



QUATERNARY LANDSCAPES

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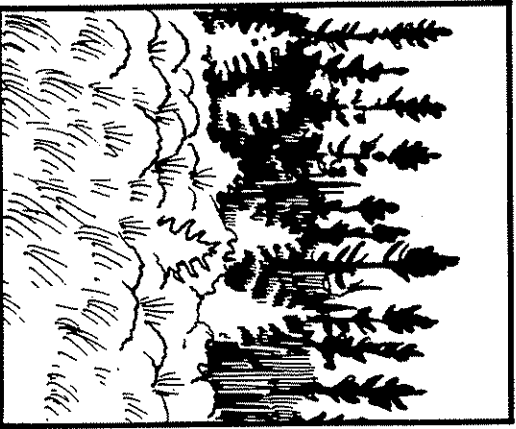
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Peat Growth

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Peatlands

Lake and marine sediments, ice caps, and peat are the main repositories of detailed information about late Quaternary landscapes. Peat, with which this chapter is concerned, is widespread, locally abundant, and easily sampled. About three-quarters of all peatlands are in the USSR and Canada; a single peatland complex in western Siberia is about 1,800 × 800 km (Walter, 1977). Peatland inventories differ in their definitions and accuracy. One recent estimate is that 297 Mha is bog-covered and 210 Mha is swamp-covered—a total of about 3.4% of the Earth's land surface (Matthews and Fung, 1987). An earlier estimate (Kivinen *et al.*, 1979) gave 420 Mha. If one assumes a mean depth of 2 m and a mean dry-bulk density of 0.1 g cm⁻³ in bog-covered areas, then there is about 240 Gt of carbon in peat—Stors (1980) estimates 300 Gt. This last is about four times the amount of carbon fixed on the Earth's land surface in a year. In a suitable environment peat accumulates moderately but conveniently rapidly: a rule of thumb is a rate of about 100 cm in 1,000–2,000 years. The record it entombs

is not confused by inwash or flow. The peat itself is predominantly the remains of plants that once grew on the surface but that have decayed incompletely—a fact that seems to have been first recognized by William King writing in 1685 (Gorham, 1953: 262): "your light spungy turf is nothing but a congeries of the threads of . . . moss . . . [which] is so quick growing a vegetable, that it mightly stops the springs, and contributes to thicken the surf especially in red bogs." The peat thus retains both a macroscopic record of the plants that formed it and a local and regional pollen record. The record may extend back 5,000–9,000 years. The record of industrialization over the last 400 years in the form of metals, soot, fly-ash particles, and the like is also retained.

Pollen analyses at intervals as close as 1 mm are now being used to investigate patterns of activity that span one or a few years only (for example, Sturhodoctir and Turner, 1983), and analyses of macroscopic remains are being used to elucidate details of ontogeny, both constructive (Janssens, 1983) and destructive (Tallis, 1985, 1987).

The rate of accumulation of peat varies greatly both in space and in time. Indeed the very idea of accumulation is widely misunderstood, as I explain later. The use of the record preserved in peat requires an understanding of the peat-accumulation process. What is accumulation? At what rate has peat accumulated? How are the small structures such as hummocks, lawns, hollows, and pools formed? How do they come to form a mosaic on the peatland surface? In what circumstances does peat-accumulating vegetation spread? Is there a limit to its spread? What part do productivity, decay, chemistry, hydrology, and ecology have in the accumulation process? Most of these questions require quantitative answers. Thirty-seven years ago Gorham, writing of the study of peatlands, recorded that "generally speaking, ecology has not yet advanced much beyond the stage of observation and description" (1953: 272). I hope to show here that we now have sufficient knowledge to begin to make quantitative predictions.

The Peat-Accumulation Process

Most peats accumulate as a consequence of waterlogging. Dead leaves, stems, and branches fall on the surface; roots grow down into the peat and die anaerobically; and mosses grow up and shade their own lower branches which then die *in situ*. Fungi, bacteria, invertebrate grazers, oxygen, and moisture at low aerobic decay, but at first the dead plant parts retain their macroscopic structure so that water can flow easily between the structural elements.

As decay weakens the dead plant matter, and as more dead matter (and perhaps a seasonal load of snow on top of unfrozen peat) is added to the surface, the structure collapses (Fig. 1). The dry-bulk density increases and, more important, the space between structural elements decreases. The hydraulic conduc-

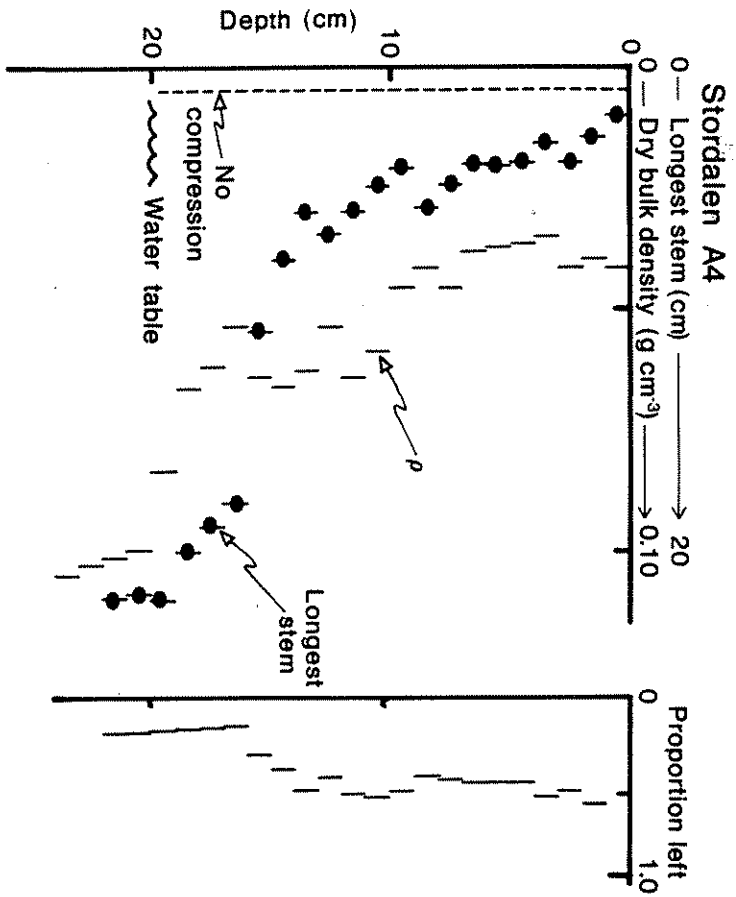


Fig. 1. Dry bulk density (ρ), length of the longest stem, and inferred decay (at right) in a core of *Sphagnum fuscum* peat from the Stordalen small mire, Abisko, northern Sweden, August 1976 (Clymo, unpublished data). The core was collected by means described by Clymo (1988). The proportion of the original dry mass left is calculated with the assumption that the extent of compaction can be inferred from the maximum length of *Sphagnum* stem in a slice. The maximum possible length was 22 cm—the width of the core—so the extent of decay below 19 cm is underestimated. See Fenton (1980) and Johnson *et al.*, (1990) for further details.

tivity decreases by several orders of magnitude. As long as precipitation and inflow (if any) exceed evapotranspiration, the water table will remain in the upper zone of high hydraulic conductivity, and water will seep away laterally. The water at the water table is oxygenated, and decay continues aerobically to a small distance below the water table. But oxygen can be replenished only by diffusion from above, and this is a slow process: the rate of diffusion of oxygen in water is barely 1/10,000th that of oxygen in air. Continuing aerobic decay therefore causes the peat to become anoxic and further decay is only by anaerobic processes, which (in peat) are much slower than aerobic ones. Consequently peat accumulates.

The accumulation of peat therefore involves an interaction between plant

productivity, hydrology, and the processes of decay. A full account would require numerous qualifications. For example, in the Arctic and Antarctic, low temperature in permafrost may substitute for anoxia as a cause of low rates of decay.

The importance of the distinction between the surface zone of aerobic decay and the underlying anoxic zone of slow decay has been gradually recognized during the last 40 years or so, as experimental measurements have accumulated. (It was suspected much earlier than this.) In translation the Russian terms for the two layers are *active* and *inactive* or *inert* (Ivanov, 1953). These terms in English are confusing because *active* means something quite different to geologists interested in permafrost than it does to ecologists, while the lower zone, far from being inactive, has crucial effects on peatland morphology. To avoid these problems Ingram (1978) introduced the general term *acrotelm* for the largely oxygenated surface layer with high hydraulic conductivity and within which the water table fluctuates, and the term *catotelm* for the underlying, permanently saturated and mainly anoxic layer of low hydraulic conductivity.

Requirements and Systems for Peat Accumulation

There are many general accounts of the sorts of peat-accumulating systems (e.g., Gorham, 1957; Moore and Bellamy, 1974; Gore, ed., 1983) and innumerable regional and floristic accounts. Of particular historic or recent importance are the works of Weber (1908) in Germany; Cajander (1913) and Euroala *et al.* (1984) in Finland; Osvald (1923), Störs (1948), and Malmer (1962) in Sweden; Crampton (1911) and Tansley (1939) in Britain; Kulczyński (1949) in Poland; Anderson (1983) in Malasia; and Rigg (1940, 1951), Conway (1949), and Heinselman (1970) in North America. The absence of any reference to Soviet work is unfortunate. The best account in English of one aspect of it—hydrological—is the translation by Thomson and Ingram of Ivanov (1975). In recent years some of the most exciting developments have been in the study of the enormous peatlands of eastern North America with their ovoid islands and water tracks. The work begins with Glaser *et al.* (1981), and Wright and Glaser (1983), and is partly summarized by Glaser (1987) and Damman and French (1987). Ideas about pool formation there have been elaborated by Foster *et al.* (1983, 1988) and Foster and Fritz (1987). This list is necessarily selective and personal. It may be supplemented by reference to the bibliographies made by Field and Goode (1981), and Gorham *et al.* (1985), and to the references in Gore, ed. (1983).

Most workers have recognized the interaction of water supply, water chemistry, and species-composition of the peat-forming vegetation. This is not the

place for another synthesis but it is worth noting a few of the characteristics generally thought to be important.

THE CHEMISTRY OF THE WATER SUPPLY

When the concentration of inorganic solutes is low, bog vegetation containing relatively few species develops. Shrubs of the heath family (Ericaceae), cotton-grasses (*Eriophorum* spp.), and especially bog-mosses (*Sphagnum* spp.) are ubiquitous. The last are particularly important because, though they can thrive only when the concentration of solutes is low, they are able to make the water around them acidic by a process of cation exchange (Clymo, 1963, 1984b); this and the low concentration of solutes make the environment unsuitable for most other plant species. Colonization by *Sphagnum* often marks profound ecological change.

The concentration of solutes may be low because the source of water is direct precipitation, or because the water has flowed over insoluble rocks, typically granite or sandstones. Where concentrations are too high for most species of *Sphagnum*, fen vegetation richer in species develops. Sedges, herbs, and trees, such as *Alnus* and *Salix*, are common.

The terms *ombrotrophic* (rainstorm-fed) and *minerotrophic* are used to describe vegetation nourished in these ways. Some authors would say that minerotrophic vegetation in parts of Finland, for example, may be more boglike than ombrotrophic vegetation in western Ireland (where *Cladium mariscus* and *Schoenus nigricans* grow in what is, by other criteria, bog). The concentration, nature, and rate of supply of solutes are the primary determinants; the source is secondary. Floristic distinctions may be subtle.

A MEANS FOR KEEPING THE PEAT WATERLOGGED

Three principal mechanisms of waterlogging are recognized. First, water may percolate through rocks or soil and emerge as springs or lines of seepage or simply as upwelling over a large area. Retention in a porous medium evens the flow rate. If water collects from a catchment and is funneled into a lower area, the effect is as if the precipitation were greater. Water of this kind often has a relatively high concentration of solutes and supports species-rich fen vegetation. But if the rocks are resistant to weathering, the emerging water may allow *Sphagnum* to establish.

A second category of water supply is that in small, relatively deep lakes. Here a mat of vegetation may encroach on the water from the edge of the lake. The water is replenished from a catchment, and the surface of the vegetation mat falls and rises as droughts and rain dictate (Green and Pearson, 1968). The water table is always about the same distance below the surface of the vegetation mat and not far below it. It is possible for *Sphagnum* and associated plants to estab-

Table 1. Electrical conductivity G_{corr} (with the contribution from H^+ removed) and pH at various points in Cranberry Moss after rain in July 1987

	G_{corr} ($\mu\text{S cm}^{-1}$)	pH
Inflow stream	390	6.5
Peripheral fen	180	5.5
Open lake	240	6.6
Lake, below floating vegetation	230	6.5
Rain	25	5.3
Hollow in <i>Sphagnum</i> mat	35	4.5
Hummock in <i>Sphagnum</i> mat	38	4.8

lish or to persist on such floating mats even when the chemistry of the lake water is unsuitable, provided that there is sufficient rain to maintain a downward washing of the mat. At Cranberry Moss on the border between Staffordshire and Cheshire in the English Midlands, a lake about 100 m across and 15 m deep is three-quarters covered by a floating mat of *Sphagnum*, *Eriophorum*, *Vaccinium oxycoccos*, and *Empetrum* about 1.5 m thick. The lake is surrounded by a 10–20-m-wide wooded fen. Drainage from fertilized fields runs in a ditch around the fen and, at one point, through a side branch into the lake. The ditch frequently floods and overflows into the fen and lake. The chemical conditions are shown in Table 1. The insulation of the surface of the floating *Sphagnum* mat from the lake water is remarkable. Areas of this kind are interesting but are usually small and of much less quantitative importance than the third kind.

The third mechanism occurs where the peat has accumulated above the regional groundwater table. Waterlogging in such circumstances implies a dynamically maintained, domed water table and precipitation as the source of water. Precipitation must exceed evaporation in most weeks in the year, but the proportion of rain days (days with 1 mm or more of precipitation) is important too. These conditions give rise to domed, raised bogs or, in constantly humid climates, to blanket bogs, both with abundant *Sphagnum*. It is astonishing that the first clear explanation in the English ecological literature of the cause of the domed water table seems to be that of Ingram (1982), though the idea had occurred to others including Weber (1908), Granlund (1932), Wickman (1951), and Ivanov (1953). Ingram pointed out that although the water table after rain would sink quickly through the acrotelm, because the hydraulic conductivity is high, it would sink very much more slowly through the catotelm. The plant structures have collapsed, the space between elements is much smaller, and the hydraulic conductivity, which is approximately related to the fourth power of the size of spaces between elements, is correspondingly and dramatically reduced. Water therefore seeps very slowly through the catotelm. The next rain

rapidly raises the water table again into the more porous acrotelm. Most ecologists—citations would be invidious—had vaguely invoked capillary forces, though Grandlund (1932) had pointed out that the height to which water could rise experimentally in peat was barely 0.5 m. This implies a radius of curvature of the meniscus of about 30 μm and spaces between elements of 0.03–0.06 mm. We know that the spaces within plant cell walls are much smaller than this, but even if they were continuous, the *rate* at which water could ascend would be determined by the fourth power law and would be inadequate to counter evaporation. Grandlund's 0.5 m is the practical limit. The same conclusion could have been reached by noting that the water table was close below or, in pools, above the bog surface and realizing that in a hole in jelly there is no water table. If the capillary explanation were adequate, a hole a handspan across in a raised bog should show a water table near the base of the bog and close to the regional water table, not close to the bog surface.

CHANGES IN TIME

The classical sequence of changes shows a shallow lake becoming filled by reed swamp, followed by fen vegetation, and this in turn replaced by bog. The whole process has been called terrestrialization. In other cases it seems that impeded drainage has allowed bog or fen to spread directly over mineral soil, often replacing forest—a process called paludification. A particularly impressive array of evidence—buried soil profiles, tree stumps, peat stratification, diatoms, and ^{14}C dates—has been assembled for the Kråkeböcken mires in Sweden (Foster and Fritz, 1987). Most boreal peatlands have probably originated by paludification (Sjörs, 1961).

It is apparent that a particular peatland may contain peat formed under different influences and to various extents at different times in the past. Some of the best examples are those now being revealed in North America. The most important difference between the peatlands of the Glacial Lake Agassiz and those studied in Europe seems to be that in the former the underlying calcareous till is included in the water-circulation patterns. A computer simulation (Siegel, 1983) suggested that recharge on a raised bog with a water table only 30 cm above the regional water table might cause water flow as deep as 15 m into the underlying till. It is salutary to discover that measurements in the field (Almendinger *et al.*, 1986; Siegel and Glaser, 1987) suggest that at some times of year water movement is upward into raised bogs in these mire complexes as well as into spring-fen and water track, and that in the *Sphagnum*-covered, raised bog, chemical conditions are unsuitable for *Sphagnum* as little as 50–100 cm below the surface, recalling those in the floating mat of Cranberry Moss (Table 1). That this delicate balance has been upset in the past is shown in places where fen vegetation has replaced bog (Glaser, 1987).

Surface Patterns

Many boreal peatlands show conspicuous surface patterns composed of the microforms hummock, lawn, hollow, and pool; Sjörs (1961) offers color photographs. The boundaries are rather arbitrary for, as Bragg (1982) showed, the frequency of surface altitudes on a regular grid shows no evidence of distinct categories. Ecological boundaries may be seen, however: the lower limit of *Calluna vulgaris* on hummocks in Europe is an example. These microforms may be organized into microtopes such as the ridge-and-flark structure (elongate hummocks and intervening pools) and a series of microtopes may form a bog mesotope. Large bog complexes are macrotopes. The arrangement of microtopes may be orderly as, for example, in the north of Scotland where Bragg and Ingram (reported in Ingram, 1987) found a series from the bog center outward of the six microtopes: perennial (large) pools, ridge-flark, hummock-hollow, dwarf sedge, dwarf shrub, and fen. This regularity has been widely recognized in the USSR (Ivanov, 1937) and seems to be found in eastern North America as well (Glaser and Janssens, 1986).

There has been much speculation about the origin of pools on raised bogs and blanket bogs, beginning with Crampton (1911:53), who believed that "they can only be due to movements in the peat." This idea was developed by Pearsall (1956), who suggested wrinkling or tearing of the surface as causes. Tearing is the likely explanation in a few cases where a peat mass is flowing very slowly over an underlying step in the rock, as it does at Muckle Moss (Pearson, 1960) and at Coom Rigg (Chapman, 1964), both in the north of England. But this mechanism is probably rare. Consensus seems to be growing that large pools on bogs develop where there is least flow of water and that they develop from hollows in which either the rate of production is lower than it is in their surroundings, or the rate of decay is higher, or both (Boatman, 1983; Hulme, 1986; Ingram, 1987; Foster *et al.*, 1988). But there is still much room for debate, and the extent of pool development differs enormously from site to site (Fig. 2). The origin of strings and flarks is in much the same state (Foster *et al.*, 1983; Foster and Fritz, 1987): there are interesting hypotheses and accumulating evidence.

For the immediate purpose it is sufficient to recognize that these surface features are widespread, though not ubiquitous. Can they be found below the surface, too? Sernander (in von Post and Sernander, 1910) suggested that in places where a mosaic of active hummocks and hollows (the "regeneration complex") exists, there might be a cyclic alternation in time of hummock and hollow leaving regular lenticular structures in peat. The evidence was slight, and the structures may have been inferred from the surface features, but the idea was accepted and used by Oswald (1923) to interpret his mainly phytosociological work on Komosse. The hypothesis was spread by Clements (1916) and by Tansley (1939), who published an account of cores from two bogs in Ireland, collected

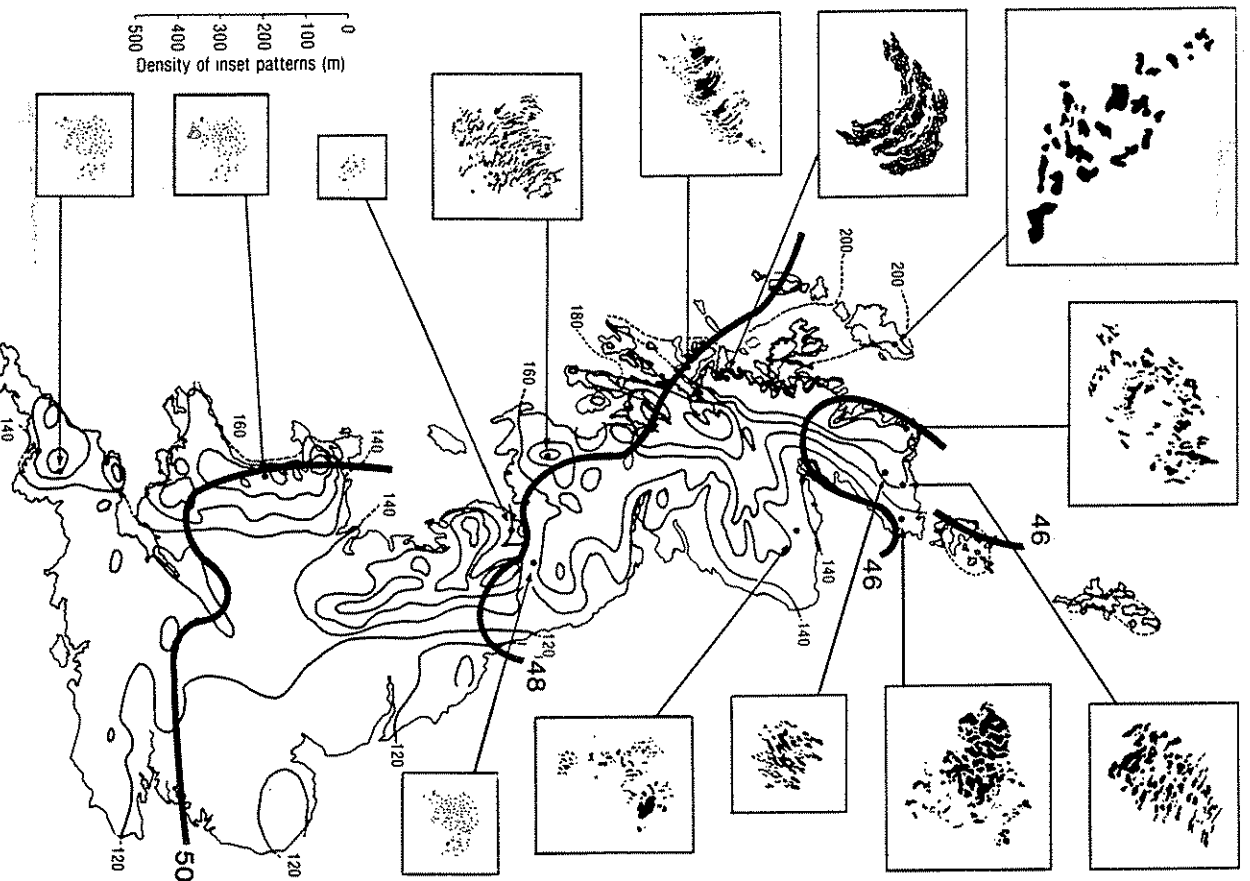


Fig. 2. The distribution of patterns of peats on bogs in Britain. The fine lines are isopleths of mean wet day yr^{-1} . The broad lines are isotherms ($^{\circ}F$) of mean daily mean temperature (46, 48, 50 $^{\circ}F = 7.8, 8.9, 10.0^{\circ}C$). From Lindsay *et al.* (1988). (With permission: Nature Conservancy Council.)

in company with and interpreted for him by Oswald. The idea was given even wider circulation by War (1947) in his influential Presidential Address to the British Ecological Society. This was its apogee. Some ecologists were already uneasy about it. First Walker and Walker (1961), then Casparie (1969), Barber (1981), and Svensson (1988) sought in vain for evidence on cut peat faces. Backéus, who also sought without success for unpublished evidence in Serlander's notebooks, comments that all the detailed work has "taken place in maritime areas where Oswald himself did not expect cyclic regeneration to play a major role" (1987:122). Yet Tansley writes, "In the summer of 1935 the author . . . [examined] . . . some Irish raised bogs in the company of Professor Oswald who interpreted the details of their vegetation and peat structure in the field. . . . A boring was made by Professor Oswald . . . in the middle of the typical 'regeneration complex' . . . A detailed record is annexed (Table XXI)" (Tansley, 1939: 688 and 690). This appears to be the only detailed evidence interpreted as supporting the hypothesis. There are few areas more maritime than Ireland. Evidence of such structures in the lower layers of peat is more dubious. Cut peat faces in these zones are less often exposed for detailed examination, and selective decay may have removed the evidence. We cannot, at present, be sure whether or not strong surface patterning is a relatively recent development.

What has emerged very clearly from the detailed work on cut peat faces is abundant evidence of subsurface structures at least as complex as those we see on the surface today. These imply bewildering local variations in space and time of plant productivity and decay. The variations are not just local. There are often "recurrence" horizons (Granlund, 1932) in peat, which can be traced laterally over a whole bog, where a layer of highly humified peat is sharply delimited from an overlying layer of less-humified peat. These horizons usually are interpreted as a response to changes in climate but are often not contemporary in bogs in the same district. There seems to be an element specific to the internal dynamics of the growth of the bog. An additional complication is that bogs at different altitudes, with different temperature and hydrologic regimes, may respond differently to the same change in regional climate if one bog is thereby moved over a response threshold while the other is not (Conway, 1948).

A particularly well documented example is Store Mosse near Vänamo in South Sweden (Svensson, 1988). Macrofossils were recorded in 2,019 samples from 49 cores, 30 on a single 1,800-m transect. Three *Sphagnum* phases were observed. Basal peats of many types of fen were replaced over large areas about 7,000 yr B.P. at a depth 4-4.5 m below the present surface by *Sphagnum* peat—mostly by *S. fuscum*-type but in some places by *S. rubellum*-type. This peat becomes more humified with remains of *Ericaceae* and *Eriophorum vaginatum*. The second *Sphagnum* phase, which begins about 2,400 yr B.P. at 3 m below the present surface, is more varied with *S. caspiata*-type replaced by *S. fuscum*- or *S. rubellum*-types. Again a highly humified layer occurs, then the

third *Sphagnum* phase begins about 1,000–1,200 yr B.P. at 2 m below the surface with *S. cuspidata*-type replaced by *S. magellanicum*-type, but with *S. rubellum*, *S. fuscum*, or *S. imbricatum*-types below present-day strings. The highly humified layers correspond with periods of low lake levels, and the beginning of the second and third *Sphagnum* phases with high lake levels (but the *S. fuscum* stage began when lake levels were low). It seems clear from this enormous mass of evidence that the changes were synchronous over a large area of the bog and most are probably attributable to change in climate, though it is not known why different species should have been favored.

We must conclude that no single hypothesis is likely to explain more than a small proportion of the observed and observable phenomena of peat growth. But we can examine the processes that contribute to peat growth, measure their rates, and try to show what consequences must follow. We should not expect to find real cases that fit our predictions exactly—peatlands are too complicated—but we may hope to find the trends we predict, in simple cases at least. It is to this that I now turn. Most of what follows is concerned with bogs because they are simpler and better known. A brief examination of surface hydrology precedes consideration of decay processes.

Hydrology of the Acrotelm

The range of conditions in the acrotelm may be understood by considering the fluctuations in the water table at the surface of a bog. A comprehensive review is given by Ingram (1983). The water table responds rapidly to rainfall. The hydraulic conductivity of the acrotelm (Fig. 3) has been measured by an ingenious field method (Brags, 1982). Conductivity decreases close to exponentially down the acrotelm, which thus behaves like a V-notch weir, as can be seen in the hydrograph shown in Fig. 4. Where the conductivity is high, the water table falls quickly. Where it is lower, it falls in steps, probably reflecting the importance of evapotranspiration during the day. A long-term summary as a residence curve is shown in Fig. 5. For half the time the water table is within a few centimeters of the mean level, but the curve is asymmetric. In droughts the water table sinks 20–30 cm. The layer between the extreme lows and the mean water table is thus occasionally oxygenated and this, one assumes, affects the rate of decay and the nature of the microorganisms. Those in the layer that is alternately oxygenated and anoxic may be facultatively anaerobic.

Decay

The immediate agents of decay—fungi and bacteria—are present in peat (Table 2). Fungal mycelia are abundant in the oxygenated zone but become much rarer

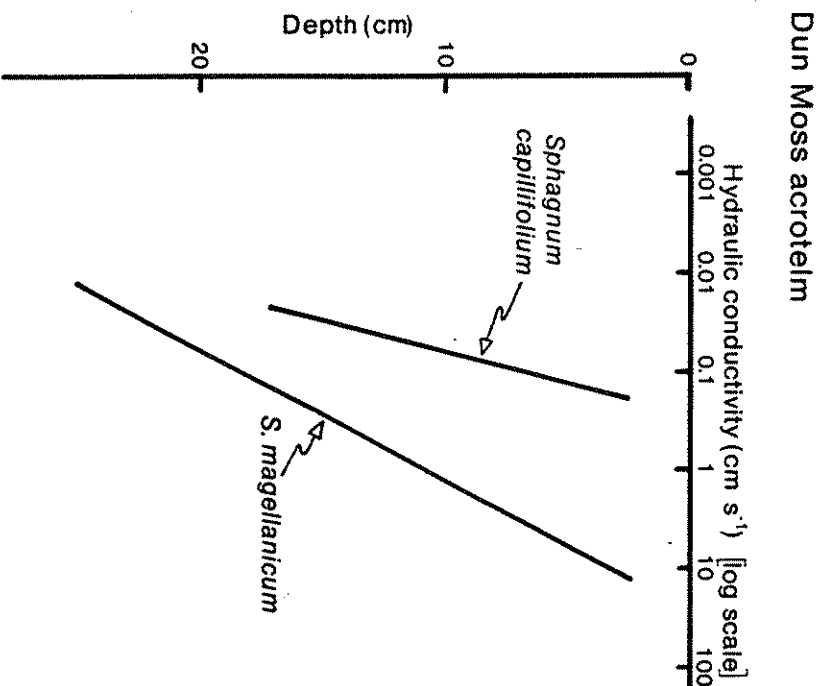


Fig. 3. Variation of hydraulic conductivity with depth in two low hummocks on Dun Moss, in the southern Grampian foothills of Scotland. The lines shown were obtained by differentiating a line, assumed to be straight, of field measurements in relation to depth (Brags, 1982). The r^2 for the field data was > 0.99 . (With permission from author.)

as one moves down into the anoxic zone. The same is true of aerobic bacteria. Anaerobic bacteria are as abundant as aerobic ones in the topmost zone—they may survive in microanoxic pockets there. In the lower layers they do not seem to become more abundant, but they do not diminish. Burgeff (1961) was unable to isolate viable bacteria from deep in the acrotelm of raised bogs, and there is a persistent though implausible belief that because *Sphagnum* can be used as a wound dressing, it and peat formed from it are sterile. Anyone who has tapped a pocket of methane deep in the peat while peat-boring may suspect that there is some microbial activity; Waksman and Stevens (1929), Waksman and Purvis

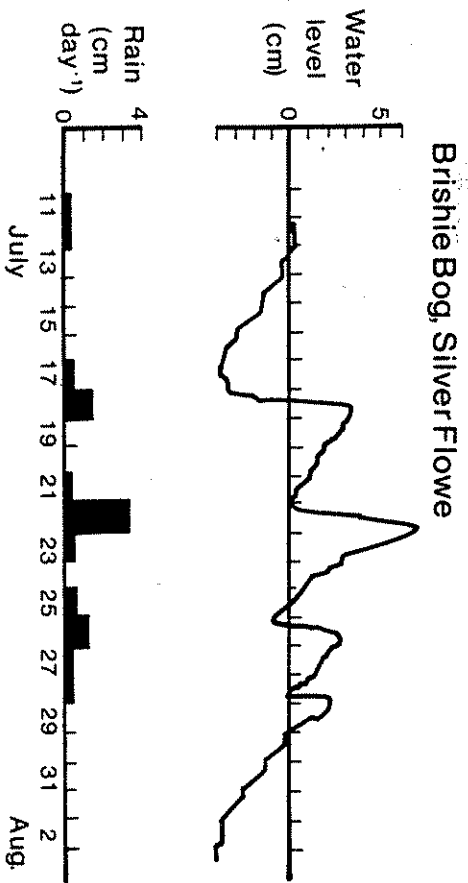


Fig. 4. Temporal variation in water level and rainfall in a pool on Brishie Bog, Wigtownshire, south-west Scotland. After Boatman and Tomlinson (1973). (With permission: *Journal of Biogeography* 10:223; originally published in *Journal of Ecology* 69 [1981]:897-918.)

(1932), and Benda (1957) all isolated anaerobic bacteria from deep in the catotelm.

In the acrotelm, invertebrate grazers may help to accelerate the rate of decay (Coulson and Butterfield, 1978). Comparison of losses of mass from litter bags with large and small meshes showed that 43% of the loss of *Calluna vulgaris* shoots was attributable to invertebrates comminuting the plants. For *Rubus chamaemorus* it was 27%, but it was only 1% for *Eriophorum vaginatum* leaves and even less for *Sphagnum recurvum*. Here is the first sign of selectivity among

Table 2. Abundance of fungi and bacteria in the surface of blanket-bog peat at Moor House, north-cm England

Depth (cm)	Zone	Fungi: stained mycelium (m g ⁻¹)	Aerobic bacteria (10 ⁵ g ⁻¹) (range)	Anaerobic bacteria (10 ⁵ g ⁻¹) (range)
0-5	"Litter"	2450	9-260	9-230
5-12	Dark brown	1030	6-150	32-200
12-20	Green-brown	750	11-76	16-500
20-32	Red-brown	200	1-42	28-260

Note: Fungal abundance was estimated by the length of stainable mycelium; bacterial potential (of many different groups) was estimated by counting colonies on nutrient agars of various sorts (Collins *et al.*, 1978). Water-table depth was about 15 cm. The red-brown zone was probably anoxic.

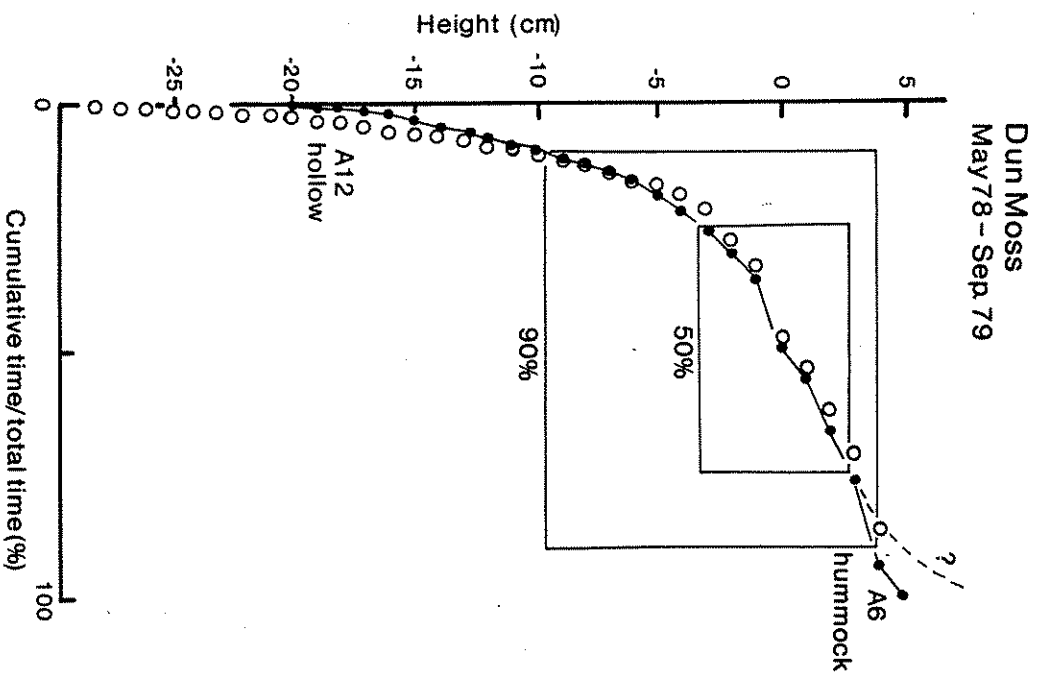


Fig. 5. Water-table residence curves for a hummock (A6) and a hollow (A12) on Dun Moss, Scotland. The vertical axis is centered on 50% residence. The small rectangle encloses 25-75% residence; the large, 10-90% residence. Measurements were made at approximately weekly intervals so occasional brief, high-water levels will have gone unrecorded. These are indicated by the broken line. From Bragg (1982, with permission from author).

species—an important factor limiting the usefulness of macrofossils in peat as indicators of the previous mire-surface vegetation.

The rate of decay in the acrotelm has been measured by a variety of methods. The loss in mass, or in tensile strength, of standard cellulose strips is useful for comparing sites; however, the strips tell little about the decay of natural materials, which are losing constituents of different kinds at different rates as the acrotelm, defined as a functional zone, gradually moves up past them. Litter bags have proved the most generally useful technique. Reviews of this sort of work have been made by Heal *et al.* (1981), among others. Three questions are frequently asked. (1) Why do some plants decay more rapidly than others? (2) How does decay rate change over time? (3) How does the rate of decay change with depth at which the material is found?

WHY DO SOME PLANTS DECAY MORE RAPIDLY THAN OTHERS IN THE SAME HABITAT?

In many studies the rate is correlated with chemical constituents of the plants. For example, Ohlson (1987) found that 45–80% of the mass of leaves of *Carex rostrata* from a spring fen and from an adjacent intermediate fen were lost in one year, and that the rate depended partly on the origin of the leaves and partly on the habitat in which they were placed. The rate of loss was correlated in various circumstances with the concentrations of nitrogen, phosphorus, and potassium. Concentrations of all three were relatively high, and the range was not great. In a survey of the results of 22 experiments on bog plants, in which the nitrogen concentrations were low and ranged from 0.5% to 2.1%, there was a positive correlation between decay rate and concentration (Clymo, 1983). There are multiple correlations between the concentration of different elements. This problem was avoided by Coulson and Butterfield (1978), who obtained plant material with increased concentrations of nitrogen or phosphorus by applying specific fertilizers to natural bog vegetation, then used material harvested from the fertilized plots for litter-bag experiments. By this means they were able to show that increasing the nitrogen concentration, specifically, increased the decay rate, but increasing the phosphorus concentration did not. The graph in Clymo (1983) can thus be treated as a regression. The loss of mass is $10\% \text{ yr}^{-1}$ at 0.7% nitrogen concentration, and 50% at 1.7%, giving a slope of 40. No doubt other intrinsic factors operate too, but chemistry seems to be of great importance.

HOW DOES DECAY RATE CHANGE OVER TIME?

The usual technique is to put out litter bags and to recover them at intervals for several years. In practice it is rare to be able to make measurements for more than five years. The results of Heal *et al.* (1978) were analyzed by Clymo (1984a), who showed that for *Rubus chamaemorus*, *Calluna vulgaris*, and *Eriophorum*

vaginatum it was not possible to distinguish between the hypotheses (1) that the rate of loss was a constant proportion of the original mass in each year for five years or (2) that it was a constant proportion of what was left at any time. The problem arises because these data have a fairly large coefficient of variation, and the two hypotheses do not become readily separable until 70–80% of the original material has disappeared, by which time other sorts of bias—collapse of the litter bags, loss of fragments, and so on—become important. It is also the case that the longer an experiment continues the more likely it is that the effects of age become confounded with changes in the environment as the acrotelm moves up past the litter bags.

HOW DOES THE RATE OF DECAY CHANGE WITH DEPTH?

Again the most frequent technique is to put litter bags at known depths. The results differ in detail (Clymo, 1965; Heal and French, 1974) but agree in showing that the rate of decay in the acrotelm is relatively high and that it declines in the catotelm (Fig. 6). The plant material placed at different depths was from a single batch, so the lower rate of decay in the catotelm must be a consequence of the different environment. It is not simply that readily decomposable material has been removed and only refractory material remains.

As the acrotelm moves up past a particular piece of organic matter, the rate of decay of the plant material changes, partly because its chemical composition changes (because of the accumulated effects of decay thus far) and partly because the thermal, hydraulic, chemical, and microbiological environment changes too. What we need to know ultimately is how the rate of decay changes as a consequence of all these factors. It may take 20–100 years for the acrotelm to pass by, and research grants do not last that long. In a few favorable cases there are indirect ways of making such measurements. The earliest, and still the best measurements, were those by Baker (1972) on the antarctic moss *Chorizondonium aciphyllum*, which, with other species of moss, forms peat banks 1–2 m deep. Annual increments of about 2 mm yr^{-1} can be identified. Baker assumed that the rate of addition of dry matter had been approximately constant and by weighing segments spanning a known age was able to calculate the rate of decay (Fig. 9, discussed below). A similar approach was used by Fenton (1980) on the same moss banks and by Johnson *et al.* (1990) on *Sphagnum* in southern Sweden. Fenton measured the angle that the moss stems make as they collapse and compared the dry-bulk density calculated from this with that measured. He assumed that differences were attributable to decay. Johnson measured stem lengths in slices of known thickness for the same purpose. It is surprising that all three found indications that decay in the acrotelm was slow near the surface, then became rapid, then slowed again. Figure 1 (apart from the top 1-cm slice)

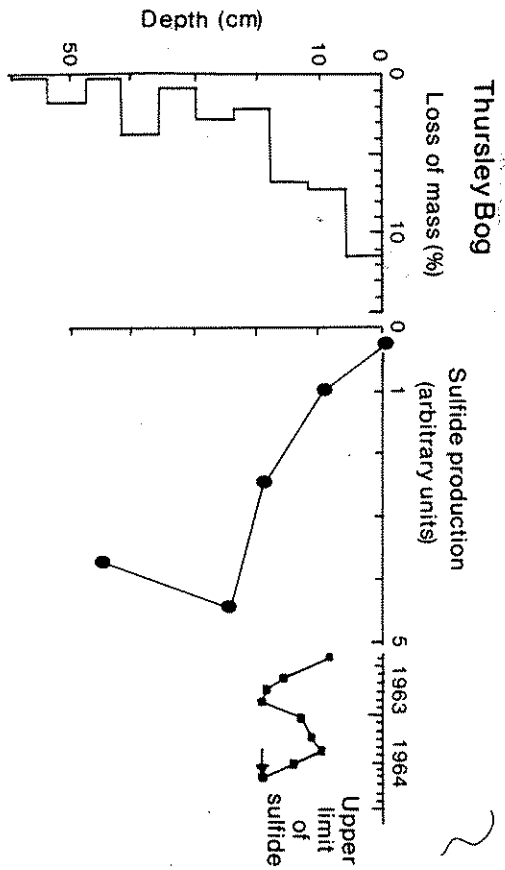


Fig. 6. Profiles in the surface of Thursley Bog, southern England, of decay rate of *Sphagnum papillosum* in litter bags, sulfide production in enrichment cultures, and seasonal upper limit of sulfide detectable on a silver wire in the field. From Clymo (1965). (With permission: *Journal of Ecology* 53: 753.)

shows the same effect. Extension of this work is hindered by lack of reliable techniques for dating samples in the acrotelm.

Before leaving the acrotelm it is worth considering the question: is the rate of decay in hollows markedly different from that in hummocks and ridges? The question is important because large pools, once formed, seem to be long-lived if not permanent (e.g., Foster *et al.*, 1988). Many contain little vegetation, and it is easy to see why they persist. In one plausible scheme a pool begins as a hollow in which productivity is less than in its surroundings, decay is more rapid, or both. It then accumulates peat less rapidly and so falls behind. But the intrinsic rate of loss of mass from bog litter put into hollows was only about half that of similar material put into hummocks (Farish and Grigal, 1985). Claricoates (unpublished) has measured the efflux of carbon dioxide and methane throughout the year from two bogs in northern England. The mean fluxes of $\text{CO}_2 - \text{C}$ ($n = 30$) from hollow, lawn, and hummock sites from which green matter had been removed were 80, 61, and $320 \text{ mg m}^{-2} \text{ day}^{-1}$ and of $\text{CH}_4 - \text{C}$ were 15, 10, and $1 \text{ mg m}^{-2} \text{ day}^{-1}$. Some of these gas effluxes would be from the acrotelm, but the strong seasonal variation implies that most efflux is from the acrotelm. The loss from hummocks is about five times that from hollows. Silvola (1986) measured much-increased rates of carbon-dioxide efflux from a Finnish bog in which the water table had been lowered. Higher rates of CO_2 efflux from

hummocks would be explained if the acrotelm there were thicker than in hollows. Certainly the water table is farther below the surface of hummocks than it is below that of hollows, though in some cases fluctuations below hollows are greater than below hummocks (Bragg, 1982).

Nils Malmer and Bo Wallén of Lund offer an interesting ecological explanation for this. Hollows commonly contain *Sphagnum* and sedges. The sedges are able to flourish in waterlogged conditions, which kill ericaceous shrubs, but the sedges lack woody stems and give little support to *Sphagnum*. By contrast, in drier conditions on hummocks, woody ericaceous shrubs are able to grow and suppress sedges. The stems provide support around which *Sphagnum* grows up. This in turn stimulates the development of newly buried stems of adventitious roots, and renders the plants potentially immortal (Forrest and Smith, 1975; Wallén, 1980). The woody structures thus maintain a thicker acrotelm than do the sedges in wet hollows, and this in turn allows a longer time for decay. Even if the productivity of the drier sites were greater, the flux of peat from the acrotelm down into the catotelm might be less than in wetter sites. The essential and striking element of this hypothesis is that the hummocks, which are higher, are adding peat to the acrotelm more slowly than are the hollows, which are lower. As the hollow slowly rises relative to the hummock, so the thickness of the hummock acrotelm decreases, and it begins to add peat to the catotelm more rapidly. There is thus a negative-feedback mechanism that prevents a hummock drawing away from a hollow but also prevents it being overtaken by the hollow. Hummocks and hollows should tend to persist, though their relative importance will be affected by climate wetness, as appears to be the case (Walker and Walker, 1961; Barber, 1981). There is an important distinction here between hollows, which have a complete vegetation cover, and pools, which do not. Pools are failed hollows.

Decay in the catotelm has not been studied widely. The rates are low and therefore not easily measured, and because they are low, they were thought to be unimportant. One obvious bacterial activity is the production of sulfide which, at the pH prevailing in bogs, is mostly in the easily detectable form H_2S . The upper limit of detectable blackening on a silver wire or on a silver-plated sheet has often been used to record the depth at which the peat has become effectively anoxic. An example of the fluctuations is shown in Fig. 6. It seems that sulfide production is at its greatest at the top of the catotelm about 20–40 cm below the surface (Fig. 7). There is a good correlation between sulfide activity and "redox potential" (Claricoates, unpublished). The amount of sulfide produced need not necessitate much decay. Direct measurements of methane efflux do imply decay, however, and have been recorded by, among others, Clymo and Reddaway (1971), Swenson (1980), Swenson and Rosswall (1984), Harriss *et al.* (1985), and Claricoates (1990). Efflux of methane from wetter sites is usually greater by a factor of 2–8, as already listed, than from sites with a lower

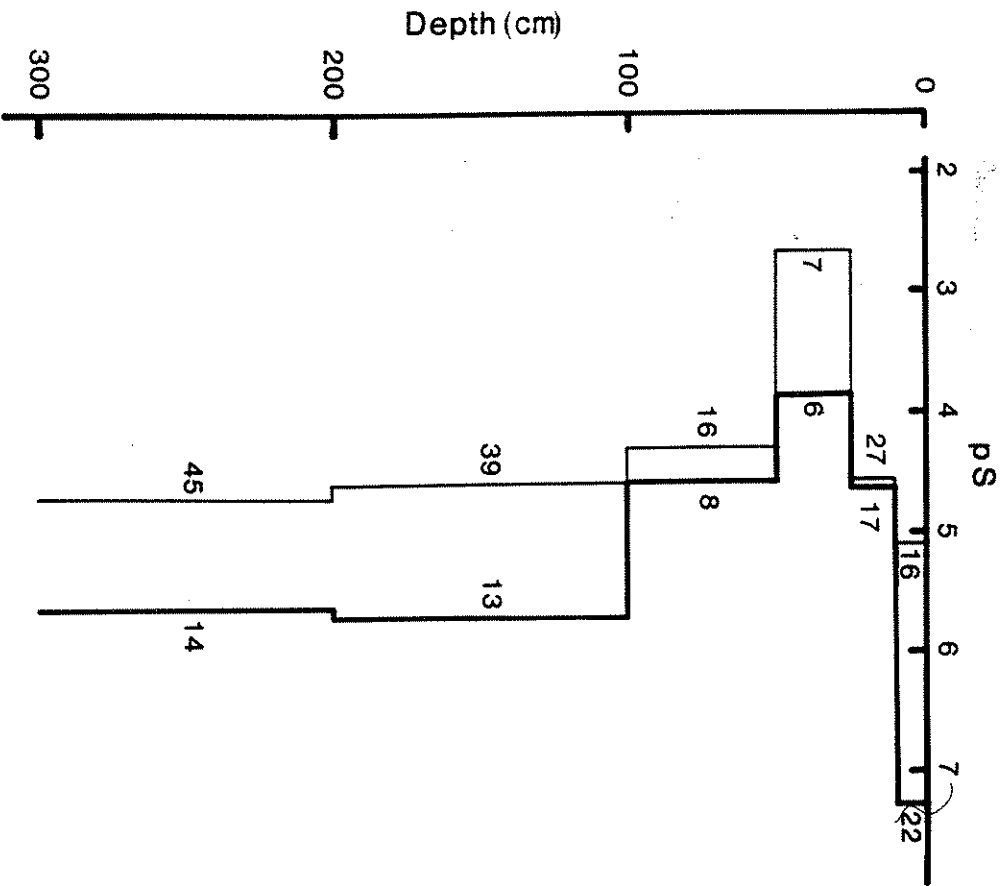


Fig. 7. Two profiles to 3 m depth of mean pS (analogous to pH) in peat at two sites at Moor House, northern England. Samples were brought to the surface and immediately placed in antioxidant buffer at high pH, thus trapping all forms of sulfide. Vertical lines plot average pS of the number of samples shown in each interval. Claricoates (1990). (With permission from author.)

water table. Erratic high values—perhaps the escape of bubbles—seem common. It is not obvious why there should be such differences if most of the methane has been produced in, and diffused from, the catotelm. It is possible that aerobic, methane-oxidizing bacteria remove gas as it passes up through a hummock. Svensson and Rosswall (1984) show that methane-producing potential is

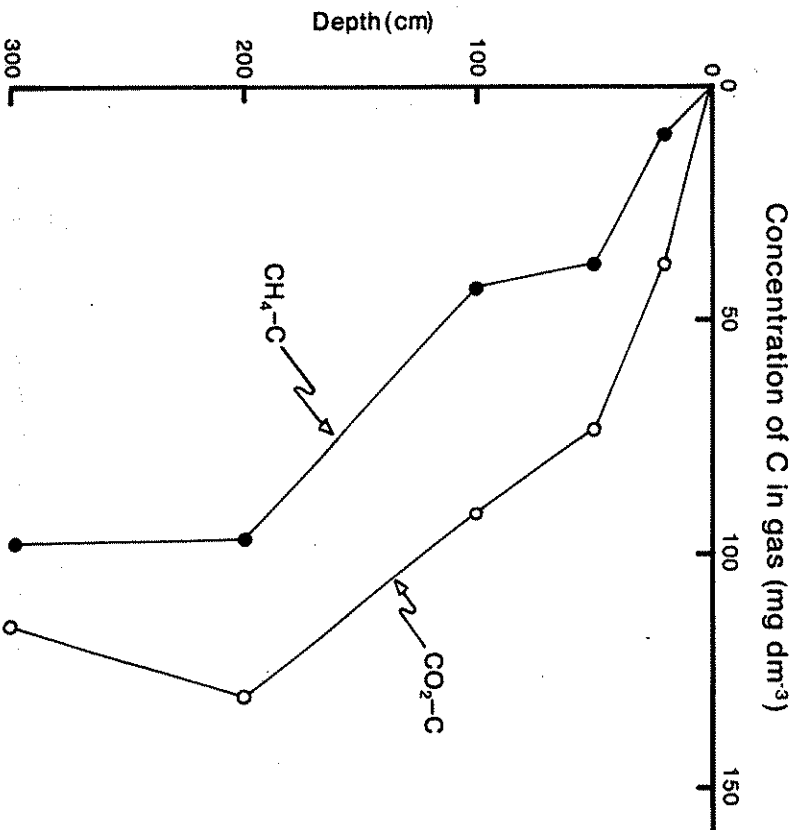


Fig. 8. Concentration of carbon from methane and carbon dioxide in peat at different depths at Moor House, northern England. Claricoates (1990). (With permission from author.)

greatest at the top of the catotelm (where pS and redox potential show minima), but they also found that methane concentration increased steadily down to 30 cm—the greatest depth sampled. Claricoates (1990) has sampled peat at much greater depths and finds that the concentrations of both carbon dioxide and methane increase with depth (Fig. 8). The only plausible explanation of such profiles is that gases are still being produced in the catotelm, and are not simply fossil. Calculations based on the assumption that gases leave solely by diffusion are consistent with a rate of decay of about 0.0002 yr^{-1} (Clymo, 1984a).

The efflux values for $\text{CH}_4 - \text{C}$ vary widely: Median values of about $20\text{--}50 \text{ mg m}^{-2} \text{ day}^{-1}$ seem common, but Hattiss *et al.* (1985) found a mean of $114 \text{ mg m}^{-2} \text{ day}^{-1}$. If this continued throughout the year it would amount to $42 \text{ g m}^{-2} \text{ yr}^{-1}$ —a significant fraction of surface productivity on bog sites. The explanation

is probably that the measurements were made in August, in which month Claricoates (1990) found methane-efflux rates were at their highest, and perhaps 2–5 times winter rates. This seasonal fluctuation again suggests that most of the efflux is of methane newly produced in an active zone just below the acrotelm, with a smaller, nonseasonal efflux of catotelm methane.

Peat Accumulation

We can now consider how in a very simple case a peat bog might accumulate peat. If we start from nothing, the earliest stages of accumulation would be something like those shown in Fig. 9(b). To construct this one must know, or surmise, how productivity and decay rate change over time. To illustrate, assume that productivity is constant (year-to-year fluctuations, which certainly occur, have little effect on accumulation). For peat bogs there are no reliable data of decay as a function of age, confounded with depth, and so on, so let us use the Antarctic *Chorisodontium* data in Fig. 9. Two approaches are possible: either to make some ecologically credible, though oversimple, assumption, or to get a good fit to these data by some ad hoc function. As an example of the first, assume that the rate of decay is directly proportional to the mass of material. This gives the exponential decay curve in Fig. 9(a). For the second, the temptation to use a polynomial must be resisted: nearly always, one will wish to extrapolate, and polynomials are generally unstable and unrealistic beyond the data used to obtain them. Polynomials include straight lines as their lowest member. The unhelpful consequences of using them for peat accumulation were shown by Jones and Gore (1978). For illustration I have used a function that swings from one asymptote to another—a "wall function." This does not go through the origin, but in practical cases is close to it—within 2% for *Chorisodontium*. It tends toward a lower asymptote, implying that part of the plant matter is totally refractory. In the very long term this may be thought to be unrealistic, but in practice would not be invoked because by that time the material would be in the catotelm, which must be considered separately.

The accumulation of peat with these assumptions is shown in Fig. 9(b). Although the two curves in Fig. 9(a) differ substantially, there is little difference in the accumulation curves over the span of these data (about 40 years). Only at 60 years do they begin to diverge greatly. Thereafter the differences increase steadily because the exponential is tending toward an asymptote at p/α with a slope of zero, while the wall function tends toward an upward slope of $p\nu$ because the wholly refractory matter of proportion ν simply accumulates.

The important point is that at some stage the acrotelm, defined by the predominantly aerobic decay processes, will have passed upward and left the peat as it now is in the quite different environment of the catotelm. The transi-

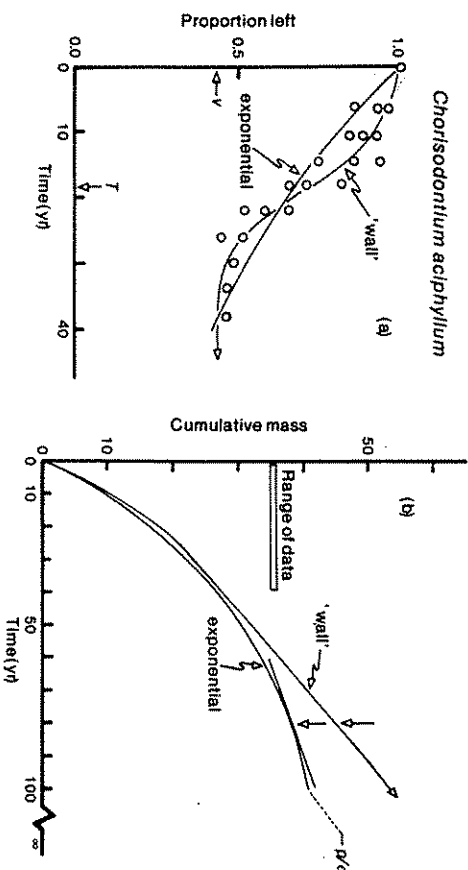


Fig. 9. (a) Decay of *Chorisodontium aciphyllum* in the maritime Antarctic. Redrawn from Baker (1972, with permission: *British Antarctic Survey Bulletin* 27: 126). The hollow curve is the best fit exponential, including 0, 1.0 as a fixed point; the sigmoid curve is the best fit of an ad hoc "wall function." (b) Cumulative mass of peat assuming constant rate of addition and decay according to the exponential or "wall function" of (a). The slope at these points is the apparent rate at which the acrotelm has finally passed by. The slope at these points is the apparent rate at which the catotelm receives matter at its top, compared with the slope at the origin which is the rate at which it enters the acrotelm by plant production. If m_t is the mass at time t , then the exponential in (a) is $m_t/m_0 = \exp(-\alpha t)$ where α controls the tightness of curvature. The "wall function" is:

$$\frac{m_t}{m_0} = 1 - \frac{(1 - \nu)}{(1 + \exp[-r(t - T)])}$$

where ν is the lower bound, T is the time of steepest descent, and r controls the curvature. The best-fit values to these data are: $\alpha = 0.0215 \text{ yr}^{-1}$, $\nu = 0.434$, $T = 18.0 \text{ yr}$, $r = 0.216$. The curves in (b) are obtained from $M_t = \int_0^t p m_t/m_0 dt$ where p is the productivity (assumed = 1.0 for illustration). For the exponential $M_t = (p/\alpha)(1 - \exp[-\alpha t])$. For the wall function:

$$M_t = p \{ \nu t - [(1 - \nu)/r] \{ \ln(1 + \exp[r(t - T)]) - \ln(1 + \exp[rT]) \} \}$$

tion will not be sharp: it may last for tens of years, and the conditions in the top of the catotelm may be sufficiently different (as Fig. 7 suggests) to justify recognizing an intermediate zone. But the difference between the acrotelm and all of the catotelm is so great that for exploratory purposes we may consider just two layers, and a sharp transition between them.

In Fig. 9(b) the transition is shown at 80 years, which for the *Chorisodontium* peat is about the age at which it is submerged by the top of the permafrost zone at 20 cm depth (Fenton, 1980). Two points of view must be considered.

The acrotelm, having reached this thickness, is now in a steady state. As it ascends, matter enters it at the top surface at a flux p (assumed 1.0 in Fig. 9),

and leaves it at the bottom at a flux given by the slope of the accumulation curve at 80 years in Fig. 9(b). For the exponential case this rate is 0.18 units of mass α^{-1} time $^{-1}$. For the wall function it is $\nu = 0.43$ flux units. For bog peats, real values are in the range 0.1–0.2 (Clymo, 1984a). The difference between input and "fallout" to the catotelm is what is lost by decay while the acrotelm is passing: 82% and 57% in the two cases here. The thickness of the wall-function acrotelm is only 19% greater than that of the exponential one, but it passes on 43% of what it receives and the exponential one passes on only 18%. The exact shape of the decay curve in Fig. 9(a) is therefore of considerable importance. Once the acrotelm is established its *accumulation* rate becomes zero because:

$$\text{input} = \text{decay} + \text{fallout}$$

There is a temptation to take the mass (on an area basis) in the acrotelm divided by the age of the bottom of the acrotelm, and to speak of that as "accumulation rate." For Fig. 9(b), that gives 0.56 and 0.48 flux units for the wall function and exponential cases. These are actually the mean accumulation rate *while the acrotelm was first becoming established*. Once established the acrotelm no longer accumulates: The catotelm is the true site of accumulation of peat.

From the point of view of the catotelm, the fallout from the acrotelm given by the slope of Fig. 9(b) is influx. This material has been modified extensively in quality and quantity from what was originally produced. Some of the surprising consequences of having mixtures of materials with different decay characteristics are explored by Clymo (1984a). If the flux into the acrotelm is constant, then so is that into the catotelm. In general the influx to the catotelm is a smoothed version of that to the acrotelm. The catotelm is dark, water-saturated, anoxic, and nearly isothermal. The contrast with the acrotelm must be similar to that experienced by a secondhand-car salesman entering a monastery.

We know little about the rate of decay in the acrotelm. About the catotelm we know nothing except that on the evidence of Fig. 8, decay does continue. We must make assumptions, see where they lead, and try when possible to compare their predictions with reality.

The simplest realistic assumptions are of constant input to the catotelm and of decay directly proportional to the mass of material accumulated. (These are the same as one set of assumptions made for the acrotelm, but the parameter values are smaller in practice.) The consequences are shown in Fig. 10. There is an asymptotic maximum depth at p'/α' (90 g cm $^{-2}$, equivalent to 9 m depth) compared with unlimited depth if there is no decay. Indeed, the depth is unlimited if there is any totally refractory material—the equivalent of $\nu > 0.0$ in the wall-function description of decay in the acrotelm. The true rate of accumulation is given by the slope of the convex curve at any time. Clearly it is p' and greatest at the start, and falls steadily toward zero as time passes. At all times

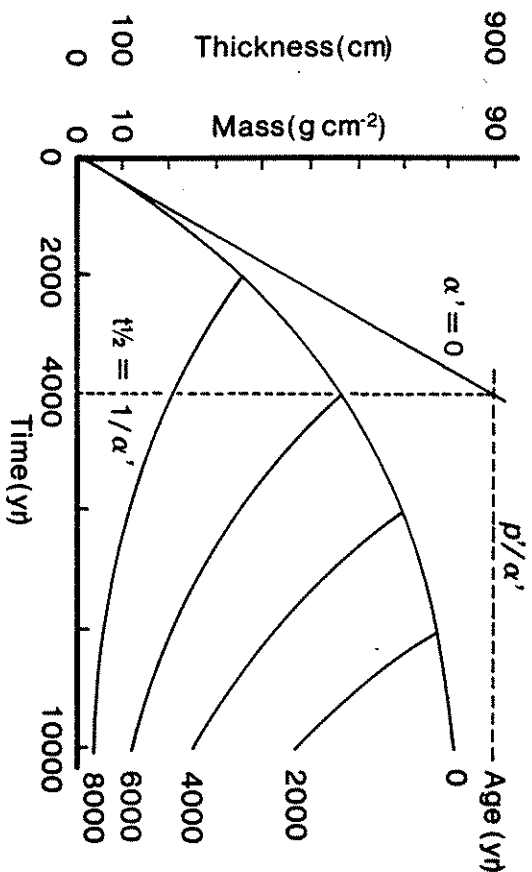


Fig. 10. Cumulative mass of peat in the catotelm assuming constant influx, p' , and proportional rate of decay, α' , with values 225 g m $^{-2}$ yr $^{-1}$ and 0.00025 yr $^{-1}$ respectively. The depth scale assumes that the dry-bulk density is 0.1 g cm $^{-3}$. The solid straight line is of slope p' and shows what would happen if there were no decay. The horizontal broken line is the asymptotic limiting thickness at p'/α' . The descending concave curves show the position of parcels of peat starting at the surface at 2,000-yr intervals and sinking because of decay below them. The formal description is that $dM/dt = p' - \alpha'M$ where M is the accumulated mass in the catotelm at time (t in the catotelm) t . From this $M = (p'/\alpha')(1 - \exp[-\alpha' t])$.

the surface of the acrotelm would be green and the influx to it would be constant, producing in turn constant influx to the catotelm. Yet the true rate of peat accumulation in the catotelm decreases steadily, and *must* do so, whatever the shape of the decay curve, provided that there is some decay and that there is no totally refractory material. The first is almost certainly true; the second is plausible. The intuitive belief that a green, healthy surface must mean rapid accumulation is difficult to uproot. Even more difficult to dislodge is the belief that accumulation rate in the past can be measured by taking the mass or depth between two horizons and dividing by the difference in age of those horizons. The danger of this practice may be seen in Fig. 10 (right side). In this case we know that the influx to the catotelm has been constant throughout, yet the application of the usual procedure would show a steadily increasing "rate of accumulation" and would no doubt invoke hand-waving reference to internal peat-bog dynamics and to an increasingly moist climate. If there is any decay then such procedures and such "explanations" must be suspect.

The pattern at the right of Fig. 10 shows one way in which the assumptions

of constant influx to, and proportional decay in, the catotelm may be tested. It is easy to show that for the assumptions given, then $M' = (p'/\alpha') (1 - \exp[-\alpha'z])$ where M' is the accumulated mass below a given horizon and z is age relative to that horizon. Again, a limit to peat depth at $M' = p'/\alpha'$ is a consequence. (The close similarity between the peat growth and the age-depth curves holds only for these assumptions.) Do we find the concave profile of age versus depth (as cumulative mass on an area basis), which Fig. 10 predicts? The assumptions are, in detail, rather implausible, so we should not expect close agreement. It was therefore astonishing to find that the best existing set of data with 55 dates on a single core (Aaby and Tauber, 1975) seemed to fit fairly closely (Fig. 11). Bulk density was not measured, so it has been inferred from the stratigraphic symbols, which agree with colorimetric estimates in showing that humification generally increases with depth, as dry bulk density is therefore inferred to do. The effect is to make the curve less concave. Other situations tend to increase its concavity: conversion from ^{14}C date to calibrated (dendrochronologic) date; dry bulk density lower at greater depth; proportion of ash increasing to significant amounts at greater depths. In Fig. 11 the data are so detailed that the temporary effects visible as recurrence surfaces are easily seen. These are no more than stumbles on a stately march through the millennia consistent with constant influx and constant proportional decay. The best-fit values are $p' = 0.005$ (s.e. = 0.001) $\text{g cm}^{-2} \text{yr}^{-1}$, and $\alpha' = 1.2 \times 10^{-4}$ (s.e. = 0.9×10^{-4}) yr^{-1} . This influx of $50 \text{ g m}^{-2} \text{yr}^{-1}$ is perhaps 10–20% of that to the acrotelm of present bog surfaces.

The same methods applied in other cases yield a mixed bag. Some are shown in Clymo (1984a), one in Smith and Clymo (1984), and others in Fig. 12. Of the 16 cases, 9 show concave curves, 4 appear straight, 1 is slightly convex, and 2 have more than one age "reversal," which, if omitted, could make them concave. Of the 5 straight and convex cases, 2 are based on depth as distance and might become more convex were their dry-bulk density known.

On balance we ought perhaps to picture the catotelm as having a limit to its depth: a limit at which the influx from the acrotelm is balanced by losses of carbon dioxide and methane from the whole of the catotelm. In any case calculation of "accumulation rate" cannot be made safely by the traditional procedure of dividing the depth or mass found today between two horizons by the difference in age of those horizons. The work of Tallis (1985) is the only case where any attempt at all has been made to allow for decay. The results were enlightening.

The Shape and Size of Raised Bogs

That precipitation has something to do with the growth and size of raised bogs has long been believed (Granlund, 1932; Wickman, 1951; Aartolahti, 1965).

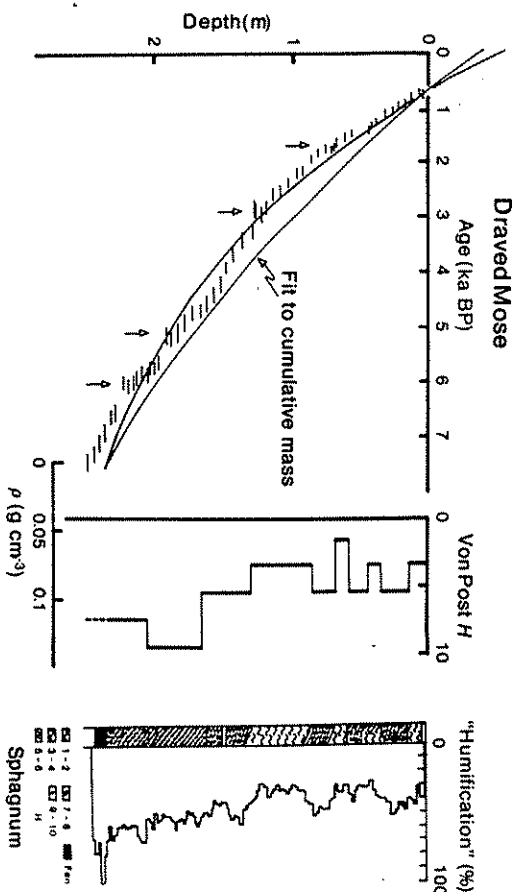


Fig. 11. Age versus depth for Draved Mose, Denmark (Aaby and Tauber, 1975). (Reprinted from Aaby and Tauber, 1975, from *Boraa* by permission of Universitets forlaget AS [Norwegian University Press].) The horizontal bars are calibrated dates with counting errors. The lower concave curve is the line of best fit to the depth-age curve using depth in linear measure. We need depth as cumulative mass (on an area basis). This was not measured but can be estimated from the humification symbols using $p' = 0.1 H + 0.04 \text{ g cm}^{-3}$ where p' = dry-bulk density and H = von Post humification (Clymo, 1983, 1984a). Stratigraphy and a colorimetric measure of humification are at the right. To the left of them are the inferred H and p' values. These were used to get another line of best fit shown above the first one and arranged to coincide with the first at the youngest and oldest points. Overall mean $p' = 0.10 \text{ g cm}^{-3}$. Vertical arrows mark "recurrence zones" where a period of slow peat growth was followed by a period of rapid growth. The surface of the peat has been cut away.

But it was only recently that Ingram (1982, 1983) pointed out that the low hydraulic conductivity of the catotelm is sufficient to account for a groundwater mound—a phenomenon well known to soil physicists, for example, Childs (1969). During periods of ample rainfall, excess water seeps laterally through the acrotelm. During droughts, however, the water table sinks into the catotelm as the catotelm begins to drain. It is probably the rare, long droughts that are critical: Ingram suggests that irreversible changes in the catotelm peat, which are known to occur on drying, may be important. The survival of the surface vegetation in such cases seems to be of equal importance. Ingram's hypothesis is that the shape of the raised bog in vertical section is determined by its hydrology, and that the acrotelm is constrained to conform to a shape determined in that way. For the simplest case of a homogeneous, isotropic catotelm, the groundwater mound should be close to a hemi-ellipse in cross section. For a raised bog

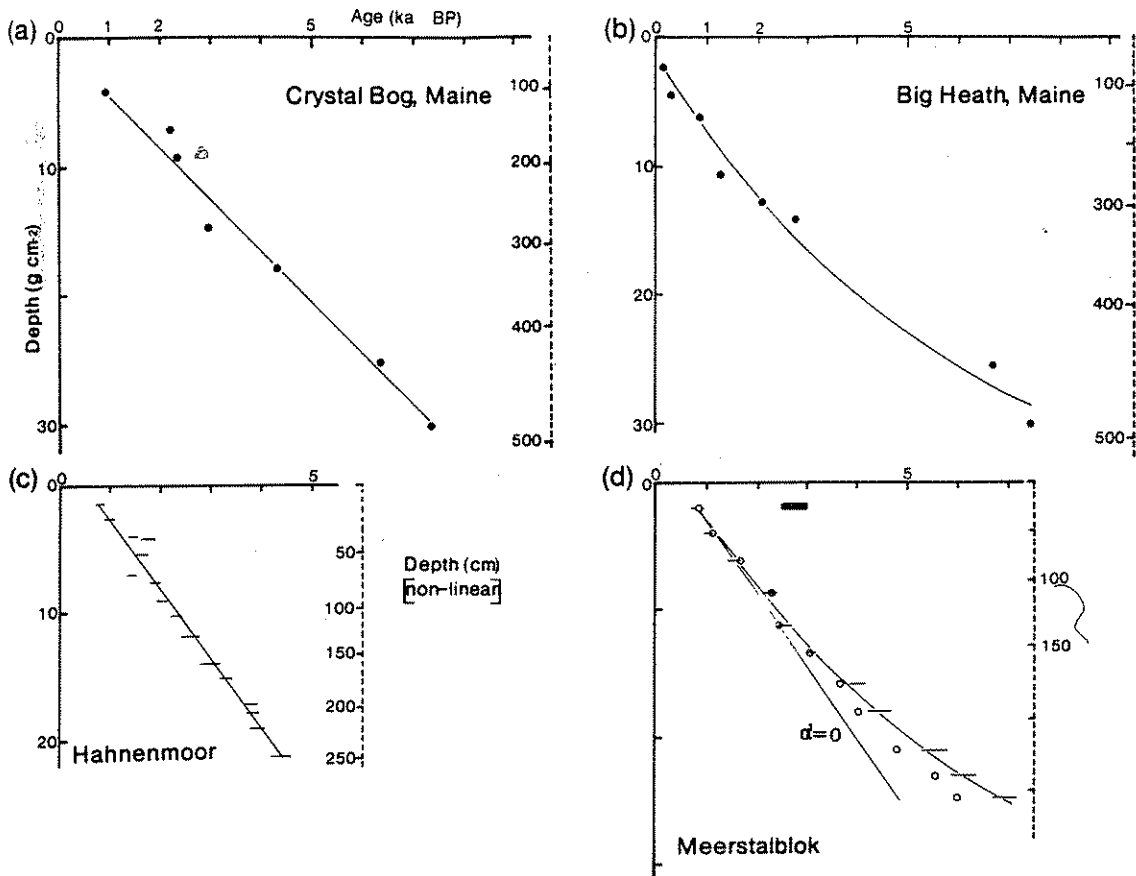


Fig. 12. Age versus depth in six bogs. In (a)-(e) the age is from calibrated ^{14}C . The left axes show depth as cumulative mass below the surface on an area basis. The broken axes at the right show the depth in linear measure at particular points, but these axes are not a simple transformation of those at the left. The model to which lines were fitted is described in the text.

(a) Crystal Bog, Maine (Tolonen *et al.*, 1983). (With permission: *Maine Geological Survey Bulletin* 33: 60.)

(b) Big Heath, Maine (Tolonen *et al.*, 1983). (With permission: *Maine Geological Survey Bulletin* 33: 60.)

(c) Hahnenmoor, Germany (Middeldorp, 1984). The bars show the counting-error limits. Middeldorp gives another less complete but strongly concave example for Engbertdijksveen, Netherlands. (With permission from the author, whose thesis concerned the variability rather than the regularity of the age/depth curve.)

(d) Meerstaiblok K2, Netherlands (Dupont, 1985, and personal communication). Bars as for *c*. The open circles are the uncalibrated ^{14}C dates; calibration makes the curves more concave. The straight line shows what would be expected if there were no decay. (With permission from the author.)

(e) Quick Moss, northern England (Rowell and Turner, 1985, with permission: *Journal of Ecology* 73: 19). The dry-bulk density was calculated from the reported colorimetric estimate of humification (*b*) as $\rho' = 0.0012 b \text{ (g cm}^{-3}\text{)}$. A plot using linear depth was markedly concave.

(f) Rotten Swamp, ACT, Australia (Clark, 1986, and personal communication, with permission). Dates were obtained from cumulative pollen density, scaled by a single calibrated ^{14}C date at 86 cm depth. Open circles are cumulative mass; filled squares are depth in linear measure but scaled to coincide with the mass scale at the oldest sample to show how the curve is made less concave using mass.

which is elliptical in plan view, with major and minor radii X and Y , then the height, h , above the regional water table is contained in:

$$\frac{U^*}{K} = b^2 \frac{(1/X^2 + 1/Y^2)}{(1 - x^2/X^2 - y^2/Y^2)}$$

where x and y are distances from the center along the major and minor axes, U^* is the net recharge in times of critical drought, and K is the hydraulic conductivity. The cross sections of two small, raised bogs in Scotland, Dun Moss and Ellegower Moss, are reasonably close to hemi-elliptical (Ingram, 1982, 1987), and the surface of Ellegower Moss gives a fit with mean deviation of 0.6 m to the equation above (Clymo, unpublished). The value of U^*/K inferred from the shape of both is about 0.001, which is close to the value calculated from separate measurements of U^* and K at Dun Moss (Ingram, 1982). This hemi-ellipse accords with early observations that the margins of raised bogs are steeper than the bog expanse—indeed the margins are recognized by the Swedish word *rand*. The margins of raised bogs, being the most accessible, are often the most damaged. The simple groundwater-mound description depends on the assumption that water flow is approximately horizontal, and this becomes more unrealistic at the margins as well.

The hemi-elliptical profile is a consequence of specific assumptions, in particular that the substratum below the peat is impermeable. In cases where the hydraulic conductivity of the substratum is similar to that of the peat, as it is thought to be in the Glacial Lake Agassiz area, for example (Siegel, 1983; Siegel and Glaser, 1987), one should not expect to find a simple hemi-elliptical profile.

Can a hemi-elliptical profile be combined with the idea of an asymptotic maximum depth, discussed in the previous section? It can, provided that one concedes that the rate at which plant mass enters the catotelm is constant only at the bog center. In the case analyzed by Clymo (1984a), the bog begins growth at a single focus on a flat, impermeable plain and gradually spreads out, maintaining the hydrological hemi-ellipse at all times. The consequences are shown in Fig. 13. One curious feature of the interaction between hydrology and decay is that the rate of growth at the edge of the bog increases steadily for a long time before decreasing again. To the unwary, ignoring decay, this effect seems even more marked (Fig. 13, left side). One must assume that the concomitant, complicated changes in the range at which the acrotelm supplies the catotelm (Clymo, 1984a) are mediated by changes in the depth or nature of the acrotelm forced by the underlying hydrological hemi-ellipse. If pool formation is a random process, so that the density of pools or perhaps their area as a proportion of the bog surface is a reflection of the length of time that a particular part of the bog has been in existence, then the density should show a pattern like that in Fig. 13b.

This sort of calculation is useful only in suggesting consequences—sometimes

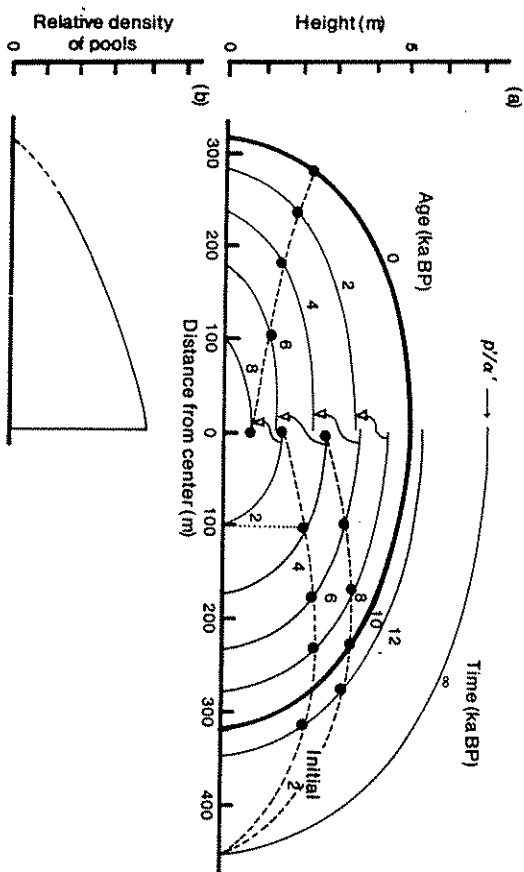


Fig. 13. (a) Hypothetical profile of the catotelm of a raised bog growing from a single focus, constrained by the hypothetical groundwater mound in droughts and by $(p/\alpha) (1 - \exp[-\alpha r])$ at the center. The vertical scale is 20 times the horizontal one. The right half shows the surface at 2,000-year intervals to 12,000 yr, and the final steady state. The left half shows the amount of growth in the first 2,000 and 4,000 yr at the bog margin as it spreads. On the left, the broken line shows the apparent growth in the first 2,000 yr at the margin if decay is ignored. (b) Relative density of pools if pool formation is a random process in space and time.

unexpected—of apparently simple and reasonable assumptions. There can be few places where bog growth starts at a single focus and spreads. One possible example is Hammarnossen, which Granlund (1932) concluded had begun growth simultaneously over its whole area but which recent work (Foster *et al.*, 1988) with ^{14}C dating indicates spread from a single focus.

What happens when growth begins at the same time over a large area, or at several or many foci that then fuse? Some indication may be obtained from the work of Granlund (1932), who recorded the length (Swedish *längd*) and maximum depth of 792 Swedish bogs. Granlund categorized the bogs by district and within district by annual precipitation. To each subset he drew a freehand "limiting" curve showing that as size increased so did depth but in a convex manner. Wickman (1951) in an influential but rather confusing article pointed out that these "limiting" curves could be considered a single family, which is a close fit to $H^2/L = C$, where H is the maximum depth of peat, L is the "length," and C is a constant. (The hemi-ellipse, however, requires that $H^2/L^2 = C$.) Wickman managed to imply that the maximum depth is determined by precipitation, and this intrinsically plausible conclusion has been widely, if uncritically,

accepted. What Granlund's "limiting" curves actually show is that there seems to be a relation between H and L but they set no maximum to H unless L is fixed.

If we return to the groundwater mound, it may be written as $U^*/K = aH^n/L^m$, where L is now the half length for a parallel sided bog with end drains (in which case $a = 1$) or L is the radius of a circular bog (with $a = 2$). The indices $m = n = 2$. This may be rearranged to give: $\log H = (m/n) \log L + \log(U^*/K\alpha)/n$. This straight line form can be tested against all Granlund's data (not his freehand "limiting" curves) and also against 115 Finnish bogs in two regional subsets (Aarolahti, 1965). There are 14 subsets of data altogether if we ignore three with 12 or fewer members. Of these, 13 have $r^2 = 0.55-0.90$, median 0.72. The values for m/n fall into two groups. For 9 subsets in Småland, southwest Häme, and north Satakunta, the values of m/n (with one exception) are in the range 0.48-0.56. For Svealand, Västerbotten, and Jämtland the values, with one exception, are in the range 0.71-0.80. It is clear that in general the relationship of these data is close to constant H^2/L or H^4/L^3 , but there is no relation to precipitation or to bog size, and the cause of these groupings is not obvious. There seems therefore to be a deficiency in height, or rather in maximum depth, of peat if one takes the lateral spread of the raised bog as given and expects a hemi-ellipse. The obvious explanation is that most of these are bogs whose lateral extent was established early in their development, probably by topography, and whose profile has not yet become hemi-elliptical.

Will it ever become hemi-elliptical? Two possibilities may be recognized. In the first the size of the bog is such that the height of the hydrological ellipse is less than the decay limit, that is, $H < p'/(a\rho')$ (where ρ' is the mean dry-bulk density in the catotelm). In this case the outer zones are the first to approach the hydrological hemi-ellipse appropriate to L , and growth there slows down. The boundary between limited growth and the central area, which is still over-wet, gradually contracts until the whole profile is hemi-elliptical. If the bog cannot spread it will just grow upward with the same profile until the $p'/(a\rho')$ limit is reached.

The second possibility is that the bog is so large that the hydrological hemi-ellipse cannot be completed before the $p'/(a\rho')$ limit is reached. For example, in lower Saxony the mean width of 64 raised bogs was 6,000 m (Eggelsmann, 1976). If a U^*/K value of 0.001 applied to them, as it does to the two bogs in Scotland, then $H = 95$ m. For $p' = 50 \text{ g m}^{-2} \text{ yr}^{-1}$, $\alpha' = 10^{-4}$, and $\rho' = 0.1 \text{ g cm}^{-3}$ —values close to those reported by Clymo (1984a)—then the $p'/(a\rho')$ limit would be 5 m. This is indeed close to the mean found by Eggelsmann, and much less than the hydrological limit of 95 m.

The center of these bogs is therefore much flatter than the hemi-ellipse appropriate to their width, and one assumes that they will never reach the hemi-elliptical profile. One may speculate (Fig. 14) that such bogs will also be wetter away from the margins, because the water table will not be driven down so far

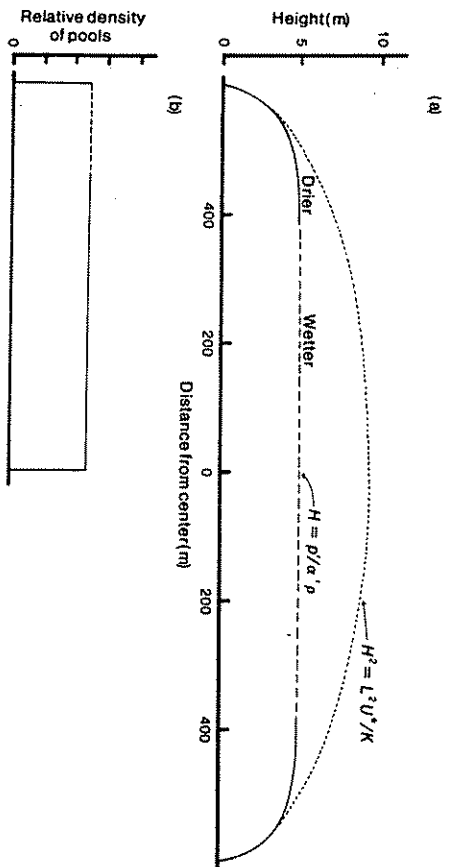


Fig. 14. (a) Hypothetical development of a raised bog of relatively large size. The dotted line is the hydrological hemi-ellipse for $U^*/K = 0.001$, $L = 300$ m. The decay limit at $p'/(a\rho')$ is for $p' = 50 \text{ g m}^{-2} \text{ yr}^{-1}$, $\alpha' = 0.001 \text{ yr}^{-1}$ and $\rho' = 0.1 \text{ g cm}^{-3}$. This depth is less than the hydrological one so the postulated limit is shown by the solid-and-dashed line, which approaches the hydrological limit at the margins but then falls well below it. (b) Relative density of pools if pool formation is a random process in space and time.

in droughts as it is in bogs that have reached the hemi-ellipse. The density of pools generated randomly in space and time would be nearly uniform across the surface (Fig. 14b), but hydrology might require a greater density of pools in the center. The gradient to drive water is less than it would be in a hemi-ellipse and may be compensated by the low resistance to acrotelm flow in pools.

In summary, U^* may be primarily determined by the requirements for plant survival in rare long droughts, and K may be primarily determined by the sort of peat. The size and profile of raised bogs may depend rather little on climate. If they are small (< 500 m across) then, it is likely that their profile will by now approximate the hydrological hemi-ellipse. But if they are larger and began growing over their whole area at once, then although their margins may be approaching the hydrological hemi-elliptical profile, their centers will not have done so because there has been insufficient time or because they have reached the decay limit, $p'/(a\rho')$. Such centers would be wetter than the margins.

We may thus glimpse how the outlines of a more exact understanding of peat growth are taking shape. But it is wise for those of us at work today to recall that, if we think we see farther than our predecessors, then so too do dwarfs on the shoulders of giants.

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