decay ( $H_0: \alpha_c = 0$ ; table 2) since the plant material passed into the catotelm. But it is interesting to find that there is no evidence of a long term drift in  $p_c$  the rate at which plant matter has entered the catotelm. (It is possible of course that  $\alpha_c$  is not zero, and that  $\alpha_c$  and  $p_c$  have both varied in a complicated and fortuitously compensating way.)

The next most detailed of the profiles is that from Laaviosuo, for which there are 11  $^{14}\text{C}$  ages from 100–9000 years (figure 8). The age against depth (as distance) relation in this case is

markedly concave, and many authors have realized that this might be because the bulk density increases with depth. For example, Aaby & Tauber (1975) and Barber (1981) refer to the possibility of autocompaction, though an increase in bulk density is not necessarily caused by autocompaction. In figure 8 it is clear that bulk density does increase, rather irregularly, with depth. This tends to straighten the age against depth profile when depth is measured as cumulative mass (figure 8), but it is still some way from a straight diagonal line. The 95% confidence interval includes most of the measured points, and the profile is clearly not linear. The value for  $p_c$ , the rate of input to the catotelm, is about  $6 \times 10^{-3} \text{ g cm}^{-2} \text{ a}^{-1}$  (about 10% that of the values of  $p_a$  given earlier) and is similar to that at Ageröds Mosse (table 2). The value of  $\alpha_c$  is about  $1 \times 10^{-4} \text{ a}^{-1}$ . It is this very small decay rate that turns the curve towards an asymptotic steady state rather than allowing peat to accumulate indefinitely. If the bulk density,  $\rho$ , were  $0.1 \text{ g cm}^{-3}$  at all depths below that measured then the steady state depth would be about 7 m.

TABLE 2. ESTIMATES ( $\pm$  STANDARD ERROR) FOR FIVE PEAT BOGS, OF THE VALUE OF  $p_c$ , THE RATE OF INPUT TO THE CATOTELM, AND OF  $\alpha_c$ , THE DECAY PARAMETER, IN EQUATION 16, AND OF THE CORRELATION BETWEEN THE PARAMETERS

(The estimation method is described in the appendix. The values for Draved Mose were calculated in two ways: by assuming that bulk density was constant throughout ( $\rho = 0.1 \text{ g cm}^{-3}$ ); and by using the stratigraphic symbols to deduce the von Post humification index  $H$ , and from that the bulk density. See text for further explanation.)

	$\frac{p_c}{\text{g cm}^{-2} \text{ a}^{-1}}$	$\frac{\alpha}{\text{a}^{-1}}$	$n$	$r$
Ageröds Mosse	$5.0 \times 10^{-3} \pm 4.4 \times 10^{-4}$	$6.5 \times 10^{-5} \pm 4.6 \times 10^{-5}$	18	0.90
Varassuo	$5.7 \times 10^{-3} \pm 1.3 \times 10^{-4}$	$1.1 \times 10^{-4} \pm 7.4 \times 10^{-6}$	11	0.94
Kaurastensuo	$3.6 \times 10^{-3} \pm 9.0 \times 10^{-5}$	$5.5 \times 10^{-4} \pm 7.0 \times 10^{-6}$	8	0.96
Munasuo	$7.8 \times 10^{-3} \pm 1.9 \times 10^{-4}$	$3.0 \times 10^{-4} \pm 1.3 \times 10^{-5}$	5	0.97
Draved Mose	$6.4 \times 10^{-3} \pm 2.8 \times 10^{-4}$	$1.9 \times 10^{-4} \pm 2.0 \times 10^{-5}$	55	0.95
( $\rho = 0.1 \text{ g cm}^{-3}$ )				
Draved Mose	$5.3 \times 10^{-3} \pm 4.0 \times 10^{-4}$	$1.4 \times 10^{-4} \pm 3.4 \times 10^{-5}$	55	0.91
( $\rho$ from $H$ )				

Other examples, all from southern Finland, are shown in figure 9. All show the same general concavity, and no more than a threefold range in  $p_c$  and  $\alpha_c$  (table 2). The data for Varrassuo seem unreliable in detail: they show apparently significant reversals of the age against depth line in two places. There seems to be no obvious explanation of this, and the estimates of  $p_c$  and  $\alpha_c$  for this site are excluded from table 2. The asymptotic,  $p_c/\alpha_c$ , steady state depths, with the same assumptions as before, are 3.5 m (Munasuo) and 7 m (Laaviosuo).

The most detailed example of a  $^{14}\text{C}$ -age against depth profile is that for Draved Mose (Aaby & Tauber 1975). There is, unfortunately, no measured profile of bulk density, so a constant value of  $\rho = 0.1 \text{ g cm}^{-3}$  was first assumed, with the result shown in figure 10. The surface of the bog has been cut, and the 'present surface' dates from about 1200 A.D. The age against depth profile is concave again. How much of this concavity is a result of increasing bulk density at greater depths cannot be determined with certainty, but an estimate can be made in the following way. There is a generally linear relation (Clymo 1983) between bulk density and humification assessed on the  $H$  scale (von Post & Granlund 1926). Different sets of data give rather different equations (figure 12), but all have  $r^2 > 0.8$ , so the relationships are fairly useful predictive ones. Aaby & Tauber used the absorbance of the brown peat extract as a measure of humification, but the relation of this to the bulk density is not known. They do not record

the  $H$  values directly but they do incorporate them in their stratigraphic symbols, and these were used to deduce the bulk density, by using the central line of figure 12. (The other lines in figure 12 give very similar results.) The  $H$  profile in figure 11 is broadly similar to the detailed profile of 'humification' determined by the colorimetric method. The age against depth as cumulative mass curve (figure 11) is still concave, as the Finnish ones were, but as the Ageröds Mosse line was not, and the estimates of  $p_c$  and  $\alpha_c$  are similar to the Finnish ones too (table 2). Of greater importance is the fine detail shown in this profile. At five places (A–E in figures 10 and 11) there is apparently a period of several hundred years with very slow accumulation at the surface, followed by a short period of unusually rapid accumulation.

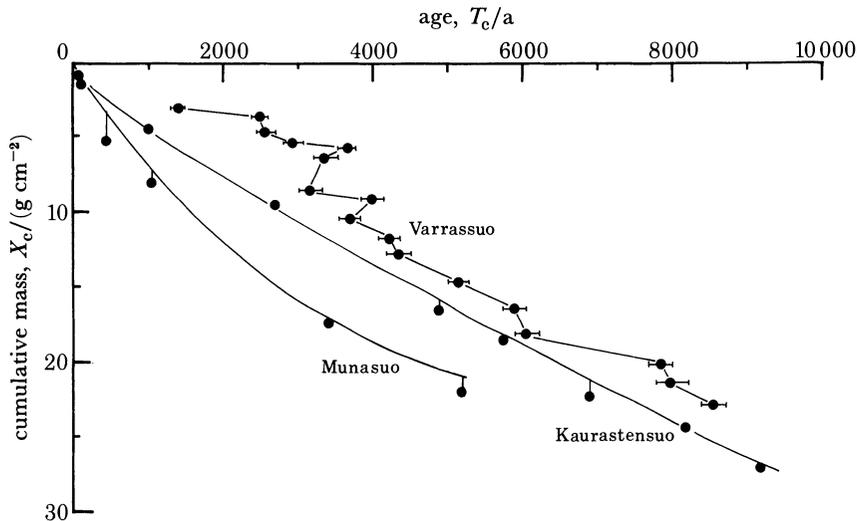


FIGURE 9. Profiles for the catotelm of three peat bogs in south Finland of corrected  $^{14}\text{C}$  age against cumulative mass below the surface. The continuous concave lines follow equation 16 and were fitted by the method described in the appendix. The parameter estimates are shown in table 2. Data for Kaurastensuo and Munasuo from Tolonen (1977) (no counting errors on  $^{14}\text{C}$  ages are given there) and for Varrassuo from Donner *et al.* (1978) and Tolonen (1979).

It would be wrong to argue that there have been no local changes in  $p_c$  and  $\alpha_c$ : the periods A–E and a mass of stratigraphic evidence already referred to, show that there are very important local changes in the peat. But the important feature of five of the six age against depth profiles in figures 8–11 is that, in spite of temporary fluctuations, there seems to be a common long-term trend and this cannot be explained by change in bulk density (whether caused by autocompaction or by other processes) as the concavity is present in profiles for which the depth is expressed as cumulative mass. It may be significant that Barber (1981) discovered to his surprise (p. 127 onwards) that the rate of accumulation of unhumified peat and of immediately underlying humified peat was much the same, in some cases at least. It may have been assumed too readily that humification is necessarily inversely correlated with the rate at which peat accumulates above and below a *sharp* transition.

There are several possible explanations for these concave curves. Any, or any combination of them, may be involved.

(1) The rate of input to the catotelm, may have increased over the long term, with superimposed short term fluctuations over several hundred years. There are three obvious possible causes of this, and they may operate individually or together:

(i) the productivity,  $p_a$ , may have steadily increased;

- (ii) the value of the decay parameter,  $\alpha_a$ , may have steadily decreased;
- (iii) the mean depth to the water table may have decreased, so that plant matter spends less time in the acrotelm, because the mean effective precipitation (i.e. precipitation – evaporation) has increased, or because the hydraulic conductance of the acrotelm has steadily decreased.

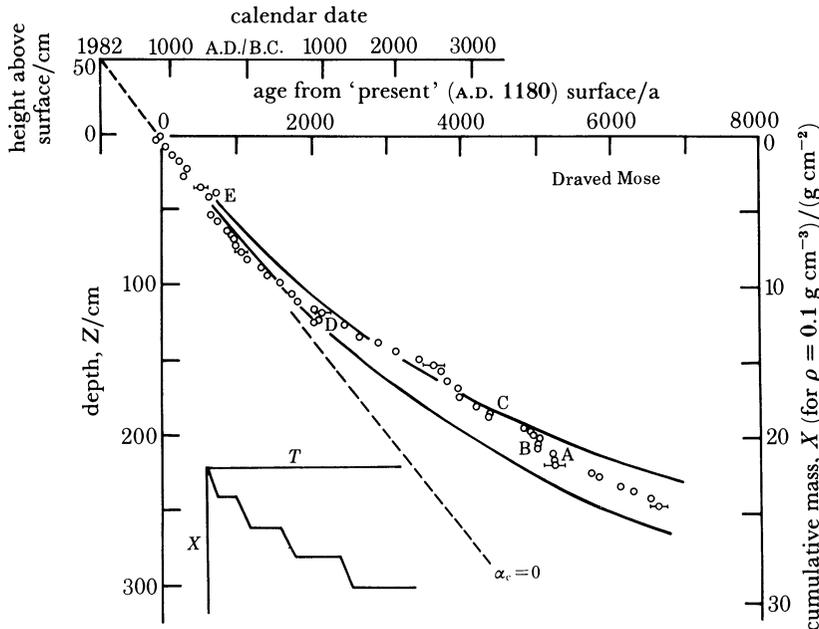


FIGURE 10. Profile for the catotelm of Draved Mose, Denmark, of corrected  $^{14}\text{C}$  age against depth as distance. The bulk density was assumed to be constant ( $0.1 \text{ g cm}^{-3}$ ). The diverging curved lines are 95% confidence limits on equation 16 using the parameter estimates in table 2. Representative points have the  $^{14}\text{C}$  counting error shown as a horizontal bar. The broken diagonal line is that which would have resulted with the same value for  $p_c$  but with no decay ( $\alpha_c = 0$ ). The asymptotic steady state ( $p_c/\alpha_c$ ) is at 337 cm depth. The surface of the bog has been cut, and the extrapolated surface of the catotelm 56 cm above the present surface is shown. A–E show places where there appears to have been a period of unusually slow growth followed by a period of unusually rapid growth – see text. Data of Aaby & Tauber (1975). Inset: hypothetical case with a series of periods of low or zero accumulation of steadily decreasing length. This pattern is *not* shown by the main graph.

The effects of climate are probably complicated. In cooler and wetter conditions one might expect (iii) to apply. If the cooler and wetter climate, operating directly and through (iii) caused an increase in the abundance of *Sphagnum* and a decrease in species such as *Calluna vulgaris* then (i) might occur at first, but probably not for long. The value of the decay parameter would become smaller – *Sphagnum* decays unusually slowly (Clymo 1983) – but such a change would probably be step-wise rather than ‘steadily’. To produce the regular concavity of the curves in figures 8–11 would require a fairly *steady* change of the sort described.

(2) The decay coefficient in the catotelm,  $\alpha_c$ , may have decreased steadily, with superimposed short term fluctuations.

(3) There may have been fairly frequent periods, of steadily decreasing length, during which input to the catotelm virtually ceased (figure 10, inset). That the halts were of decreasing length is essential, and they must not have been followed by compensating periods of increased  $p_c$ , i.e. they must not be of the form that periods A–E in figure 10 apparently were.

(4) The rate of input to the catotelm,  $p_c$ , and the value of the decay parameter,  $\alpha_c$ , may have been constant and the rate of loss of mass may have been proportional to the total amount of matter,  $X_c$ . (These are the assumptions made in fitting lines in figures 7–11.)

Mechanisms (1) and (3) are consistent with the assumption that there is no decay in the catotelm; (2) and (4) are not.

Almost all previous attempts to calculate so-called peat ‘accumulation’ rates have assumed that the first mechanism is the only one, without regard to causes (i)–(iii). Such calculations have assumed that there was no decay in the catotelm ( $\alpha_c = 0$ ), and when authors have realized that it is the depth as cumulative mass that is important they have usually assumed that the bulk density is constant. Of the mechanisms outlined above, the first three require a rather special tailoring of the changes in  $p_c$  and  $\alpha_c$  over a long period, 5000–9000 years, if they are to give a fairly good fit to equation 16. The fourth mechanism is engagingly parsimonious, but so is the steady state theory of the Universe.

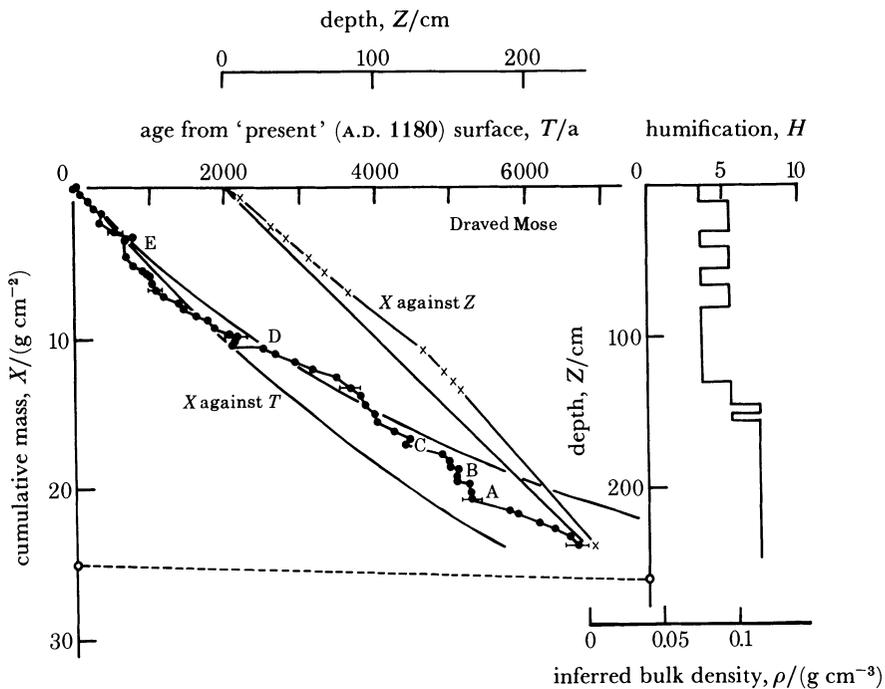


FIGURE 11. Profile for the catotelm of Draved Mose, Denmark, of corrected  $^{14}\text{C}$  age against estimated depth as cumulative mass below the surface. The diverging curved lines are 95% confidence limits on equation 16 using the parameter estimates in table 2 and calculated by the method described in the appendix. Representative points have the  $^{14}\text{C}$  counting errors shown as a horizontal bar. The asymptotic steady state ( $p_c/\alpha_c$ ) is shown by the horizontal line at  $33 \text{ g cm}^{-2}$ . The histogram shows the profile of humification ( $H$  scale, von Post & Granlund 1926) deduced from the stratigraphic symbols (Aaby & Tauber 1975). These were converted to bulk density using the central regression in figure 12, shown as the axis at the bottom. The straight diagonal line is the relation between the two depth measures for constant bulk density ( $0.1 \text{ g cm}^{-3}$ ) assumed in figure 10; the adjacent crosses are for the bulk density calculated from stratigraphic symbols used in this figure. The broken line at the bottom links corresponding points on the depth scales (compare figure 7). A–E as in figure 10.

At least these observations may clear the ground for reconsideration of the question of peat ‘accumulation’ rates and of the need for more detailed measurements. For example, figure 12 shows that there is a variety of types of profile of bulk density,  $\rho$ . A few resemble the Munasuo profile and are low (about  $0.04 \text{ g cm}^{-3}$ ) throughout. Most, however, show a general increase with depth, sometimes with step-wise increases. If humification usually increases with age, as appears to be the case, and if the increase in bulk density is an indirect consequence of chemical change, then the correlations of both the von Post humification,  $H$ , and  $\rho$  with the ‘rate of

peat depth accumulation' recorded by Tolonen (1979), are readily understandable as being no more than incidental correlates of age and of equation 16.

These concave age against depth-as-cumulative-mass curves are all from southern Fennoscandia. Are such patterns more widespread? There is some evidence to show that they are.

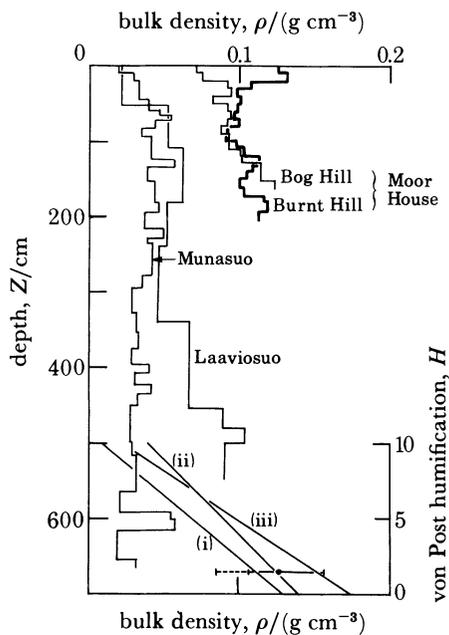


FIGURE 12. Representative profiles of bulk density,  $\rho$ , against depth as distance. At the bottom are three regressions between  $\rho$  (dependent variable) and von Post  $H$  value of humification (von Post & Granlund 1926). The horizontal bar shows the mean, standard deviation and extreme values of  $\rho$  for 45 assorted south Pennine peats (Tallis & Switsur 1973). Sources for bulk density profiles: Munasuo (Tolonen 1977); Laaviosuo (Tolonen 1979); Moor House, Burnt Hill (R. S. Clymo, unpublished); Moor House, Bog Hill (Jones & Gore 1978). Other examples are given in figures 7 and 8, and by Tolonen (1979) and by Jones & Gore (1978) though the tabular and graphic expressions of the same data by these last authors do not agree. Sources for  $\rho$  ( $\text{g cm}^{-3}$ ) against  $H$  regressions: (i) Tolonen (1979)  $\rho = 0.012 H + 0.01$ ; Clymo (1983) using data from Päivänen (1969)  $\rho = 0.10 H + 0.04$ ; (iii) Olsen (1968)  $\rho = 0.015 H + 0.023$ .

For example, Aaby & Tauber (1975) assembled the 'rate of depth accumulation' for  $^{14}\text{C}$ -dated levels in 24 raised bogs in northern Europe, and plotted these against age. There was a very clear indication of a concave trend, similar to those in figures 8–11. On the other hand, the data from 22 British peat bogs (Walker 1970) showed no clear pattern. (Walker used many pollen-dated horizons, and his figure 7 contains some points not in his table 9, and omits others that are in table 9. But the same conclusion holds for the full set of data.) There are a few other cases where more than ten  $^{14}\text{C}$ -dated horizons are recorded for a single peat bog, though the position of the cores on the bog is not clear. They are shown in figure 13. Featherbed Moss seems to be clearly concave, but the lowest four points were taken from a different site 24 km distant, and cross correlated on peaks in the proportion of *Plantago* pollen (Tallis & Switsur 1973). Scaleby Moss may be concave in the lower part (Godwin *et al.* 1957), with four groups of points, but the topmost group, which is about 1 m above all the others, is not on the concave line. Finally, Red Moss is nearly linear, but, as Hibbert *et al.* (1971) comment, 'the rate of growth of the deposit ... is seen to be not quite linear'. In none of these cases is the profile

of bulk density known, and if it were then the concavity would probably be reduced or even reversed.

There are a great many other cases where five to ten  $^{14}\text{C}$  ages and depths are recorded. In many of these there is some indication of a concave relationship, but the lack of a bulk density profile and the small number of dated horizons make these cases no more than suggestive.

The interest of those who study peat has, for good reasons, tended to concentrate on changes and differences within a peat profile. The possibility that some important processes have changed little in 5000 years or so has been neglected. We need more, and more detailed, age against depth-as-cumulative-mass profiles from a wide variety of locations.

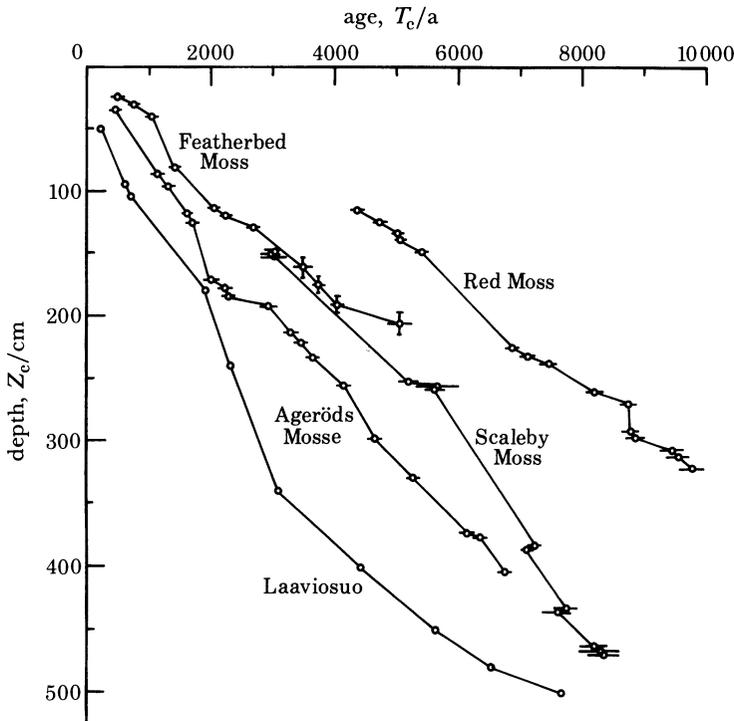


FIGURE 13. Profiles in the catotelm of three English peat bogs of the calibrated  $^{14}\text{C}$  age against depth as distance. The Ageröds Mosse and Laaviosuo data are repeated from figures 7 and 8 for comparison. Horizontal bars show the  $^{14}\text{C}$  counting errors. Sources: Laaviosuo (Tolonen 1979); Ageröd's Mosse (Nilsson 1964); Featherbed Moss (Tallis & Switsur 1973); Scaleby Moss (Godwin *et al.* 1957); Red Moss (Hibbert *et al.* 1971).

We may also ask: for what length of time is the model of equation 16 valid? To answer this question we need older, which probably means deeper, peat deposits for which the age against depth profile is known. Most deposits are less than 10 m deep, but a few are very much deeper. For example, Menéndez Amor & Florschütz (1964) and Florschütz *et al.* (1971) describe one at Padul in the Sierra Nevada of southern Spain that is 72 m deep, and van der Hammen *et al.* (1965) and Wijmstra (1969) describe another, Tenagi Philippon in northeastern Greece, that is at least 62 m, and perhaps as much as 120 m, deep. Both deposits have accumulated in unusual circumstances and contain alternating layers of 'peat with detritus' and 'calcareous mud' (also described as 'lake marl'). The deposits appear to span several glacial and interglacial periods, and at least one deposit shows no evidence of a hiatus. The profiles of  $^{14}\text{C}$  age against depth for the uppermost layers, which are all that can be dated by the  $^{14}\text{C}$  method, are shown in figure 14. None of the four accounts of the two sites gives any indication of the

nature of, or of the plants that formed, the peat, and the bulk density is not recorded. But it seems clear from figure 14 that these peats contained, or were transformed to contain, a component that is much more refractory than most of the original plant matter. Whether this fraction decays at an extremely slow rate or is totally refractory cannot, at present, be determined. There may be an infinite regress of progressively more refractory components. The

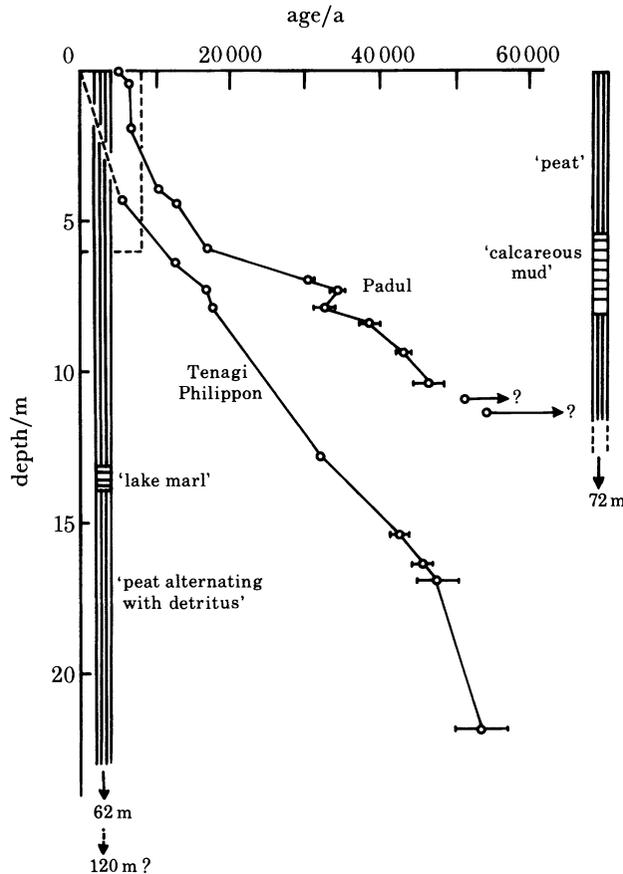


FIGURE 14. Profile of <sup>14</sup>C age against depth in two very deep peat deposits. The stratigraphy at the right and the upper curve are for a deposit at Padul in the Sierra Nevada of southern Spain (Menéndez Amor & Florschütz 1964; Florschütz *et al.* 1971). The deposit is 72 m deep and contains 15 alternating bands of 'peat' and 'calcareous mud'. The top 10 m are shown. The stratigraphy at the left and the lower curve are for a deposit at Tenagi Philippon, Greece (van der Hammen *et al.* 1965; Wijmstra 1969). The deposit is at least 62 m, and perhaps 120 m deep and contains alternating bands of 'peat alternating with detritus', 'very hard peat' and 'lake marl'.

The age and depth scales on this diagram are much smaller than those on earlier ones, the approximate boundary of which is shown by the broken line in the top left corner.

worst case is of a totally refractory component. Equation 16 may be supplemented with a term to describe this component which, notionally, enters the catotelm at a rate  $p_r$ , though it may in reality be produced by transformations within the catotelm. It is then the case that

$$X_c = \frac{p_c}{\alpha_c} (1 - e^{-\alpha_c T_c}) + p_r T_c \tag{17}$$

and when  $T_c$  becomes very large ( $> 50,000$  years) this gives

$$X_c \rightarrow \frac{p_c}{\alpha_c} + p_r T_c \tag{18}$$

From figure 14 it can be seen that this component probably forms considerably less than 1% of the original mass, but it does apparently allow the continued *very* slow accumulation of peat. If this were generally true of peat forming communities then the idea of a steady state depth in the very long term (more than 50 000 years) would be incorrect. It would have to be replaced by the idea that the 'steady state' depth is approached, apparently asymptotically, for about 50 000 years, but thereafter the depth continues to increase, albeit very slowly.

(b) *The fate of decayed plant matter*

If the rate of decay,  $\alpha_c$ , in the catotelm is finite though very small then it is necessary to explain how mass is lost from the system. Suppose the plant is transformed, either directly by very slow chemical reactions or indirectly through the activities of microorganisms, into soluble compounds. If these compounds stay in position they still contribute to the mass: if the mass is to decrease then they must leave the system. The hydraulic conductance of humified peat is small and the rate of flow of water and solutes through it is probably very low (Ingram 1982). Whether it is negligible or not is difficult to determine because the solution that has flowed through the catotelm is usually diluted by the generally much larger volume of solution that has flowed superficially through the acrotelm, which has a high hydraulic conductivity. We need measurements of the concentration of organic solutes in runoff at times of minimum discharge from a raised bog. Such measurements do not exist, but a crude calculation may be made by using measurements of the concentration of dissolved organic carbon in water from samplers in a blanket peat face (M. Hornung, unpublished results). The concentration was about 4–8 mg l<sup>-1</sup> for 12 weeks before the flow stopped for 6 weeks during a drought, and 11–17 mg l<sup>-1</sup> in the 6 weeks after the flow began again. The raised bog Dun Moss is hemi-elliptical in longitudinal section and of maximum depth 8.2 m (Ingram 1982). The mean depth is therefore  $8.2 \times \pi/4 = 6.4$  m. Suppose the peat were of average bulk density 0.1 g cm<sup>-3</sup> and that the improbably large amount of 500 mm of precipitation drained through the catotelm in a year and emerged with a dissolved organic carbon concentration of 10 mg l<sup>-1</sup>. The amount of carbon removed would correspond to  $\alpha_c = 2 \times 10^{-5} \text{ a}^{-1}$ . This is an order of magnitude less than the values of  $\alpha_c$  inferred from the age against depth curves (table 2).

The other obvious way by which mass might escape is upwards by diffusion or as gas bubbles. The concentration of methane is often high and it is well-known (e.g. Dalton 1802) that bubbles that can be ignited are present in waterlogged vegetable matter. If all the matter that decays is converted to methane, what is the likely rate of production in the catotelm? Suppose  $\alpha_c = 2 \times 10^{-4}$  (table 2), and that  $\rho = 0.1 \text{ g cm}^{-3}$ , then the volume rate of production of methane (at n.t.p.) is about  $0.028 \text{ cm}^3 \text{ cm}^{-3} \text{ a}^{-1} = 0.028 \text{ a}^{-1}$ . At 5 m depth, where the pressure is about  $1.5 \times 10^5 \text{ Pa}$ , the solubility of methane in water is about  $0.066 \text{ cm}^3 \text{ cm}^{-3}$ . Within a few years therefore the peat would become supersaturated with methane, and one would expect bubbles of gas to form. At 5 m depth these would be at a pressure of about  $1.5 \times 10^5 \text{ Pa}$ , and if they 'floated' upwards their volume would increase until they either redissolved in unsaturated parts of the peat profile or escaped from the surface. Diffusion would occur too. The diffusion coefficient of gases such as nitrogen, oxygen and hydrogen in water is about  $2 \times 10^{-5} \text{ cm}^2 \text{ s}^{-1}$ , which seems very small. But expressed in a more relevant unit of time it is  $630 \text{ cm}^2 \text{ a}^{-1}$ . The diffusion coefficient of methane in peat is about  $500 \text{ cm}^2 \text{ a}^{-1}$  (R. S. Clymo, unpublished results).

The full problem of the calculation of the profile of concentration of methane (and perhaps of the 20-fold more soluble carbon dioxide) is daunting. The main features to be included are

zero concentration at the surface of a slab of peat whose lateral extent is large compared with its thickness. The upper boundary of the peat moves slowly upward, following equation 16. Gas is produced continuously throughout the slab of peat and moves in three ways: by diffusion; by mass flow in solution in the interstitial water; and by mass flow upward in gas bubbles. The peat may rest directly on virtually impermeable rock, in which case the movement of gas is entirely upward or sideways. If the peat rests on a more permeable substratum there may be both diffusion and mass flow in solution downwards as well (Siegel 1983). For the present purpose – that of showing whether diffusion alone could remove the mass that has decayed – a much simpler problem, which can be solved analytically, is sufficient. Carslaw & Jaeger (1947) consider the temperature (analogous to concentration) in a slab of fixed thickness with heat (analogous to gases) being produced continuously throughout it, and with the temperature kept at zero at both faces of the slab. Heat produced just above the centre of the slab will all flow upwards, and that produced just below the centre will all flow downwards: the centre of the slab behaves as if it were impermeable to heat. The peat catotelm, of depth  $Z_c$ , and assumed to rest on an impermeable base, can be considered as the top half of the slab. After substitution and translation of the heat problem variables by the gas concentration ones we get the defining equation:

$$\frac{dC}{dT} = \frac{d}{dZ} \left( D \frac{dC}{dZ} + G \right), \quad (19)$$

and the solution of this (Carslaw & Jaeger 1947) is

$$C = \frac{G}{2D} Z(2Z_c - Z) - \frac{32Z_c^2}{\pi^3} \sum_{n=0}^{n=\infty} \frac{1}{(2n+1)^3} e^{-(D(2n+1)^2\pi^2 t/4Z_c^2)} \sin \frac{(2n+1)\pi Z}{2Z_c}, \quad (20)$$

where  $C$  is the concentration of gases in solution,  $G$  is the rate of gas production per unit volume of peat,  $Z$  (in the range  $0-Z_c$ ) is the depth below the top of the catotelm, and  $D$  is the coefficient of diffusion of gas in peat. As  $t \rightarrow \infty$ , the profile of  $C$  becomes

$$C \rightarrow \frac{GZ(2Z_c - Z)}{2D} \quad (21)$$

and at the peat base, where  $Z = Z_c$ , then,

$$C \rightarrow GZ_c^2/2D. \quad (22)$$

At the base the concentration is proportional to the square of the depth, inversely proportional to the diffusion coefficient,  $D$ , and directly proportional to the rate of production,  $G$ .

These equations were evaluated assuming that the gas was methane with the values of  $D$  and  $G$  already given above, to give the concentration profiles of methane in peats of different thickness after various times (figure 15). The proportion of all the methane produced that is still in the peat after various times is also shown.

The problem is rather artificially constrained, and the particular value of  $D$  may be inaccurate, but several points do seem to be clear.

(i) The profile of concentration is steeper the nearer the surface. (It appears relatively shallow in figure 15 because of the logarithmic scale.)

(ii) There is a steady state profile which is approached asymptotically with time. Within 1000 years the profile is not far from the final steady state one, so the lack of a moving boundary in the problem is not serious.

(iii) The proportion of all the methane produced which is still in the peat is high to begin with and declines asymptotically towards zero. After a long time the rate of methane efflux is nearly that of  $p_c$ .

(iv) After a long time in peat more than 50 cm down in the catotelm the concentration of methane calculated in this way exceeds, and at several metres depth greatly exceeds, the solubility of this gas in water. Even if there is some supersaturation, therefore, one would expect bubbles of gas to appear. If there are bubbles, then the profile of concentration of gas in solution in the supersaturated zone should be nearly linear – a consequence of Henry’s law.

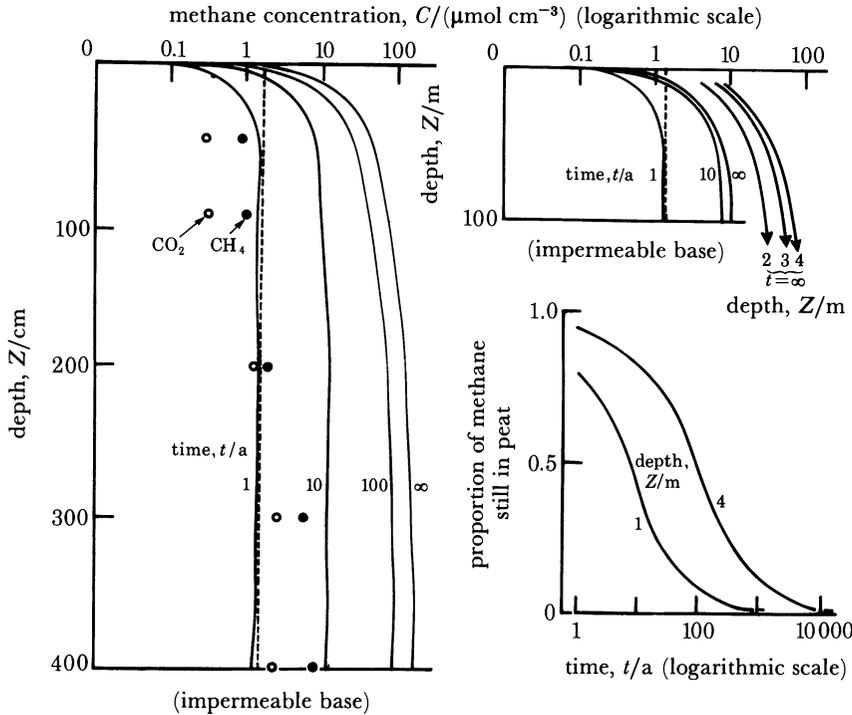


FIGURE 15. Calculated profiles of methane concentration, according to equation 20 and if the appearance of gas bubbles is ignored, after various times in a 4 m deep peat column (left) and a 1 m deep peat column (top right). The top 1 m of the limiting curves for three other depths is also shown at the top right. The dashed line shows the saturation limit for methane in water. On the 4 m graph are shown the concentration of methane (●) and of carbon dioxide (○) measured in peat from Coom Rigg Moss, Northumberland (see text). At the bottom right is shown the calculated proportion of all the methane produced that is retained in peat columns of two depths as a function of time.

The appearance of bubbles might increase the efflux (by mass flow) or decrease it (if the bubbles could not move through peat). But if the bubbles did not move then the base of the peat would, in time, become little more substantial than a foam. This does not happen and it seems probable, therefore, that a substantial amount of methane does escape in bubbles. Even if it did not do so, however, the material that has decayed could have moved to the surface by diffusion, and then escaped. All the observed carbon dioxide (figure 15) could remain in solution. The assumption that matter can escape from the peat – even deep peat – during decay thus seems to be plausible.

Indeed the existence of a greater concentration of methane at greater depths in the peat may now be used as evidence that decay *does* continue in the catotelm. The mere presence of methane

at depth is not sufficient: it could be 'fossil methane' formed just after the peat was engulfed by the catotelm and persisting *in situ*. But the efficacy of diffusion, illustrated in figure 15, is clearly such as to eliminate this possibility, and in any case an increasing concentration with depth could be explained only if there had been a dramatic decline in the rate of methane production.

It is not easy to collect adequate samples on which to measure the concentration of gases in peat, but a technique has been devised to do this (J. Claricoates, unpublished). The samplers were very thin rubber cylinders housed in a protective cage of expanded aluminium and connected to a long piece of thick-walled plastic tube. The cage and collapsed rubber cylinder were pushed down to a known depth in the peat, the cylinder was inflated with nitrogen calculated to expand it at the known pressure to its unstretched volume of 150 cm<sup>3</sup>, and the tube at the bog surface was stoppered. Gases in the peat diffused through the thin rubber into the gas phase in the collector. After several months the collector contents were transferred to a syringe and analysed by gas chromatography. The concentration in the gas phase is probably less than it is in the peat, but should be proportional to it, and this is sufficient for the present purpose. A representative profile is shown in figure 15: the concentration of methane *does* increase markedly with depth.

In short, it seems that decay at depth does continue, and that the gaseous products can probably escape by diffusion, aided perhaps by mass flow in solution and as bubbles.

#### 5. ACROTELM AND CATOTELM TOGETHER

The age of peat in the catotelm may be estimated from the concentration of <sup>14</sup>C, but reliable methods for establishing the age of peat in the acrotelm, in the range 1–200 years, are only now being developed. The moss-increment method (Malmer 1962; Clymo 1970; Pakarinen & Tolonen 1977) has been checked against the <sup>210</sup>Pb method by El-Daoushy *et al.* (1982), who show a profile of the top 90 cm of a hummock of *Sphagnum fuscum* on the Finnish peat bog Kunonniemensuo. In the lowest part (figure 16) there is satisfactory agreement between the age estimated by the moss-increment method, by <sup>14</sup>C dating, and of a single level identified by the appearance of cereal pollen and cross-dated by a varved sediment in an adjacent lake (Vuorinen 1978 and unpublished results). These data were fitted by the minimization technique described in the appendix to a model similar to that specified in equations 23 and 24, but with one component only. This model therefore contained four parameters representing productivity and decay in the acrotelm and catotelm:  $p_a$ ,  $\alpha_a$ ,  $p_c$  and  $\alpha_c$ . There were 22 dated levels, which leaves 17 degrees of freedom for the minimization. Eight different combinations of starting value and step size were tried. All but one converged on the same solution. (The odd 'solution' was a very poor fit and was clearly no more than a local minimum.) The best solution, though it was scarcely better than the other six, is shown in figure 16 and the parameter values are given in table 3.

The fit to the data is good; with four parameters and such a simple curve this is not surprising. An arbitrary polynomial with four parameters gave as good a fit. The relatively low precision of the parameter estimates results from this too. But the estimated values of  $p_c$  and  $\alpha_c$  fall in the range already found for the catotelm (table 2). The value of  $p_a$  (240 g m<sup>-2</sup> a<sup>-1</sup>) is in the likely range as well. The value of the acrotelm decay coefficient,  $\alpha_c$ , is 0.02 a<sup>-1</sup> which is lower than the values recorded for several temperate zone peat bogs, but in the range for Arctic ones

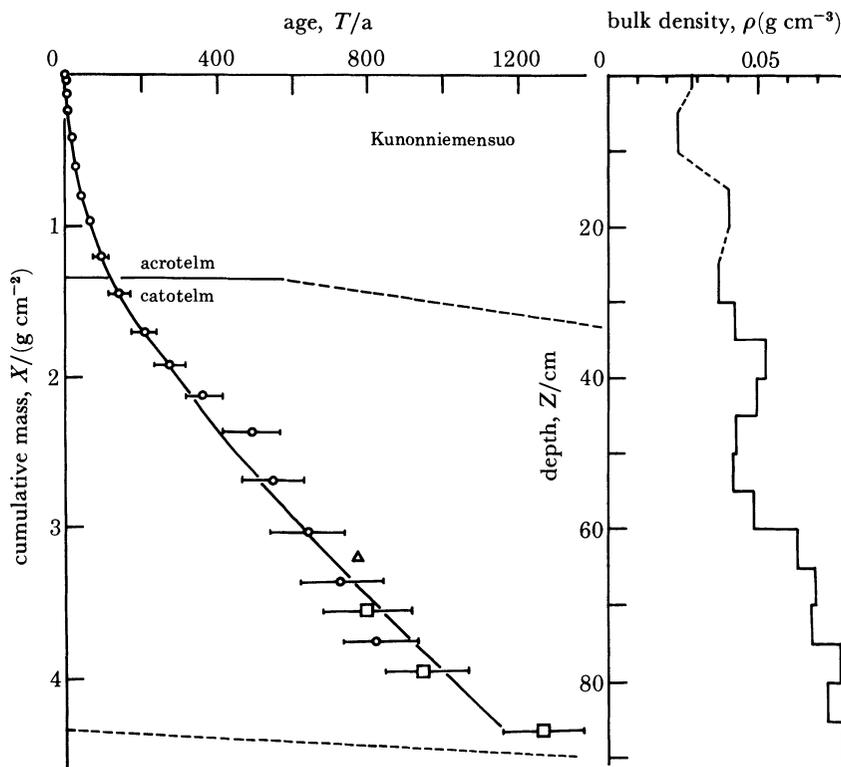


FIGURE 16. Profile for the acrotelm and catotelm of the peat bog Kunonniemensuo, southern Finland, of age against depth as cumulative mass below the surface, and of bulk density. The continuous line is that, estimated by the method described in the text, which gave the parameter values in table 3. Confidence limits are not given because some of the errors are not parabolic. Most of the age estimates were by the moss-increment method (El-Daoushy *et al.* 1982), that agrees well with the <sup>210</sup>Pb method on the same profile. Squares are <sup>14</sup>C estimates, and the triangle is for a horizon identified by the increase in cereal pollen (J. Vuorinen, unpublished results) and cross-dated to a varve-dated horizon in a nearby lake (Vuorinen 1978). Bars show the standard error. The horizontal full line shows the estimated boundary between the acrotelm and catotelm, at  $t_A = -\ln(p_c/p_a)/\alpha_a$ . The broken lines connect corresponding depths on the cumulative mass and distance scales. The bulk density values were supplied by K. Tolonen (unpublished results).

TABLE 3. ESTIMATES OF THE VALUE OF THE PRODUCTIVITY AND DECAY PARAMETERS,  $p_a$ ,  $\alpha_a$ ,  $p_c$  and  $\alpha_c$ , AND OF THEIR CORRELATION, FOR THE ACROTELME AND CATOTELME OF KUNNONIEMENSUO, FINLAND

(The age at 22 depths was known. The standard error is shown, but for the acrotelm parameters the fitted surface is not parabolic so that the + and - errors are shown separately. The range of estimates of  $p_c$  and  $\alpha_c$  in other peat bogs (from table 2) is also shown.)

	value	standard error		range
$p_a/g\text{ cm}^{-2}\text{ a}^{-1}$	$\dagger 2.4 \times 10^{-2}$	$+ 1.2 \times 10^{-2}$	$- 6.2 \times 10^{-3}$	—
$\alpha_a/a^{-1}$	$1.5 \times 10^{-2}$	$+ 1.5 \times 10^{-2}$	$- 6.4 \times 10^{-3}$	—
$p_c/g\text{ cm}^{-2}\text{ a}^{-1}$	$3.6 \times 10^{-3}$	$\pm 1.0 \times 10^{-3}$		$3.6\text{--}7.8 \times 10^{-3}$
$\alpha_c/a^{-1}$	$5.0 \times 10^{-4}$	$\pm 1.2 \times 10^{-4}$		$0.7\text{--}5.5 \times 10^{-4}$

estimated steady state depth  $8.5\text{ g cm}^{-2} \approx 105\text{ cm}$  if  $\rho = 0.07\text{ g cm}^{-3}$ .

	correlation matrix		
	$\alpha_a$	$p_c$	$\alpha_c$
$p_a$	0.95	0.38	0.25
$\alpha_a$	—	0.58	0.42
$p_c$	—	—	0.95

† equivalent to  $240\text{ g m}^{-2}\text{ a}^{-1}$ .

(Heal *et al.* 1981) and particularly for *Sphagnum fuscum* (Clymo 1978). The quotient  $p_c/p_a$ , which is the proportion of plant matter that survives passage through the acrotelm, is 0.15. This is consistent with the values between 0.1 and 0.2 reported by Heal *et al.* (1975), by Moore *et al.* (1975), and by Pakarinen (1975). As in the earlier cases,  $p$  and  $\alpha$  are highly correlated (table 3), but other correlations (between acrotelm and catotelm parameter estimates) are much smaller.

The fitted values of the parameters serve to identify the depth of the acrotelm too (figure 16). It is  $33 \pm 9$  cm, and at that depth the peat is 125 years old. The depth of the summer water-table is not known, unfortunately, but it is interesting that a fairly sharp increase in bulk density occurs at about 60 cm depth, indicating perhaps that a capillary fringe of water is sufficient to keep a layer of peat about 30 cm deep in a predominantly anaerobic state in summer.

## 6. A TWO COMPONENT TWO LAYER SIMULATION

The sort of effects to be expected if the processes considered so far (excepting the possible very long-term accumulation of refractory material) are combined can be shown in a simulation. The model has an acrotelm and catotelm and two components. The values of  $p_{1,a}$ ,  $p_{2,a}$ ,  $\alpha_{1,a}$  and  $\alpha_{2,a}$  can be chosen at will. The depth of the acrotelm can be specified, and this then determines  $p_{1,c}$  and  $p_{2,c}$ , but  $\alpha_{1,c}$  and  $\alpha_{2,c}$  can also be chosen at will, thus giving seven variables. The model for the acrotelm can be specified as:

$$\sum_{i=1}^{i=2} \frac{p_{i,a}}{\alpha_{i,a}} (1 - e^{-\alpha_{i,a}t}) - x_A = 0, \quad (23)$$

and this can easily be solved by iteration to give the time,  $t_A$ , needed to accumulate the specified mass in the acrotelm. (This is the time needed subsequently for matter to pass through the acrotelm.) The input to the catotelm is then

$$p_c = \sum_{i=1}^{i=2} p_{i,a} e^{-\alpha_{i,a}t_A}. \quad (24)$$

This model was used to get the results shown in table 4. Case A represents the 'standard' conditions, and the other cases may be considered as 'experiments' in which one or more of the variable values has been changed. In the standard case the two components have equal values of  $p_a$  of  $360 \text{ g m}^{-2} \text{ a}^{-1}$ . The total  $p_a$  is rather high for a bog but low for some other peat accumulating systems such as fens. In the acrotelm component 1 decays at twice the rate of component 2. The depth of the acrotelm is set at 12 cm. These values determine that the time spent in the acrotelm,  $t_A$ , is about 15 years. The acrotelm steady state depth is about two thirds of that which would have been reached if there were no catotelm to truncate the development of the acrotelm. The input to the catotelm is only  $21/72 \simeq 1/3$  of  $p_a$ , and more than two thirds of this is of component 1. The set values for decay in the catotelm are one hundredth those in the acrotelm, and the component decay rates are in the same ratio as in the acrotelm. The final steady state depth is about 3 m, and the peat has reached about 80% of this value after 2500 years (94% for the faster decaying component 1; 77% for component 2). At the steady state about one sixteenth of the *total* mass is of component 1 (which had productivity equal to that of component 2) and in the oldest peat component 1 forms an even larger proportion. For the catotelm alone the quotient of the mass of the components after a time  $t_c$

in the catotelm is:  $p_{1,c} e^{-\alpha_{1,c} t_c} / p_{2,c} e^{-\alpha_{2,c} t_c} = \exp \{ \ln (p_{1,a} / p_{2,a}) + t_c (\alpha_{2,c} - \alpha_{1,c}) \}$ , which for case A and  $t_c = 2500$  years gives component 1 as less than one tenth of component 2. For  $t_c = 5000$  years then component 1 is down to less than 2% of component 2. And this is with equal initial productivity and only a two fold difference in decay rate.

The other cases may now be examined. If the productivity of component 1 (case B 1) is doubled the steady-state depth increases to 6 m; if that of component 2, which decays more slowly, is doubled the depth increases to 9 m. In *both* cases the proportion of component 1 increases, mainly because in both cases the time spent in the acrotelm is reduced: from 15 to 8 and 7 years respectively. If the productivity is halved (B 3, B 4) the opposite effect is produced. In the extreme case (B 4) there is no catotelm at all.

The next three cases (C 1–C 3) double or halve the rate of decay in the acrotelm. In the C 1, the doubling of the rate for the slower decaying component 2 again has the effect of eliminating the catotelm. The importance of slow decay *of at least one component* in the acrotelm, as a means by which *other components* may survive into the catotelm is obvious. This is again shown in C 3, where the decay of the more resistant component 2 is slowed even further.

The experiments in D 1 and D 2 show the effects of a reduction in the rate of decay in the catotelm. Again, changes to the more slowly decaying component 2 are particularly effective in changing the steady state depth of peat.

Finally, the experiments in E 1–E 4 show the dramatic effects of a small change in the depth of the acrotelm on both the depth of peat and on the proportion of the components. If the boundary is raised by 4 cm this increases the steady state depth to 5 m and promotes component 1 to one fifth of the final mass; if the boundary is lowered by the same amount this reduces the steady state depth to about 1 m and the proportion of component 1 to less than one tenth of the total.

From all these simulations it is apparent that reducing the time spent in the acrotelm is the most important means by which the total depth of peat can be increased. Selective survival of the components is not so simply governed however.

## 7. TEMPERATURE FLUCTUATIONS AND THE RATE OF DECAY

It is well known that temperature affects the rate of decay, but less so that the amplitude and frequency of fluctuations may, in themselves, have significant effects if the relation between decay rate and temperature is non-linear, as it usually is. The reason is easily understood. Suppose there are two environments that have the same mean temperature, but in one the temperature is constant while in the other it fluctuates. Suppose also that the rate of decay of a specific plant material has a concave relationship with temperature (figure 17), and that the response to a change in temperature is very rapid, compared with the frequency of fluctuations. In the constant temperature environment this material will decay at a constant rate. But in the fluctuating environment an hour spent at, say, 5 °C below the mean temperature is more than compensated by an hour spent at 5 °C above the mean temperature, so that the overall loss is greater than it is in the constant temperature. This would not be so if the rate against temperature relationship were linear: it is the non-linearity that produces the difference.

A simple simulation suggests that this effect may be surprisingly large. For illustration we need a decay rate against temperature curve and knowledge of temperature fluctuations. There

TABLE 4. SIMULATION FOR A TWO COMPONENT (1, 2), TWO LAYER MODEL OF THE ACCUMULATION OF DRY MATTER AS PEAT

(Symbols:  $\rho$ , productivity/(g cm<sup>-2</sup> a<sup>-1</sup>);  $\alpha$ , decay rate coefficient/a<sup>-1</sup>;  $x$ , accumulated mass/(g cm<sup>-2</sup>);  $z$ , depth/cm assuming that in the acrotelm (subscript a) the bulk density,  $\rho$ , is 0.05 g cm<sup>-3</sup> and in the catotelm (subscript c) it is 0.1 g cm<sup>-3</sup>;  $t_A$ , time/a, peat spends in the acrotelm when it has reached its steady state thickness;  $Q_{2500}$ , proportion of the final steady-state of the whole system reached after 2500 years. The total mass and depth in the acrotelm and catotelm at  $t = \infty$  ( $x_A + x_{c,\infty}$  and  $z_A$  and  $z_{c,\infty}$ ) are shown as  $x_{tot}$  and  $z_{tot}$  respectively. The first example, A, may be considered as the 'standard'. Examples B-E are sets of experiments in which one or more of the seven parameter values that must be supplied (shown in bold) is changed. Values that are the same as those for A, whether supplied or resulting, are shown by a tilde (~). The experiments are of variation in: B, productivity; C, acrotelm decay parameters,  $\alpha_a$ ; D, catotelm decay parameters,  $\alpha_c$ ; E, acrotelm depth.)

case	$\rho_a$	$\alpha_a$	$x_A$	$z_A$	$t_A$	$\frac{x_A}{x_{\infty}}$	$\rho_c$	$\alpha_c$	$x_{c,\infty}$	$Q_{2500}$	$x_{tot}$	$z_{tot}$	notes
A	1	<b>0.12</b>	0.25			0.83	0.006	<b>0.0012</b>	5.2	0.94	5.4		
	2	<b>0.036</b>	<u>0.35</u>			0.59	0.015	<b>0.0006</b>	24.9	0.77	25.2		
	1+2	0.072	<b>0.6</b>	12	14.7	0.67	0.021		30.0	0.81	30.6	312	standard
B1	1	<b>0.072</b>	0.37			0.62	0.028	~	22.9	0.94	23.3		
	2	~	<u>0.23</u>			0.38	<u>0.022</u>	~	<u>37.1</u>	0.77	<u>37.3</u>		
	1+2	<u>0.108</u>	~	~	8.0	0.50	0.050	~	60.0	0.84	60.6	612	$\rho_{a1} \times 2$
B2	1	~	0.18			0.58	0.015	~	12.5	0.94	12.7		
	2	<b>0.072</b>	<u>0.43</u>			0.35	<u>0.047</u>	~	77.5	0.77	<u>77.9</u>		
	1+2	0.108	~	~	7.3	0.40	0.062	~	90.0	0.80	90.6	912	$\rho_{a2} \times 2$
B3	1	<b>0.018</b>	0.14			0.94	0.001	~	0.8	0.95	1.0		
	2	~	<u>0.46</u>			0.76	<u>0.009</u>	~	14.2	0.77	<u>14.6</u>		
	1+2	<u>0.054</u>	~	~	24.1	0.80	0.010	~	15.0	0.79	15.6	162	$\rho_{a1} \times \frac{1}{2}$
B4	1	~	0.30			1.0	0	~	0	1.0	0.30		
	2	<b>0.018</b>	<u>0.30</u>			1.0	0	~	0	1.0	<u>0.30</u>		
	1+2	0.054	~	~	$\infty$	1.0	0	~	0	1.0	0.6	12	$\rho_{a2} \times \frac{1}{2}$
C1	1	~	0.30			1.0	0	~	0	1.0	0.30		
	2	~	<u>0.30</u>			1.0	0	~	0	1.0	<u>0.30</u>		
	1+2	~	~	~	$\infty$	1.0	0	~	0	1.0	0.6	12	$\alpha_{a2} \times 2$
C2	1	~	0.15			0.99	0.0001	~	0.1	0.98	0.3		
	2	~	<u>0.45</u>			0.75	<u>0.0090</u>	~	<u>14.9</u>	0.77	<u>15.4</u>		
	1+2	~	~	~	23.2	0.80	0.009	~	15.1	0.78	15.7	163	$\alpha_{a1} \times 2$
C3	1	~	0.23			0.77	0.008	~	6.9	0.94	7.1		
	2	<b>0.03</b>	<u>0.37</u>			0.31	<u>0.025</u>	~	<u>41.6</u>	0.76	<u>41.9</u>		
	1+2	~	~	~	12.2	0.40	0.033	~	48.5	0.80	49.1	496	$\alpha_{a2} \times \frac{1}{2}$

case	$p_a$	$\alpha_a$	$x_A$	$z_A$	$t_A$	$\frac{x_A}{x_\infty}$	$p_c$	$\alpha_c$	$x_{c,\infty}$	$Q_{2500}$	$x_{tot}$	$z_{tot}$	notes
D1	1	~	~			~	~	<b>0.0006</b>	10.3	0.78	10.5		
	2	~	~			~	~	~	<u>24.9</u>	0.77	<u>25.2</u>		
	1+2	~	~	~		~	~	~	35.2	0.79	35.8	363	$\alpha_{c1} \times \frac{1}{2}$
D2	1	~	~			~	~	~	5.2	0.94	5.4		
	2	~	~			~	~	~	<u>74.6</u>	0.39	<u>74.9</u>		
	1+2	~	~	~		~	~	~	79.7	0.43	<u>80.3</u>	809	$\alpha_{c2} \times \frac{1}{3}$
E1	1	~	0.18			0.60	0.014	~	12.0	0.94	12.2		
	2	~	<u>0.22</u>			0.37	<u>0.023</u>	~	<u>38.0</u>	0.77	<u>38.2</u>		
	1+2	~	<b>0.4</b>	8	7.6	0.44	0.037	~	50.0	0.82	50.4	508	acrotelm (8 cm)
E2	1	~	0.22			0.72	0.010	~	8.4	0.94	8.6		
	2	~	<u>0.28</u>			0.47	<u>0.019</u>	~	<u>31.7</u>	0.77	<u>31.9</u>		
	1+2	~	<b>0.5</b>	10	10.7	0.56	0.029	~	40.0	0.81	40.5	410	acrotelm (10 cm)
E3	1	~	0.28			0.92	0.003	~	2.5	0.95	2.8		
	2	~	<u>0.43</u>			0.71	<u>0.011</u>	~	<u>17.5</u>	0.77	<u>17.9</u>		
	1+2	~	<b>0.7</b>	14	20.6	0.78	0.014	~	20.0	0.80	20.7	214	acrotelm (14 cm)
E4	1	~	0.29			0.98	0.001	~	0.7	0.96	1.0		
	2	~	<u>0.51</u>			0.84	<u>0.006</u>	~	<u>9.3</u>	0.78	<u>9.8</u>		
	1+2	~	<b>0.8</b>	16	31.1	0.88	0.007	~	10.0	0.80	10.8	116	acrotelm (16 cm)

are no long-term experiments on the effects of controlled temperatures on the rate of decay of peat-forming plants, but there are several sets of data relating the rate of oxygen consumption ('respiration') to temperature: Heal *et al.* (1981) summarized them. All show a concave relationship over a 25–30 °C range of temperature similar to that to which the plants are naturally exposed. The measurements were made in respirometers: those for 1–3 year old *Rubus chamaemorus* leaves (Rosswall 1974) are shown in figure 17. The experiments were not totally

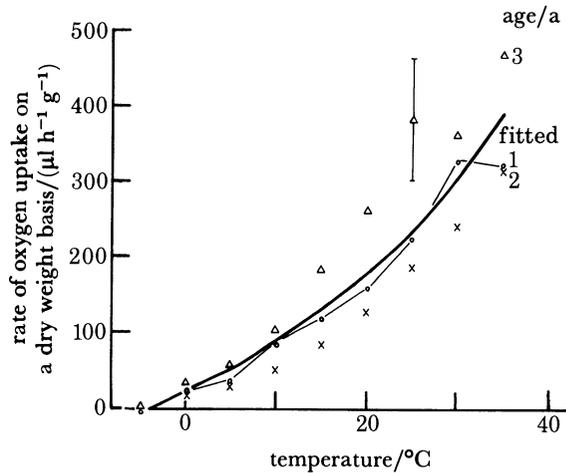


FIGURE 17. Rate of consumption of oxygen by *Rubus chamaemorus* leaves from Stordalen, Abisko (north Sweden), in a Gilson respirometer, in relation to temperature. The temperature began at  $-5^{\circ}\text{C}$ , and every 24 hours was raised by  $5^{\circ}\text{C}$ . There were three ages of leaf (1, 2 and 3 years old) and three replicates of each age. Representative ranges are shown by vertical bars. The proportion of the original leaf dry mass remaining after 1, 2 and 3 years was 0.72, 0.79 and 0.52 respectively. The curved line was fitted to all the data by using  $\hat{\alpha}_u = b(s + e^{\beta u})$ , and minimizing  $\Sigma(\hat{\alpha}_u - \alpha_u)^2 / \alpha_u$  by the method described in the appendix, where  $u =$  temperature ( $^{\circ}\text{C}$ ),  $\alpha_u =$  the measured rate of oxygen consumption per unit dry mass of leaf ( $\mu\text{g}^{-1} \text{h}^{-1}$ ),  $\hat{\alpha}_u =$  calculated rate, and  $b$ ,  $s$  and  $\beta$  are parameters with estimated values:  $b = 142 \mu\text{g g}^{-1} \text{h}^{-1}$ ;  $s = -0.86$ ;  $\beta = 0.0324^{\circ}\text{C}^{-1}$ . Data from Rosswall (1974).

satisfactory in that the temperature was, for technical reasons, raised systematically by  $5^{\circ}\text{C}$  increments from the lowest value to the highest and not randomized (or even stepped down again). The changes were made at 24 hour intervals, and rates measured at the end of each period. There is, too, a puzzling increase in rate for 3 year old leaves. But the general *shape* of the curves, which is their most important characteristic in the present context, is similar. So is that of other dead plant materials (Heal *et al.* 1981). The integrated loss over a whole year, considered shortly, is similar to that measured directly, so the absolute rates are probably fairly reliable in spite of the technical shortcomings of the experiments and the unnatural conditions in the respirometers.

An exponential curve was fitted to these data (appendix, figure 17). It is interesting to see that oxygen uptake occurred when the temperature was  $0^{\circ}\text{C}$ .

For the simulation the temperature was assumed to fluctuate sinusoidally with superimposed 24 h and 365 day periods. The temperature at chosen depths was calculated assuming that the peat was a homogeneous isotropic solid (appendix). The rate of 'respiration' was assumed to respond instantaneously to a change in temperature and with no long-term adaptation to the seasonal march of temperature. The resulting equation (appendix) was integrated numerically for 365 days at 1 h intervals. Nearly identical results were obtained with a 30 min

interval. Four simulations were made, using factorial combinations of daily and yearly amplitude of 15 and 25 °C. The total decay was evaluated at 0, 2, 4, 8, 16, ... 256 cm depth and for mean temperature -10 to +10 °C at 5 °C intervals. The results are shown in figure 18.

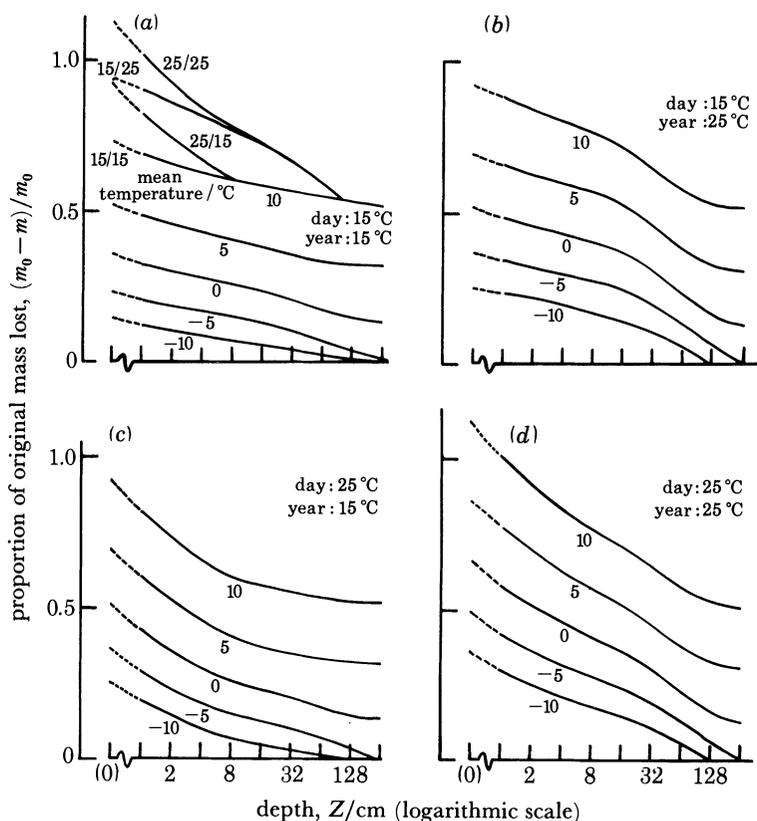


FIGURE 18. Simulated loss of mass of leaves of *Rubus chamaemorus* with the respiration rate against temperature response shown in figure 17. The respiratory quotient was assumed to be 1.0 and the plant to be wholly composed of carbohydrate. The temperature at the surface was assumed to fluctuate sinusoidally daily and yearly, with independent amplitudes, and the fluctuation propagated as if in a homogeneous isotropic solid (appendix). Four combinations of daily and yearly amplitude are shown: (a) 15, 15 °C; (b) 15, 25 °C; (c) 25, 15 °C; (d) 25, 25 °C. The equations were integrated, with a 1 hour time step, for ten depths (0, 1, 2, 4, 8 ... 256 cm) and for five mean temperatures (-10, -5, 0, 5, 10 °C). The 10 °C results for (b)-(d) are repeated in (a) to allow comparison.

The assumptions made are not as close to reality as might be wished, so it is encouraging to find that the calculated loss over a year at 4-8 cm depth and a mean temperature of 0 °C was 0.3-0.45 compared with losses measured in the field in these conditions of 0.2-0.3 (Rosswall 1974). Nevertheless, the results in figure 18 are best used to show the likely relative importance of different factors and not to give accurate predictions of values. In any one simulation the curves are in order of mean temperature, as would be expected. In all cases the rate of decay decreases with depth. For the larger *daily* amplitude this effect is greatest near the surface; for the larger *yearly* amplitude the difference is almost as large at 16 cm depth as it is at the surface. These differences reflect the fact that daily fluctuations are attenuated about  $(365)^{\frac{1}{2}} \approx 19$  times more than yearly ones are.

At relatively high mean temperature, all parts of all the curves are well above the zero line:

the range of values is about  $0.5\text{--}1.2\text{ a}^{-1}$ . But at lower *mean* temperature the range is proportionately much greater: for  $0\text{ }^{\circ}\text{C}$ , appropriate for northern Canada, Fennoscandia and Russia, the range for the  $15\text{ }^{\circ}\text{C}$  daily and  $25\text{ }^{\circ}\text{C}$  yearly fluctuation is three fold, from  $0.52\text{ a}^{-1}$  at the surface to  $0.16\text{ a}^{-1}$  at  $64\text{ cm}$  depth.

Temperature *fluctuations*, as such, have not previously been considered as a factor affecting the rate of peat accumulation. It now seems that the effect of fluctuations at low *mean* temperature may be just as important as the mean value itself in helping to account for peat formation. A quite shallow concavity in the rate of decay against temperature relation can produce large effects.

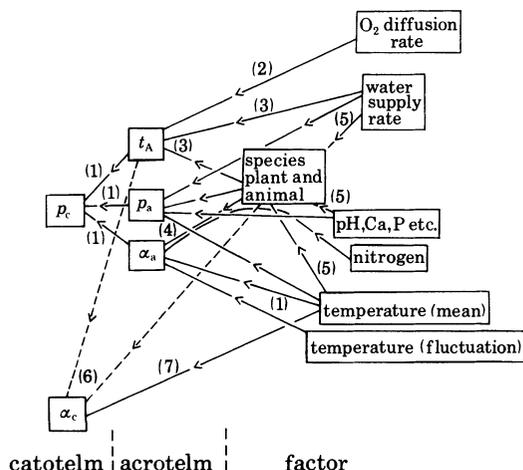


FIGURE 19. Schematic relationships of factors and the parameters affecting peat accumulation. The importance of the links differs and, for any one link, depends on circumstances. The diagram is certainly incomplete. Numerals refer to the notes that follow. (1) Considered earlier in this article. (2) Oxygen flux less than rate of consumption is the main cause of anaerobic conditions and the existence of a catotelm (but not in Antarctic moss-banks). It is shown as affecting time spent in the acrotelm. (3) Water supply affects the depth of the water table (Ingram 1982), and so does the speed at which plant parts collapse. (4) The rate of decay is determined partly by the plant species, partly by the activity of small invertebrates, partly by 'nutrition', and specifically – as shown by the curved arrow – by the nitrogen concentration in the plant matter (Coulson & Butterfield 1978; Clymo 1983). (5) Which plant and animal species live at the surface is determined by a large number of factors, most of which not only select a particular spectrum of species but also have direct effects on  $p_a$  and  $\alpha_a$ . (6) Largely speculative: the decay coefficient in the catotelm may be affected by the nature of chemical compounds that survive passage through the acrotelm; the species of plant may also have a similar direct effect. (7) In Antarctic moss-banks permafrost creates the catotelm – there is no anaerobic zone. In the Arctic the catotelm may result from anaerobic conditions overlying permafrost (Sonesson 1980).

## 8. DISCUSSION

### (a) *The causes of peat accumulation*

It is clear that many factors may influence the establishment and maintenance of a peat accumulating system. If the analysis in this article is near the truth then the real *accumulating* system is the catotelm, and the cardinal values are those of the parameters  $p_c$  and  $\alpha_c$ , the rate of input to the catotelm and the catotelm decay parameter. The factors that are known, or that may be inferred, to affect these values are shown diagrammatically in figure 19, which speaks for itself.

*(b) Implications for the interpretation of stratigraphy*

The surface of many, perhaps most, peat bogs has a complex microtopographic variation of wetter and drier (usually higher) patches. To some extent the pattern of these may be understood as a consequence of hydrology (Ivanov 1981). Each microtopographic feature has its characteristic assemblage of species, and these are the raw material that, after selective decay, becomes peat. It seems beyond doubt that during post glacial times there have been major changes in climate. In those cases where detailed evidence has been sought (for example Walker & Walker 1961; Casparie 1969; Barber 1981), it is clear that there have been substantial changes in the species composition of peat over fairly large areas of the same bog, and in one case at least these changes were simultaneous. Long-term observation of the surface of peat bogs also shows conspicuous changes. For example, some of the pools on Burnt Hill, Moor House, northern England, contained *Sphagnum cuspidatum* in 1960 and now contain *S. magellanicum* or *S. papillosum* (personal observations). A similar change has occurred on the Åkhult mire, southwest Sweden (N. Malmer, personal communication). In time these changes should appear in the stratigraphy as fairly abrupt transitions. On Burnt Hill the cause is a gradual lowering of the water table in the pool complex as an erosion channel cuts back into one arm of a sinuous interconnecting set of long narrow pools.

There seems to be no reason, therefore, to doubt that widespread changes in vegetation do occur and that these may be reflected in equally sharp transitions in the proportion of macroscopic remains in the peat. But the examples given in this article show that other interpretations of changes, particularly the slow ones, are possible. Such changes may reflect selective decay rather than widespread climatic change. It seems also that the older the peat the more cautious one should be in using the macrofossil composition as an indication of the vegetation at the time that the peat was laid down. The examples in this article, particularly the simulations in table 4, show that ten fold changes in the relative proportion of different components are possible, perhaps even probable.

The simulation with two components and two layers may be modified to allow the effects of climatic change to be examined. One may postulate that a cooler wetter climate makes the acrotelm shallower (reduces  $x_A$  in table 4) and changes the values of  $p_{1,a}$  and  $p_{2,a}$ . This represents a change in plant productivity, or, in an extreme case, a replacement of one species by another. The choice of values is so unfettered by knowledge of which are relevant, however, that it is not justifiable to give detailed results: they are very varied and in a fair proportion of cases unexpected. An increase in the productivity of one component while the other(s) remain the same may result in either an increase or a decrease in the proportion that it forms of the acrotelm peat, depending on its effect in accelerating or decelerating the passage of all components through the acrotelm. This effect may be enhanced or diminished by a concomitant change in the depth of the acrotelm. In short, the specific composition of peat may not always respond in such a simple way to 'wetness' or to internal dynamics as has often been assumed.

*(c) The maximum depth of peat and hydrological effects on growth*

The thesis proposed here is that the maximum depth that a peat deposit can reach in 50 000 years or so is determined by the value of  $p_c/\alpha_c$ , or by some similar expression if there are two or more distinct components. Yet it is widely believed, mainly as a result of an analysis by Wickman (1951), that the maximum height of bog peat in general, and of a raised bog cupola

in particular (because the analysis is simpler), is determined almost solely by what Wickman (1951) called 'effective ... rainfall'. 'Height' in this context means the highest possible point on the bog plain relative to that of the water in lagg runoff streams, and 'effective rainfall' is the 'difference between ... rainfall and the amount of water evaporated and lost along the surface'. It is unclear what is intended by this last phrase: Wickman imagined that 'the precipitation falling on an ombrogenous bog partly evaporates ... directly or indirectly, i.e. with the help of the respiration [sic] of the peat-forming plants; partly runs away along its surface; and partly penetrates the surface, moving from the plane [sic] to the margin'. Wickman recognizes that there is an upper layer of little-humified peat of high hydraulic conductivity overlying a more humified layer of lower conductivity. He assumes 'that the low-humified peat is exclusively responsible for the transportation of water from the plane to the margin'. Yet, while assuming that some water runs away 'along' the surface he 'excludes ... water transport to a notable extent by open channels'. He appears to be considering that part of the precipitation that is not lost by evaporation and that runs off *through the acrotelm*. For this he deduces that at the steady state, when the 'discharge',  $U'$ , from the bog is equal to the 'effective precipitation' over the whole bog area, then 'if the size of the bog is constant' (probably meaning that it is circular and of given radius,  $R$ ):

$$H_m^2 = AU', \quad (25)$$

where  $H_m$  is the maximum height of the bog plain above the discharge on the margin and  $A$  is a parameter. (These symbols are not Wickman's: they are chosen to facilitate later comparisons.) The physical dimensions of  $U'$  and  $A$  are unclear but are considered later. Wickman also concluded that for constant  $U'$  then

$$H_m^2 = bR, \quad (26)$$

where  $b$  is another parameter. He used the maxima abstracted by Granlund (1932) from an extensive series of records of the height and diameter of Swedish peat bogs to show that equations 25 and 26 are followed remarkably closely for the maximum recorded heights if  $U' \simeq$  (annual rainfall - 480) mm. His paper is titled 'The maximum height of raised bogs ...', and in the abstract he states that 'the maximum height of an "ideal" raised bog is proportional to the square root of the annual rainfall and to the square root of the "diameter" of the bog'. It is probably these statements which have occasioned the belief that the maximum height of a raised bog is determined by the 'effective rainfall'. Yet what Wickman showed, in theory and in Granlund's abstracted curves, was that

$$U' \simeq cH_m^2/R, \quad (27)$$

where  $c$  is a parameter whose value,  $10.3 \text{ a}^{-1}$ , summarizes Granlund's data. For a given value of  $U'$  there is a relation between  $H_m$  and  $R$ , *but no maximum is set to either*: it is only if both  $U'$  and  $R$  are arbitrarily fixed by the observer that  $H_m$  is determined, and nature is not so restrictive.

Wickman pointed to the agreement between the *shape* of the theoretical and the observed relationships, but he failed to calculate the parameter values, particularly that of  $c$  which is related to the hydraulic conductivity and should therefore allow a test of his assumptions about where the water is moving.

Recently, Ingram (1982, 1983) has arrived at much the same conclusion and has

reconsidered the problem of the shape of the water-table in a raised bog. He considers the groundwater discharge,  $U$ , defined by the hydrological budget

$$P - E - U - G - \Delta W = 0 \tag{28}$$

where  $P$  = precipitation,  $E$  = evapotranspiration,  $G$  ( $\ll U$ ) = leakage through the rock below the peat, and  $\Delta W$  = change in storage. All except the last are flux densities, and by a suitable choice of time interval the last can be made zero if required. (It seems likely that the  $U'$  in Wickman's analysis is similar to, if not identical with, Ingram's  $U$ .)

Ingram points out that the survival of a peat mass is likely to be determined by the ability it has to withstand the worst conditions, and these are likely to occur during the occasional drought. He implies that droughts are important because irreversible changes occur in the peat when it dries. It seems just as likely that it is the death from drought of plants in the living surface that is important, but whatever the reason, attention is focused on those times when the water table is unusually low. Ingram assumes that the water flow is then almost all through the more humified catotelm, which he assumes to be isotropic, with relatively low hydraulic conductivity. Rycroft *et al.* (1975) suspected that the flow of water through moderately or highly humified peat did not conform with Darcy's law. But later work (Ingram 1983) has shown that most of the apparently non-Darcyan behaviour is a consequence of a storage effect, so that for small hydrostatic pressure gradients the peat mass may be treated as a porous medium to which Darcy's law does apply. In these circumstances, Ingram (1982) shows that for a raised bog in a parallel-sided valley, with runoff from the two ends but not from the sides, the water table should be hemi-elliptical in longitudinal vertical section (figure 20):

$$\frac{U}{k} = \frac{H^2}{2Ll - l^2}, \tag{29}$$

where  $H$  is the height of the bog surface,  $2L$  is the length of the bog,  $l$  is the distance from either end, and  $k$  is the hydraulic conductivity. For a circular raised bog of radius  $L$  then a similar equation holds:  $U/k = 2H^2/(2Ll - l^2)$ . (This groundwater mound equation has been known to soil physicists for some time.) For one raised bog, Dun Moss, for which the data exist, this expectation is close to observation. It follows from equation 29 that at the centre of the bog, where  $l = L$  and  $H = H_m$ ,

$$\frac{U}{k} = \frac{H_m^2}{L^2}. \tag{30}$$

This is similar to the relationship shown by Wickman's analysis of Granlund's data, summarized in equation 27. The only difference is the appearance of  $L^2$  in place of  $R$ . This difference is attributable to Wickman's assumption of a circular peat mass: if his argument is applied to a parallel-sided bog with runoff at the ends only then  $R$ , which now represents the half-length  $L$ , is replaced by  $(\pi R^2/2\pi R)^2 = R^2/4$ , and the equations 27 and 30 become functionally the same. If  $k = 4c\eta$ , where  $\eta$ , a length, has the value 1.0, they become identical.

Yet the other assumptions are very different: Wickman seems to have been concerned solely with flow in the acrotelm, assumed to be of high conductivity, while Ingram assumed flow was in the catotelm of low conductivity.

For Dun Moss, the values of  $H_m$  and  $L$  gave the value of the dimensionless quantity  $U/k$  (equation 27) as  $1.0 \times 10^{-3}$ . The mean precipitation,  $P$ , was  $951 \text{ mm a}^{-1}$ . The measured value in the driest of ten hydrological years was  $530 \text{ mm}$ . The value of  $U$  in the same year was

187 mm a<sup>-1</sup>, and the mean measured value of the hydraulic conductivity,  $k$ , was  $5 \times 10^{-4}$  cm s<sup>-1</sup>. These give an independent estimate of  $U/k$  of  $1.2 \times 10^{-3}$  (Ingram 1982).

Granlund's data may be used to calculate  $k = 4c\eta = 1.3 \times 10^{-4}$  cm s<sup>-1</sup>, which is about one quarter of the mean value measured by Ingram. Granlund's data would lead one to expect that a bog of the size of Dun Moss (about 500 m long) in a parallel sided valley, with runoff at the ends only, would have a maximum depth of about 6.8 m, compared with the actual value of 8.2 m.

The various values of  $k$  range from  $1.2 \times 10^{-4}$  (indirect, from Granlund's data) to  $8 \times 10^{-4}$  cm s<sup>-1</sup> (maximum measured by Ingram). All these values are about two to four orders of magnitude smaller than those recorded for unhumified peat but on the high side for decomposed peat, for which values of about  $10^{-4}$  to  $10^{-7}$  cm s<sup>-1</sup> seem to be common (Ingram 1983). The whole analysis is approximate, however, and the real system is certainly more complex than is allowed here.

In summary, it seems that Wickman may have hit on the correct functional relationship between  $U$ ,  $H$  and  $R$  (or  $L$ ) but for the wrong reasons, and that the value of  $k$  supports Ingram's view that it is movement through the catotelm in dry years that is important in determining the shape of the water table. Granlund's extensive set of data can then be used to support Ingram's thesis.

The development of a peat mass in ideally simple circumstances may now be considered. Suppose that the peat develops in an infinitely long parallel sided valley, with all groundwater discharge at the two ends of the bog. (The same argument would apply to a circular mass on an infinite plane with discharge all round the perimeter). Peat formation may begin at a number of separate places, and the peat may grow outwards and fuse, or it may start from a single focus. Much the same considerations apply, so I follow a single peat mass. Suppose that the value of  $U$  in the occasional drought year, say one in every 20 years, remains the same. The peat can accumulate until in these drought years the centre of the cupola reaches  $H_m$  appropriate to the present value of  $L$ , and the water table is then hemi-elliptical in longitudinal section. In subsequent wetter years the water table will be rather higher, and perhaps more so in some places than in others. Because the water table is closer to the surface then the value of  $p_c$  will be greater so peat (and height) accumulation will be greater. At the next drought such places will be under greater stress: negative feedback will thus tend to keep the surface of the bog vegetation not far above the drought water table, though the exact distance above may be systematically greater in some parts of the bog than in others. The only escape is then for  $L$  to increase: the bog must extend along the valley. This it can do, as there is no obstruction. As it already has a shape that is close to hemi-elliptical in longitudinal section the bog will therefore tend to extend along the valley (perhaps incorporating other foci) and to increase  $H_m$  according to equation 30. This process is shown in figure 20a, and there is no hydrological constraint to the indefinite extension of the bog along the valley. But the process of decay discussed earlier would put an eventual limit at a depth (as cumulative mass) at the central highest point of approximately  $p_c/\alpha_c$ , and hydrology would then prevent further extension along the valley. *The maximum possible depth would be set by  $p_c/\alpha_c$ , not directly by hydrological variables.*

If the channel has obstructions at the end, as if it were an enormous rectangular pit, then peat would expand as before until it reached the end barriers (as shown in figure 20b). At this point  $L$  could no longer increase, but there is no reason why the pit should not continue to accumulate peat all over at the same rate as long as the discharge were always at the surface

of the peat at the ends of the pit. The drought-ellipse and value of  $H_m$  above this discharge level would be maintained until eventually the attainment of the  $p_c/\alpha_c$  cumulative mass again froze the shape and size in the seeming sameness and phrenetic activity of 'running on the spot'.

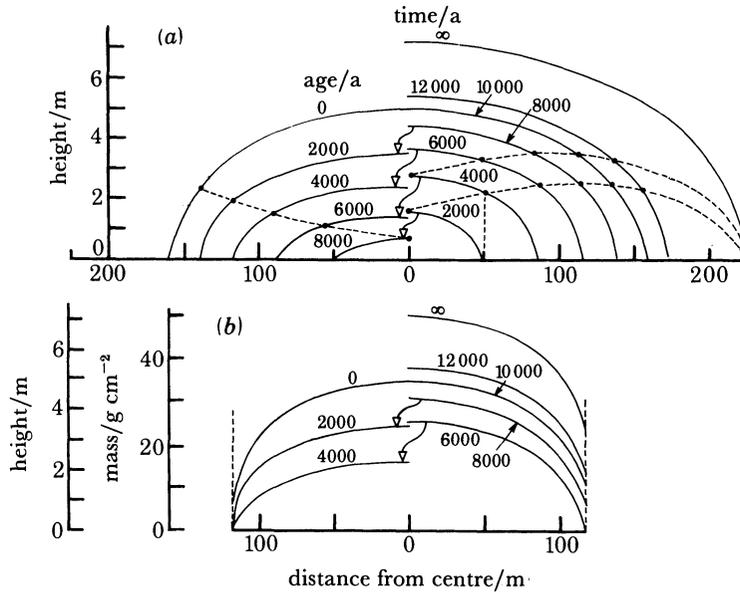


FIGURE 20. Hypothetical longitudinal section of peat accumulating according to equation 34 in a flat-bottomed parallel-sided valley (a) of unlimited length and (b) with permeable barriers 118 m from the centre. The peat reaches these after 6000 years and accumulates thereafter with the same shape, i.e. the surfaces are all parallel, towards the steady state (the topmost curve). The right side of each diagram shows the position of the surface at the time at which it formed. The left side shows, for the single specific time of 10000 years, the position of the older surfaces by that time; each has sunk to the position shown by the unfilled arrow because of decay of peat below the original surface. The broken lines on the right half of (a) show the depth of peat 2000 and 4000 years respectively after peat began to accumulate at that spot. The curves are convex and show that the maximum rate of accumulation in the lower peat occurs at the edge of the peat mass after about 10000 years. The broken line on the left half of (a) is a similar line for the apparent rate of accumulation in the lower peat. This curve is concave (for the time shown) and is the one that someone who assumed that there is negligible decay in the catotelm would mistake for the corresponding broken line (for 2000 years) on the right. This 2000 year slab is used for illustration. Instantaneous values (of  $p_c/p_c$ ) are shown in figure 22. The mass accumulation is independent of the bulk density,  $\rho$ , but if  $\rho$  is constant then the height scale is directly proportional to the mass scale. The vertical scale used is 20 times the horizontal one. The parameter values used were chosen as representative (table 2, figures 7, 8, 11, 12, and the Dun Moss value of  $U/k$  - see text). The values are:  $p = 0.006 \text{ g cm}^{-2}$ ;  $\alpha = 0.00012 \text{ a}^{-1}$ ;  $\rho = 0.07 \text{ g cm}^{-3}$ ;  $U/k = 0.001$ .

This description, and figure 20, assume that peat growth in the bog centre follows equation 13, an assumption made plausible by the results in figures 7-11 and in tables 2 and 3. But it is apparent from the broken lines in figure 20 that the pattern of growth away from the centre of the bog is different from that at the centre. For the first few millenia, the further out that the bog spreads the more rapid is the rate of peat accumulation when the ground is first covered. At any one spot the rate at first is higher than it was at the same stage of peat accumulation at the centre. But eventually the rate when ground is first covered begins to decrease, and in the final steady state the rate at the edge would be zero.

It is necessary now to formalize these matters. It is convenient to be able to refer to a fixed position along the bog axis, relative to the original focus of growth (where  $H = H_m$  and equations 13 and 16 hold). Let this distance be  $v$ . Then equations 29 and 30 give

$$H = (H_m^2 - v^2 U/k)^{\frac{1}{2}} \tag{31}$$

The sensitivity of peat growth behaviour to distance from the centre of the bog may be examined by calculating the distance from the centre for which  $H/H_m$  is greater than some specific value, i.e. that the surface is so nearly as high as that at the centre that it is behaving very similarly to it. By substituting in equation 31 it follows that for  $H/H_m = 0.9$  and  $U/k = 10^{-3}$  (the Dun Moss value) then  $v = 14 H_m$ , and from equation 30 it follows that  $L = 32 H_m$  and  $v/L = 0.44$ . If the lowest 3 m of peat were ignored then one might hope to observe the consequences of equation 13 with little disturbance by hydrological effects anywhere within about 100 m of the bog centre.

The full equation describing the pattern of growth in figure 20 is obtained by using  $H = x_c/\rho_c$  and substituting equation 13 in 31 to give

$$H = \left\{ \left[ \frac{p_c}{\alpha_c \rho_c} (1 - e^{-\alpha_c t}) \right]^2 - v^2 U/k \right\}^{\frac{1}{2}} \quad (32)$$

An illustrative example of these equations, using realistic parameter values, is shown in the right half of figure 20.

The age against depth curve for any point on the surface can also be derived (appendix (e), equation A 15). The isochrones for a single time (10000 years) are shown as the left half of figure 20, and the effect on age against depth curves at various points on the surface is illustrated in figure 21. The pattern relative to the central curve is quite complicated, with concave and convex sections, but the differences from the central curve are small except in peat that was near the edge of the bog when it formed, i.e. it is near the base of the peat now. Other specific times give different age against depth curves, except at the centre, but between 2000 and 20000 years (for the parameter values used) the same general features are seen.

In equation 32, as in all previous ones,  $p_c$  is the rate at which mass passes into the catotelm and is constant at the bog centre. But it is obvious from the broken lines in figure 20 that the rate at which matter accumulates when the ground is first covered by the spreading bog is *not* constant. As the decay parameter is constant it must be that the rate at which matter passes into the catotelm at points other than the centre is a variable,  $\tilde{p}_c$ . This is a consequence of the assumption that the *shape* of the bog in section is determined by hydrology. The equation for this variable is developed in appendix (e), and the values of  $\tilde{p}_c/p_c$  for the same peat system as that in figure 20 are shown in figure 22. The variation of  $\tilde{p}_c/p_c$  is quite complicated. In the first few millenia it exceeds 1.0 at all points away from the central highest point, and by a lot at the bog margins. After about 7000 years (in this example) the value falls slightly below 1.0 away from the centre, but still exceeds 1.0 towards the margins. This tendency becomes more marked as time passes and eventually the value falls steadily away from the centre with no more than a very short, though steep, marginal upturn to values above that at the centre. This analysis assumes constant climate and that the bog shape is determined by hydrology. The variation in  $\tilde{p}_c$  must therefore result from variation in the characteristics of the acrotelm: in  $p_a$ ,  $\alpha_a$ ,  $t_A$  (the steady state time for matter to pass through the acrotelm), or from some combination of these. These might be found in the field as different growth rates of the same species as occur near the bog centre, as a change in species composition, as a difference in the acrotelm depth, or as some combination of these. There may be systematic differences between the centre and the margin of a peat bog in the amplitude of the fluctuation of the water table. More attention is indicated to the behaviour of the water table and the plants at the margins of peat bogs.

If  $p_c/\alpha_c$  does limit depth to about 10 m, then for  $U/k = 1.0 \times 10^{-3}$ , i.e. for mean precipitation about  $1000 \text{ mm a}^{-1}$ , the maximum distance across a circular cupola of raised bog peat, for which  $U/k = 2 H_m^2/L^2$ , would be about 0.9 km. The effect of a generally wetter climate, if it increased  $U$  in critical years would be to give a water table that was generally nearer the surface. This might have three effects: it might favour plants able to grow well in wetter conditions (for

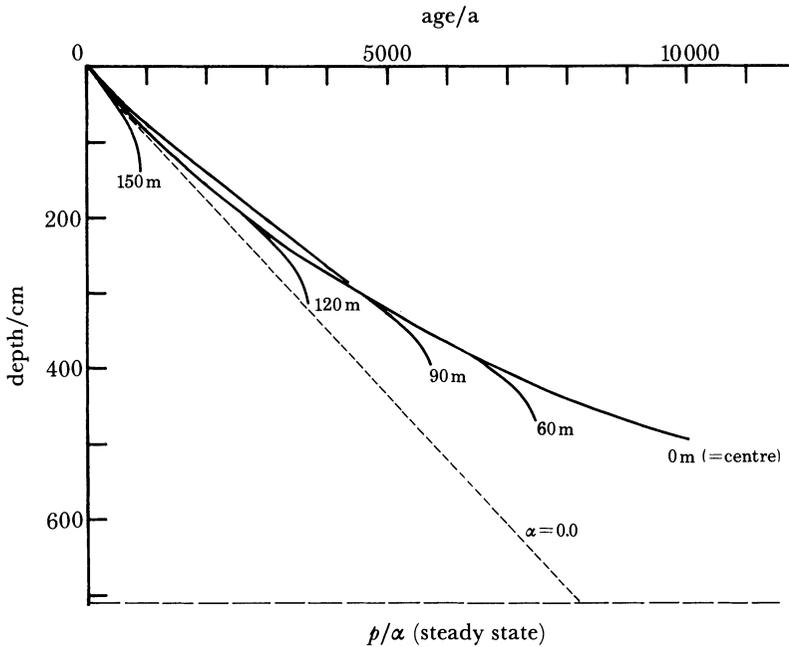


FIGURE 21. Age against depth profiles, similar to those in figures 7–11, for several points along the axis of the hypothetical raised bog shown in figure 20. The profiles are for the single time of 10000 years and are calculated from equation A 15. The profile at 60 m from the centre follows the central one closely, but becomes convex in the lower peat. The 90 and 120 m profiles are sigmoid, starting above the central one and falling below it in the lower peat. The differences from the central profile are small except close to the base of the peat. For earlier times, 4000 years for example, the differences are slightly larger and all the curves fall below the central one.

example *Sphagnum* and *Erica tetralix* over *Calluna vulgaris*); it would decrease the average time that plant matter spent in the acrotelm and thus increase  $p_c$ ; and as a consequence peat would accumulate faster. Because  $p_c$  was larger, the maximum depth of peat and hence the distance across the cupola should be greater, and because  $U$  is larger the distance across the cupola when that depth is approached should be larger.

It is always possible, of course, that catastrophic failure as a bog ‘burst’ or ‘flow’ may prevent the  $p_c/\alpha_c$  limit being reached. Blanket bog failure, particularly on steep ( $5\text{--}20^\circ$ ) slopes, is well documented. But it is not clear that failure of this kind is the rule. More common is the development of gullies and erosion. These alone could limit the peat to a depth less than the  $p_c/\alpha_c$  limit. They may have more complicated effects too by increasing the depth of the acrotelm (thus decreasing  $p_c$ ) and by changing the species composition.

These hypotheses about bog growth can be tested in various ways. One way would be to examine the depth of the acrotelm and the value of  $p_c$  across a raised bog. Another way would be to construct detailed age against depth profiles at several points from the centre to the margin

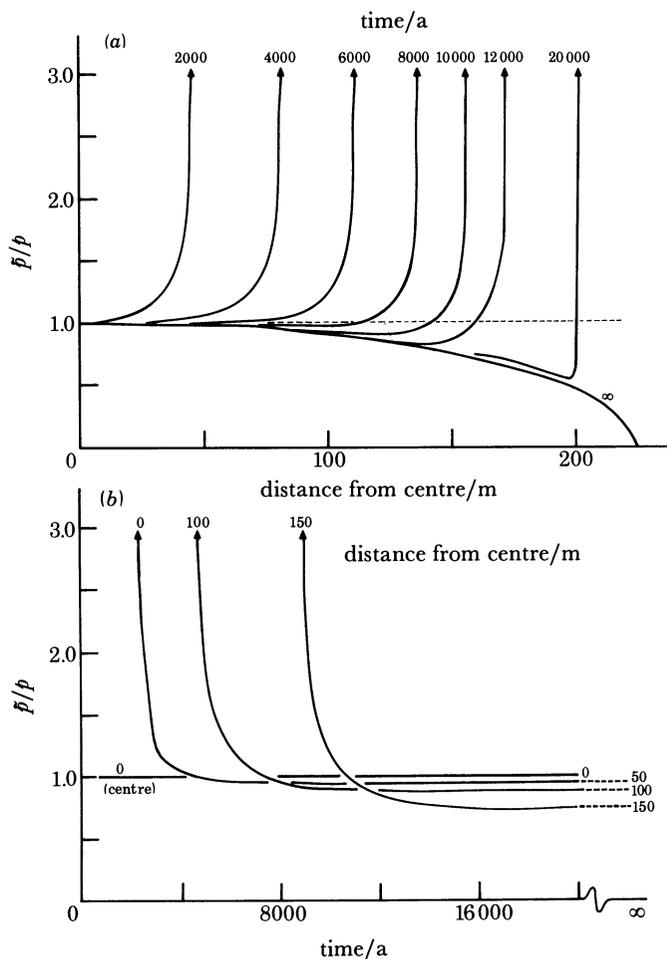


FIGURE 22. Values of the rate at which matter passes into the catotelm, relative to that of the central constant value  $p_c$ , for the hypothetical raised bog shown in figure 20. The values were calculated from equation A 16. (a) As a function of distance,  $v$ , from the centre along the long axis. Curves for times at six 2000 year intervals and at 20000 years are shown, as is that for the final steady state. Until about 7000 years all values exceed 1.0. Thereafter the value falls from the centre, but rises progressively more steeply at the edge. (b) As a function of time,  $t$ , for four distances along the centre axis. The steady state values are shown at the right.

of a raised bog such as that just considered, and to make such measurements on a series of such bogs of differing  $U$  and  $L$  (or  $R$ ). Whether such a project is practicable or not remains to be seen.

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9. APPENDIX

(a) *Linear and exponential decay*

Let  $m$  be the proportion of the original mass,  $m_0$ , left after time  $t$ , then for linear decay,

$$m'/m_0 = 1 - \alpha' t, \tag{A 1}$$

and for exponential decay

$$m/m_0 = e^{-\alpha t}, \tag{A 2}$$

where prime (') indicates the linear assumption and  $\alpha'$  and  $\alpha$  are the appropriate decay parameters. Some of the considerations governing the use of these description may be revealed by asking, for a given value of  $t$  and  $\alpha$ , what value of  $\alpha'$  will make the shaded area (figure 3a) above the exponential and below the straight line equal to that below the exponential and above the straight line. The value of this area gives some indication of how similar the descriptions are: when it is small they give similar results; when large the two may be distinguishable. The problem amounts to stating that  $\int_0^t m'/m_0 dt = \int_0^t m/m_0 dt$ .

General results, independent of  $\alpha$  and  $\alpha'$ , may be got if the time axis is scaled in half-lives (or doubling times if  $\alpha$  and  $\alpha'$  are positive). Let  $\tilde{T}$  represent the time in half-lives and  $\phi = -\ln(1/2)$ , then  $\tilde{T} = \alpha t/\phi$ ,  $m/m_0 = e^{-\phi\tilde{T}}$  and  $m'/m_0 = 1 - \alpha'\phi\tilde{T}/\alpha$ . It follows that  $e^{-\phi\tilde{T}} = 0.5^{\tilde{T}}$ .

By substituting and integrating between  $\tilde{T} = 0$  and  $\tilde{T} = \tilde{T}_s$ , where  $\tilde{T}_s$  is the chosen specific time, we get

$$\alpha' = \frac{2\alpha}{\phi\tilde{T}_s} \left[ 1 + \frac{(e^{-\phi\tilde{T}_s} - 1)}{\phi\tilde{T}_s} \right]. \tag{A 3}$$

The value  $\tilde{T}_z$ , at which  $m'/m_0 = 0$ , i.e. when, according to the linear model, all the matter has decayed, is obtained by substituting  $\alpha'$  to give

$$\frac{m'}{m_0} = \frac{2(1 - e^{-\phi\tilde{T}})}{\phi\tilde{T}} - 1 = 0, \tag{A 4}$$

and solving numerically to give  $\tilde{T}_z = 2.29911 \dots$ . Further substitution shows that when  $m'/m_0 = 0$ ,  $m/m_0 = 0.20319 \dots$ .

We now ask, for what value  $\tilde{T}_c (\neq 0)$  is  $m' = m$ , i.e. where do the lines intersect? By substitution it follows that

$$1 - \frac{2\tilde{T}_c}{\tilde{T}} \left[ 1 + \frac{(e^{-\phi\tilde{T}} - 1)}{\phi\tilde{T}} \right] - e^{-\phi\tilde{T}_c} = 0. \tag{A 5}$$

For  $\tilde{T} \gg 1$  it can be shown directly that  $\tilde{T}_c \rightarrow \tilde{T}/2$ . For  $\tilde{T} \ll 1$ , substituting the exponential terms by their series expansions, and ignoring cubic and higher powers of  $\tilde{T}$ , gives  $\tilde{T}_c \rightarrow 2\tilde{T}/3$ . For intermediate values of  $\tilde{T}$  the equation must be solved numerically; for  $\tilde{T} = \tilde{T}_z$ , then  $\tilde{T}_c = 0.638 \tilde{T}$ .

The area,  $A$ , between the lines is obtained by integration as

$$A = 2\tilde{T}_c - \frac{2\tilde{T}_c^2}{\tilde{T}} \left[ 1 + \frac{(e^{-\phi\tilde{T}} - 1)}{\phi\tilde{T}} \right] + \frac{2}{\phi} (e^{-\phi\tilde{T}_c} - 1). \tag{A 6}$$

The mean deviation,  $D$ , is then  $D = A/\tilde{T}$ , and is a function of  $\tilde{T}$  alone. It is shown at the base of figure 2b.

(b) *Proportion of one component in a two component mixture*

As before, assume exponential decay so that  $m_1 = m_{1,0} e^{-\alpha_1 t}$  and  $m_2 = m_{2,0} e^{-\alpha_2 t}$ , where the subscripts identify the component and time. Expressing time,  $\tilde{T}_1$  in half-lives for component 1 gives  $m_1 = m_{1,0} e^{-\phi \tilde{T}_1}$  and  $m_2 = m_{2,0} e^{-\gamma \phi \tilde{T}_1}$  where  $\gamma = \alpha_2/\alpha_1 = \tilde{T}_2/\tilde{T}_1$ . (Note that  $\tilde{T}_2$  and  $\tilde{T}_1$  are not themselves the half-lives, but a given time expressed in an appropriate number of half-lives.) The proportion that  $m_1$  forms of the total left at any time is:

$$\frac{m_1}{m_1 + m_2} = \frac{m_{1,0} e^{-\phi \tilde{T}_1}}{m_{1,0} e^{-\phi \tilde{T}_1} + (1 - m_{1,0}) e^{-\gamma \phi (\tilde{T}_2 - \tilde{T}_1)}}. \quad (\text{A } 7)$$

For simplicity, suppose that there are equal amounts of both components to start with, so that  $m_{1,0} = m_{2,0}$ . Then

$$\frac{m_1}{m_1 + m_2} = \frac{1}{1 + e^{-\phi(\tilde{T}_2 - \tilde{T}_1)}} = \frac{1}{1 + 2^{-(\tilde{T}_2 - \tilde{T}_1)}} = \frac{1}{1 + e^{-(\alpha_2 - \alpha_1)t}}. \quad (\text{A } 8)$$

The second (general) and fourth (specific) forms of this relationship are shown in figure 4. From the third form it follows that for  $\tilde{T}_2 - \tilde{T}_1 = 1, 2, 3, 4 \dots$  the proportion that  $m_1$  forms of the whole is  $2/3, 4/5, 8/9, 16/17 \dots$ . For  $m_1/(m_1 + m_2) = 0.8$ , then  $\tilde{T}_2 - \tilde{T}_1 = 2$ , and  $(\alpha_2 - \alpha_1)t = -2 \ln(1/2) \simeq 1.4$ .

(c) *The age profile in the catotelm*

Suppose the catotelm contains a single component that is added at a constant rate per unit area and that decays exponentially according to  $dx/dt_c = -\alpha_c x$  where  $x$  is the amount of peat per unit area, then the amount of peat left after a time  $t_c$  is  $x e^{-\alpha_c t_c}$ . The whole bog may be considered from the *surface* (rather than the base) as a series of slices each of which has decayed for different times, and, in the limit,

$$X = \int_{t_c=0}^{t_c=T} p_c e^{-\alpha_c t_c} dt_c, \quad (\text{A } 9)$$

where the capitals  $X$  and  $T$  represent mass of peat and time respectively measured *downwards* from the present surface, at which  $X = 0$  and  $T = 0$ . This gives

$$X = \frac{p_c}{\alpha_c} (1 - e^{-\alpha_c T}). \quad (\text{A } 10)$$

The 'surface' is of course an arbitrary level, and the equation holds for any level provided that age and mass below that level are measured relative to that level.

Given a particular set of data for age at known depth (measured as cumulative mass below the surface) equation A 10 may be fitted and the value of  $p_c$  and  $\alpha_c$  estimated. A function,  $F$ , is defined that measures the badness of fit between the observed points and those calculated using arbitrarily chosen values of  $p_c$  and  $\alpha_c$ . This function is then minimized. A description of the procedure is given by Clymo (1978).

The method used here was the simplex of Nelder & Mead (1965) incorporated in the C.E.R.N. computer program D506 called MINUTS. The location of a minimum was refined by a variable metric method (Fletcher 1970), and the true errors estimated. The function,  $F$ , to be minimized included both deviations in cumulative mass for known age and deviations in age for known cumulative mass, as both are subject to sampling errors. Both components

were given approximately equal weight by standardizing by half the appropriate range. This gave a range for the standardized mass and time,  $X^*$  and  $T^*$ , from 0.0 to about 2.0. Specifically,

$$F = \left\{ \sum_{i=1}^{i=n} \left[ \frac{(X_i^* - \hat{X}_i^*)^2}{X_i^* + 0.5} + \frac{(T_i^* - \hat{T}_i^*)^2}{T_i^* + 0.5} \right] \right\} / n, \quad (\text{A } 11)$$

where the hat (^) indicates the calculated value. The addition of 0.5 avoided giving excessive importance to points near the origin. This function proved to give a single well defined minimum that was nearly parabolic, so that the standard error could be estimated. The minima were all in narrow diagonal valleys (the parameters were highly correlated) because the general slope is determined by  $p_c/\alpha_c$ , and the deviation from a straight line (which determines  $\alpha_c$ ) is not great. Other standardizations were used with very similar results. Weights inversely proportional to the error on individual points were applied in a few cases, but the results were nearly the same as with unweighted data and are omitted. Confidence limits were calculated in the way described by Hayward & Clymo (1982).

In theory, the minimum information needed to calculate  $p_c$  and  $\alpha_c$  is the age at three depths ( $T_1, T_2$  and  $T_3$ ), one of which may be the present surface of the catotelm, and the mass of peat, between any two levels, say  $X_{1,2}$ , between the top and the middle levels, and  $X_{1,3}$  between top and bottom levels. It is easy to show by substitution in equation A 10 that

$$\theta e^{-\alpha_c(T_3-T_1)} - e^{-\alpha_c(T_2-T_1)} - \theta + 1 = 0, \quad (\text{A } 12)$$

where  $\theta = X_{1,2}/X_{1,3}$ . This equation has two solutions: one is the trivial  $\alpha_c = 0$ ; the other can be found by numerical methods; simple Newton-Raphson and bisection methods are both suitable. The value of  $p_c$  may then be found by substitution in equation A 10.

(d) *Decay as a function of depth and thermal regime*

Suppose the peat is a homogeneous isotropic mass infinite in extent but finite in depth, and suppose that the surface temperature is caused to vary sinusoidally with a diurnal cycle superimposed on a yearly one.

Let the temperature at time  $t$  and depth  $Z$  be  $u_{t,z}$  then Carslaw & Jaeger (1947) show that

$$u_{t,z} = \bar{u} + A e^{-Z/W} \sin(\Omega t - Z/W) + a e^{-Z/w} \sin(\omega t - Z/w) \quad (\text{A } 13)$$

where  $\bar{u}$  is the mean temperature;  $A, a$  are the surface amplitude of the yearly and diurnal temperature changes  $\Omega, \omega$  are the yearly and diurnal frequencies, so that  $\Omega = 2\pi F = 2\pi/H$  and  $\omega = 2\pi f = 2\pi/h$ , where  $F, f$  are the frequency and  $H, h$  are the length of year and day respectively. The daily damping depth,  $w$ , is given by  $w = (2K/\omega)^{1/2}$ , where the thermal diffusivity,  $K$ , is defined as  $K = \lambda/\rho C$ . The thermal conductivity is  $\lambda$  and the specific heat is  $C$ . The yearly damping depth  $W$ , is similarly defined, and it follows that  $W = w (365.3)^{1/2} \approx 19 w$ . Let rate of decay as a function of temperature be  $\alpha_u$ . Then a description of the relation is given by

$$\alpha_u = b \{s + \exp(\beta u_{z,t})\}, \quad (\text{A } 14)$$

where the coefficients (fitted by minimization in the same general way that  $p_c$  and  $\alpha_c$  were) are:  $b$  = scale expansion factor;  $s$  = vertical shift;  $\beta$  = shape factor ( $\text{degree}^{-1}$ ). The temperature of zero decay,  $u'$ , is given by  $u' = \ln(-s)/\beta$ . To ensure that  $\alpha_u$  is effectively zero at all temperatures below  $u_u = 0$ , but that the transition is continuous, the cutoff function

$y = 1/\{1 + \exp[-\eta(u-u')]\}$  is used as a multiplier. With  $\eta = 150$  then  $y$  switches from within 1% of 0 to within 1% of 1 as  $u$  goes from 0.03 °C below  $u'$  to 0.03 °C above it.

The proportion of matter lost at depth  $Z$  between  $t_1$  and  $t_2$  is then obtained by numerical integration of  $\alpha_u y$  with the appropriate values of  $u$  given by equation A 13.

(e) *Dynamics of a raised bog*

Suppose that the peat bog develops in a flat-bottomed parallel-sided valley; that in longitudinal section it is hemi-elliptical (equation 29) for hydrological reasons; and that the height of the central (highest) point for which  $p_c$  and  $\alpha_c$  are constant is given by equation 13. (Much the same is true for a circular cupola of peat developing on a large flat plain, except that for a given height the bog is twice as far across.) The validity of these assumptions is discussed in section 8c where equation 32 describing the longitudinal section of such a bog in terms of the distance  $v$  from the centre is given.

The age against depth profile at any point on such a raised bog may be derived. In what follows the catotelm subscript  $c$  is omitted for simplicity. The height of the present surface at time  $t$  and at  $v$  from the centre can be obtained from equation 32. The height of the surface at the same point but at an earlier time,  $\tau$ , can also be obtained. But this old surface has had  $T = t - \tau$  in which to sink by decay of the peat below it and its present height must therefore be lower by a factor  $e^{-\alpha T}$ . It follows that the age ( $T$ ) against depth as cumulative mass ( $X$ ) relation is

$$X = \frac{p}{\alpha} \left\{ [(1 - e^{-\alpha t})^2 - \phi^2]^{\frac{1}{2}} - e^{-\alpha T} [(1 - e^{-\alpha(t-T)})^2 - \phi^2]^{\frac{1}{2}} \right\}, \quad (\text{A } 15)$$

where  $\phi^2$  represents  $v^2(\rho^2\alpha^2U/p^2k)$ . This relation is plotted in figure 21, using the same parameter values as were used to construct figure 20. This equation, unlike equation 7, contains both  $t$  and  $T$ : it is necessary to know when the peat began to accumulate. If age against depth profiles were known for several values of  $v$  on the same bog then it would in principle be possible to treat the time when peat began to accumulate as a parameter and to estimate it by minimization in the way already described. In practice, as figure 21 shows, the differences from equation 16 (which is true for the bog centre only) are likely to be small, so the estimate would be a poor one.

Although  $p_c$  is a constant and represents the rate at which matter passes into the catotelm at the bog centre, the rate elsewhere is, in general, not constant. Represent it by  $\tilde{p}_c$ , and omit the catotelm subscript henceforth for convenience. Because  $dx/dt = p - \alpha x$  at all times and places (by definition) it follows that  $\tilde{p} = dx/dt + \alpha x$ . This may be obtained by differentiation as

$$\frac{\tilde{p}}{p} = \frac{e^{-\alpha t}(1 - e^{-\alpha t})}{[(1 - e^{-\alpha t})^2 - \phi^2]^{\frac{1}{2}}} + [(1 - e^{-\alpha t})^2 - \phi^2]^{\frac{1}{2}}, \quad (\text{A } 16)$$

where  $\phi^2$  is as before. This equation has two independent variables,  $t$  and  $v$ . It is shown in figure 22 using the same parameter values as were used to construct figure 20.

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