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The ecology of peatlands

R. S. Clymo

About 3% of the Earth's land surface is covered with peat. There are many sorts of peatland, divided primarily on whether they rely entirely on precipitation (bogs, usually acid) or receive some water from mineral soils (fens, sometimes alkaline and calcareous). Bogs have a thin skin of plants and porous peat through which surplus water can drain easily. This skin overlies a much deeper denser peat, much less permeable to water, and anoxic. The rate of decay is therefore very slow, but it is not negligible: together with hydrological constraints it controls the size and shape of peat bogs. Surface patterns of hummocks and hollows are often conspicuous. Hollows may develop into pools and facilitate erosion. The chemistry of bog water and the profile of metal concentrations are subjects of current interest.

Introduction

Imagine an English deciduous woodland as the days in autumn shorten. Leaves die and fall. For a time there is a rustling carpet but by the following summer little is left. Ash leaves decay rather quickly; beech and oak last longer. A shallow scrape in the surface of the soil shows that below the intact dead leaves are fragments of leaf, and below them is a thin layer of black humus overlying mineral soil. The combined depth of the organic layers is rarely more than 10 cm and often much less. The decomposition of organic matter thus revealed is as important, and just as much taken for granted, as the disposal of sewage and waste by human communities. Only when the process fails do we think about it. Peat, which is usually more than 90% organic matter, is a special case of the partial failure of decomposition. The depth of peat ranges from a few centimetres to 10 m or more. In many parts of the world peatlands (an alternative collective term is 'mire') are fragmentary, and have until recently been ignored in inventories or included with the surroundings in which they are set.

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Estimates of the total area of peatlands have therefore increased: the latest is that 420 Mha (3% of the Earth's land surface) is peat-covered. About three-quarters of all peatland is in the U.S.S.R. and Canada. A single peatland complex in Western Siberia covers approximately 1800 × 800 km. About 10% of the British Isles is peatland, but this is only 0.7% of the world total. If the mean depth of all peatlands were 1.0 m then there would be about 170 Gt of carbon in peat. This is about one quarter of all readily accessible vegetable carbon on the Earth's land surface, and about 3 times the amount fixed on land by photosynthesis in a year. There is a lot of peat.

Almost all mires accumulate peat because they are waterlogged, with consequent low rates of decay. There are some, such as the moss banks of the Antarctic Signy Island, where the rate of decay is low because they are permanently frozen a short distance below the surface or are unusually dry beneath productive vegetation. One of the most bizarre 'peats' is the 3.3 m deep accumulation of wind-blown leaves and of dung of the recently-extinct giant ground-sloth (*Mylodon*) in a cave in Patagonia.

The cause of waterlogging is usually that precipitation exceeds evaporation during most of the year, but peat also develops in places where a high water table is constantly maintained by other means.

The accumulation of peat is an intrinsically interesting process. It is generally true that the further down one goes in a peat bog the older the peat is: stratigraphy reflects chronology. Peat is therefore interesting to archaeologists and historians of vegetation. The sort of record made depends on the ingenuity and resources of the worker: pollen and macrofossil analysis has been used for 50 years or more; use of the temperature-dependent deuterium:hydrogen ratio is a more recent development. There is locally strong interest in mining peat for fuel, for horticulture and for medical use, and Hobbs[16] has reviewed its increasing interest to engineers (whose first thought is to remove it or to avoid it). The literature about peatlands is scattered and in many languages—English, German, the Scandinavian languages, Finnish and Russian are probably the most important.

The peat-forming process

Plant matter becomes available for peat-formation in one of four main ways. (1) In those mires which are entirely dependent on precipitation for their water supply it is common to find large amounts of the bog-moss (*Sphagnum*). This has no roots. It grows at the top, producing branches which live for about a year before they become so densely shaded by more recently formed branches above that they die, *in situ*. The top of the plant behaves as if it were a machine extruding a product below it and being gradually raised up thereby. (2) Leaves and branches of plants that are rooted in the peat die and fall onto the surface. (3) Underground stems (rhizomes) form just below the surface and eventually die. (4) Roots grow down into older peat and eventually die *in situ* but, anachronistically, they are younger than the peat into which they become incorporated.

The first three sorts of material are attacked by fungi and bacteria (perhaps aided by invertebrate animals) in the presence of oxygen and water. Different species attack different chemical constituents and at different rates. Fatty cuticles tend to survive longer than does cellulose, for example. The spatial incidence of attack is erratic too: *Sphagnum* leaf cells may develop holes in the walls rather than disintegrating completely. Most important is the fact that different plant species lose their integrity (and probably their substance) at very different rates. In a series of elegant experiments Coulson & Butterfield[9] showed that *Rubus chamaemorus* (cloudberry) leaves decay rapidly, and even faster when invertebrates are allowed to eat the leaves; the rate of decay of *Calluna vulgaris* (common heather or ling) is lower but is still increased when invertebrates can eat the leaves; the rate for *Sphagnum recurvum* is low—only 15% yr^{-1}—and is unaffected by invertebrates. Coulson & Butterfield also increased the natural concentration of phosphorus and nitrogen in plants, separately, by a fertilizer treatment and found that the subsequent decay rate of leaves put onto unfertilized bog was increased only by the nitrogen enrichment. As a result of all these differences the composition of macroscopic fragments of plants soon becomes distinctly different from that in the parent vegetation which continues to grow on the surface above.

On *Sphagnum*-dominated bogs this differential decay has little effect on the overall structure, just as individual bricks may be knocked at random from a wall without the wall collapsing. The space between the structural components of the peat is relatively large and water flows easily both vertically and horizontally: the hydraulic conductivity is high.

Eventually there comes a point, however, where the whole edifice collapses. It may be a seasonal load of snow which triggers the collapse: in *Sphagnum*-dominated bogs a layer of nearly horizontal moss-stems may often be seen. Whatever the cause or speed, this change is a crucial one. The space *between* structural elements becomes much smaller. There is a power-relation (approximately fourth power) between the size of spaces and hydraulic conductivity. If the peat mass were protected from precipitation it would eventually drain down towards the surrounding water table. But in normal circumstances precipitation exceeds evaporation. Whatever small amount of water is lost by drainage from the lower collapsed peat is rapidly replaced and excess runs off laterally through the upper uncollapsed peat. The lower peat thus remains waterlogged. It used to be thought that capillarity was the main cause of waterlogging. The current view is that we cannot tell what capillarity might do in humified peat (where is the 'water table' in a jelly?) but we can see that the reduction in hydraulic conductivity is a sufficient explanation by itself. Ingram,[18] who has done more than most to advance this view, has also coined the terms 'acrotelm' for the upper layer of high hydraulic conductivity and 'catotelm' for the lower, waterlogged layer. New terms are often unnecessary but here they replace the older 'active' and 'inert' or 'passive' which were positively misleading.

Micro-organisms are active in the top of the catotelm. They use up the oxygen. This may be replaced by diffusion from above but the diffusion coefficient of oxygen in water is about 1/10,000 that of oxygen in air, and the micro-organisms use up the oxygen faster than it can be replaced by diffusion from above: the catotelm lives permanently beyond its means, and is therefore anoxic. It contains micro-organisms which live anaerobically. Decay continues, but at a much slower rate than in the acrotelm.

The whole chain of events may be summarized as: aerobic decay → structural collapse → much lower hydraulic conductivity; this and excess precipitation → waterlogging → lower rate of transport of oxygen; this and micro-organisms → anoxic conditions → much slower anaerobic decay.

The sorts of peat-forming systems

It is generally agreed that climate, hydrology and the supply of dissolved inorganic solutes interact with vegetation over time to produce a variety of structures on several scales. A typical example of the complexity is shown in Fig. 1. But each country has its own range of these structures, and it also has one or more national classifications which are only partly applicable to other countries.

Those mires that depend for their water and solutes on precipitation alone are 'bogs': they are 'ombrotrophic' (Greek: rainstorm-fed). If part of the water has flowed through or over mineral soil the mire is a 'fen' and is 'minerotrophic'. Bogs are usually strongly acid ($\text{pH} < 4.5$) and calcium-poor. Minerotrophic fens are less acid (pH 4.5–6.5) and more calcium-rich. Rich fens are often fed by calcareous water of pH 6.5 and high calcium ion concentration. Many mires have a pattern, of scale 2–20 m, in which 'hummocks' of peat and vegetation which may be 20–60 cm above the general level alternate with flat 'lawns' just above the water table and with 'hollows' which are water-filled for part of the year or 'pools' which are water-filled for most or all of the year. In some cases the hummocks are ombrotrophic bog in a matrix of minerotrophic fen hollows. Such a system would be a 'mixed mire'.

There is a continuous scale of minerotrophy. In much of the continental Boreal zone the soils are so leached that water which has flowed through them and has perhaps been mixed with precipitation is still little better than distilled water. It often contains less in solution that does rainwater in oceanic areas. At the other extreme is water which has flowed through calcareous or agricultural soils. The most ombrotrophic sites contain few species—perhaps *Sphagnum fuscum* and *Calluna vulgaris* on hummocks, *Sphagnum cuspidatum* and *Carex limosa* (a sedge) in hollows. More minerotrophic sites contain these species, other species of *Sphagnum*, other dwarf shrubs, and other 'sedges' (in the wide sense) including *Eriophorum* (cotton 'grass'). The most minerotrophic sites contain a large number of species; ten to thirty in a single 1 m^2 sample is common.

Trees are rare on oceanic bogs but may be common on some sorts of continental bog. In Finland many mires are considered (and managed) as forest. In Europe *Pinus*

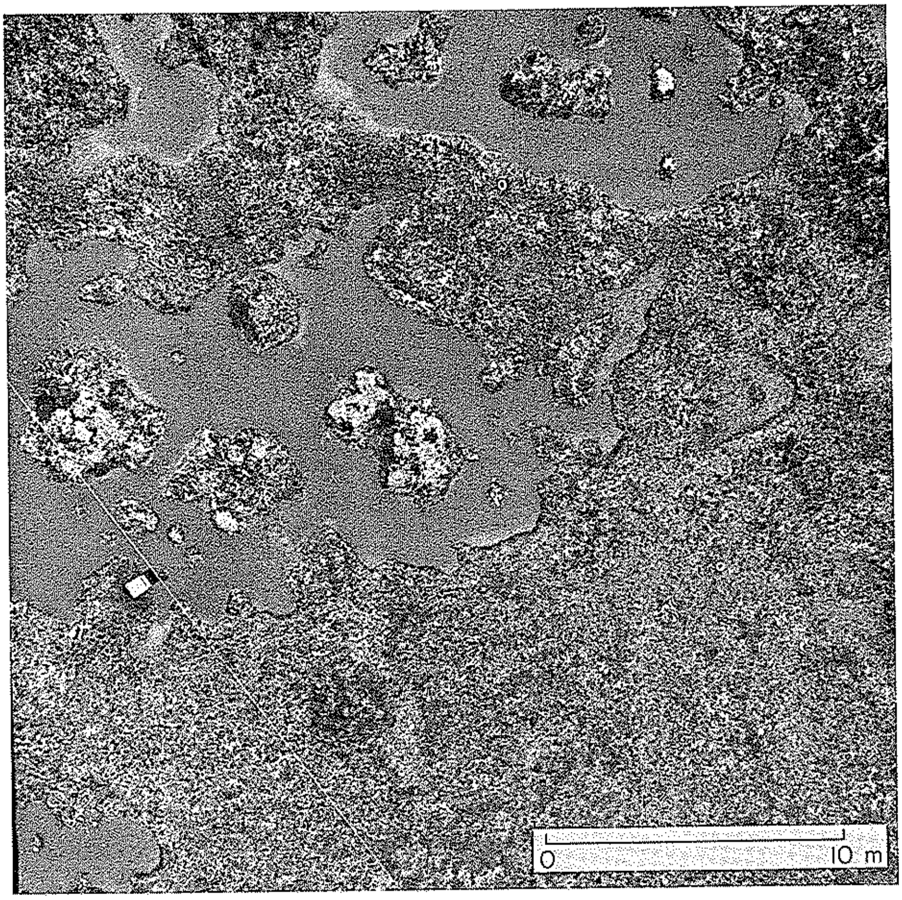

Fig. 1. Part of the Silver Flowe mires (Galloway, Scotland) photographed from a balloon at about 61 m altitude. The white line is one of the balloon guy ropes; the white rectangle houses a water-level recorder. The mosaic of vegetation and hydrology can be seen. (Photograph by D. A. Goode and D. J. Boatman.)

sylvestris (Scots pine) is found on the least minerotrophic sites, *Picea abies* (spruce) on more minerotrophic sites, and *Alnus* (alder) and *Salix* (willow) on the most minerotrophic. In North America the trees are most often *Larix laricina* (tamarack) or *Picea mariana* (black spruce).

A few of the commoner sorts of larger scale structures are described briefly and in simplified form in what follows. The articles in Gore[13] and in Moore[21] give much fuller descriptions, and Gorham[14] gives a fascinating account of early views of peatlands. The early classification into two groups—the quick and the dead—has not survived in spite of its attractive simplicity.

Raised mire

There is a central very gently sloping dome or cupola of peat, typically 0.5–1.5 km across and perhaps 0.5–10 m above the surrounding mineral soil. Around the edge is a relatively steeply sloping 'rand'. At the base of the rand there is usually a wet 'lagg fen' through which water, running off the surrounding mineral soil as well as the central bog, is channelled. Suboceanic raised mires may have a forested rand but the trees on the main bog dome are small and sparse.

Three main sorts of treeless raised mire are recognized. Plateau mires have a nearly level central expanse with irregular hollows or pools in a reticulate pattern. Concentric mires have their highest point near the centre and 'eyebrow' pools forming concentric arcs around the highest point, very clear from the air but confusing on the ground. Eccentric mires (Fig. 2) have similar pool systems but with the highest point some distance from the centre of the bog.

In Finland these three types occur in order as one travels north and away from the south coast. The boundaries can be correlated with climatic features affecting wetness. There is a similar change from plateau to other types of raised mire away from the coast in Maine and New Brunswick. In Labrador the same three components occur in a different order.

Some raised mires have followed a succession from open water in a shallow lake to fen, then to fen woodland ('carr') and finally to bog. But this succession (the process has been called 'terrestrialization') is not always found: many bogs seem to have developed directly on mineral soil previously occupied by forest or swampy woodland. Peat-accumulating vegetation has often spread out from a former lake to invade larger surrounding areas: a process which has become known as 'paludification'.

Blanket mire

In upland Britain, western Ireland, western Norway, southern Newfoundland and perhaps the southernmost tip of Chile the climate is so constantly humid that peat accumulates not only on flat land but even on slopes up to 20°. The vegetation contains many bog species, particularly *Sphagnum*, but because there is so much rain these blanket mires also contain species which would elsewhere be recognized as minerotrophic. The western Irish examples are known for the occurrence of *Schoenus nigricans* (black bog-rush) and *Cladium mariscus* (saw-sedge) which elsewhere are found in fens. Blanket mires often develop hummocks and pools over 1.5–3 m of peat. But the topography of the underlying ground and the likelihood of heavy and prolonged rain make them liable to catastrophic slides, flows or bursts.

Aapa mire

Aapa, the Finnish word for 'vast', is appropriate to describe the moderately minerotrophic fens which are usually found to the north of the raised mire zone. Typically they form in a wide nearly flat valley. Across the line of water flow are long, often 0.5–1 m high, ridges (strings, kermis). The vegetation is that of an ombrotrophic

Fig. 2. Oblique aerial view of an ombrotrophic mire (one of the Silver Flowe mires). The dark patches are pools. They are concentric about the highest point, which itself is eccentric. The pool complex is about 200 m across. (Photograph by permission of the Ordnance Survey.)

hummock, but the ridge may be 1–2 m wide and 50–400 m long (Fig. 3). Between the ridges are the flat, very wet, minerotrophic sedge- and *Sphagnum*-filled lawns and hollows known as flark or rimpi. The steeper the slope, the closer together are the strings.

Rich fen

Where the water is highly calcareous, rich-fen may form. The vegetation is species-rich and very varied.

Fig. 3. Aerial view of an aapa mire (in Korvanen, Finland). The dark patches are wet flarks (rimpis) and the light ones are long hummocks (strings, kermis). (Photograph by permission of the Finnish Army General Staff.)

Palsa mire

In the arctic one finds mounds raised 1–8 m above the surrounding peatland. These palsas contain alternate layers of peat and pure ice. The ice layers seem to increase gradually in thickness and it is this that produces the mound. The ground around the palsa thaws in summer, and the palsa is in a delicate thermal balance. A small change in the climate or environment may cause the ice to melt and the whole structure to collapse, leaving a water-filled hole.

Schwingmoor

A carpet of sedges, *Sphagnum* or reeds grows out from the edge of a fairly deep small lake. It may leave a central area of open water or cover the whole surface. The surface remains in the same place but the peat is displaced downwards. The weight of trees may depress the surface, waterlogging roots and killing the trees. Groves of the standing dead testify to the dangers of 'success'. One may stand on a sedge and *Sphagnum* carpet, flex one's knees a few times, and see waves travelling away in the vegetation. This schwingmoor development is still described in textbooks as if it were typical of all mires; it is not. Schwingmoors are rare. Of all the types of peatland they approach most closely the public perception of bogs immortalized in Conan Doyle's Great Grimpen Mire, which began 'upon the thin peninsula of firm, peaty soil which tapered out into the widespread bog. . . . [The] path zigzagged . . . among those green scummed pits and foul quagmires which barred the way. . . . Lush slimy water-plants sent an odour of decay and a heavy miasmatic vapour into our faces, while a false step plunged us more than once thigh-deep into the dark quivering mire, which shook for yards in soft undulations around our feet. Its tenacious grip plucked at our heels as we walked, and when we sank into it it was as if some malignant hand was tugging us down into those obscene depths, so grim and purposeful was the clutch in which it held us.'

Other mires

Many other types of peat-accumulating system have been recognized within the Boreal zone. There are also series of very different systems in, for example, the Everglades of Florida and the coastal zone of the Malesian islands. Amongst these are the ombrotrophic raised forest-bogs of Sumatra and Sarawak, dominated by giant trees of *Shorea*. The peat may be more than 17 m deep. These tropical forest peats with low ash concentrations may be the closest analogues that we have today of the precursors of Carboniferous tropical coals. Conaghan[8] makes the interesting suggestion that the present-day arctic palsas may be analogues for Australian Permian boreal coals.

Mire complexes

Some mires are very large and include a series of distinctive units. The Red Lake Peatland in Minnesota may serve as an example. The area is about 80 × 15 km. It contains raised mires in a matrix of strings and flarks reminiscent of aapa fen. But the matrix also contains 'teardrop islands' covered by *Picea mariana* or *Larix laricina* forest, and rich fens where calcareous water upwells. Glaser *et al.*,[12] who describe the area, note that similar complexes occur in the Hudson Bay area and in other parts of Canada.

It is possible to deal with only a few of the areas of active interest to mire ecologists. What follows is biased towards bogs because they are the most extensive and best-worked mires.

Hydrology

In normal circumstances a shallow hole dug in a peat bog fills rapidly with water. The smaller the hydraulic conductivity the smaller the hole must be if the water table is not to take a long time to reach equilibrium. A typical 'residence curve' (the proportion of time the water table spends above a given height) is shown in Fig. 4 and a typical hydrograph in Fig. 5. The stepped part of the hydrograph results because evaporation occurs more rapidly during the day than at night. Both the residence curve and the hydrograph imply that hydraulic conductivity decreases with depth, but it is only recently that Bragg[2] has used an ingenious flume formed in the acrotelm in the field, with minimal disturbance, to show that the hydraulic conductivity declines approximately

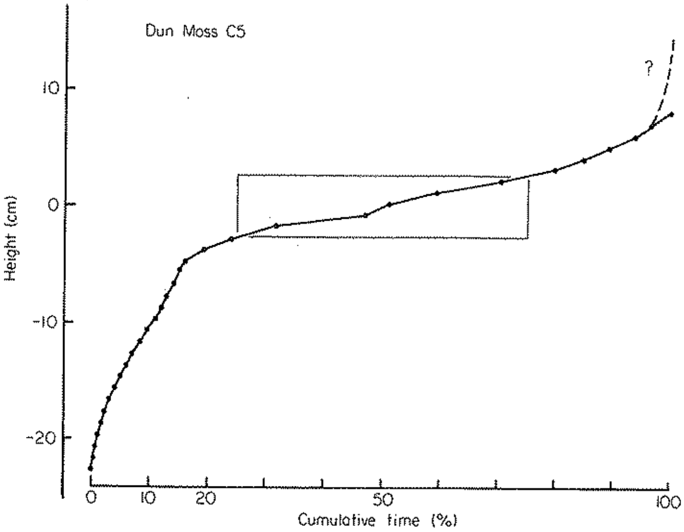

Fig. 4. Water table residence curve at Dun Moss, Scotland (after Bragg[2]). The curve was constructed from spot measurements at intervals. Occasional very high transient values will not have been recorded. They are represented by the broken line. The height is centred on 50% time. The rectangle includes half the total time (from 25% to 75%).

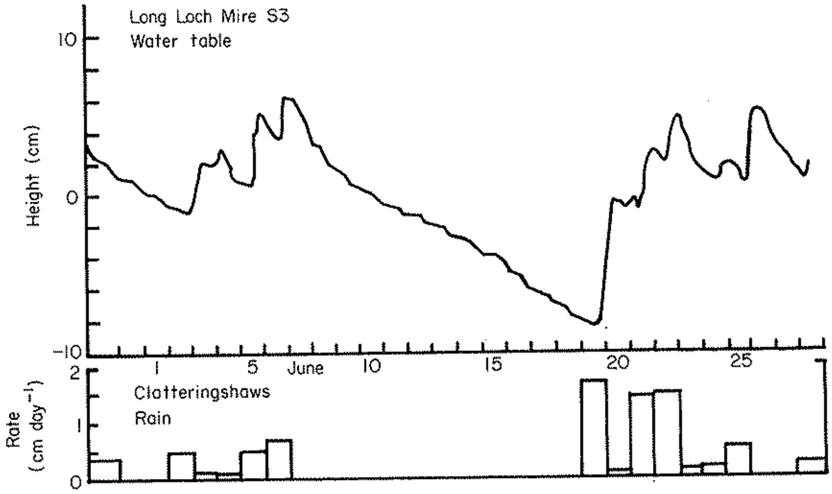

Fig. 5. Hydrograph for a site on the Silver Flowe, Scotland (from Boatman[1]). The rapid response to rain is evident. The curve is stepped during the rainless period because evaporation during the day is at a much greater rate than during the night.

logarithmically down to 30 cm depth in the peat. This corresponds to the zone within which the dry bulk density increases approximately linearly from 0.03 to 0.10 g cm^{-3}. The whole acrotelm has characteristics similar to those of a V-notch weir: the higher the water rises the easier it is for it to flow away. A consequence of differences in hydraulic conductivity (and storage) profile in different types of acrotelm is that the water table below a large hummock fluctuates less than it does below adjacent pools: the pool water table is above the hummock one in wet weather, but below it in dry weather. There is some evidence that in droughts the whole bog may shrink vertically by a few centimetres.

It will probably be obvious by now that the famed ability of peat bogs to act as 'sponges' mopping up heavy rain is very limited if not entirely mythical. The first rain after a long dry period may be effectively absorbed, but once the acrotelm is recharged the ability to retain further water is small. There is a delay in runoff, however, and stream flows are less flashy than they would be from bare rock or eroding peat.

In the catotelm the hydraulic conductivity is much lower than it is in the acrotelm —typical values measured with seepage tubes at 1 m depth are 10^{-5}–10^{-4} cm s^{-1}. This has important consequences for the shape of raised bogs.

The shape and size of raised bogs

In 1932 Granlund[15] measured the height and diameter of raised bogs in areas of different precipitation in Sweden. He suggested that in a particular climate there was a limiting relation between height and diameter, and he drew freehand curves for this relation. These curves were later found to be very close to hemi-ellipses. They were widely misunderstood until Ingram[17] pointed out that the water table in a *single* homogeneous peat mass should follow the groundwater mound equation:

$$\frac{U}{K} = \frac{ah^2}{(L^2 - \ell^2)} \tag{1}$$

with $a = 1$ for a parallel sided bog and runoff streams at the end; $a = 2$ for a circular bog with peripheral drainage. The equation gives the height, h, of the peat mass above the runoff stream at a distance ℓ from the centre for a peat mass $2L$ long (or of radius L) related to the dimensionless hydrological quotient of the runoff U and hydraulic conductivity of the catotelm, K. In ordinary times much of the water falling on a raised bog runs off through the acrotelm. What matters for the shape is probably the extraordinary times of long droughts, represented by $U^* \ll U$, when the acrotelm is almost dry and runoff is mostly through the catotelm. Ingram suggested that irreversible changes following drying of the top layer of the catotelm might damage its structure, but it seems just as likely that it is the death of plants on the surface which would be limiting. In wet years one supposes that some plants may cause peat to begin to accumulate above the hemi-elliptical limit but they will not get far before a dry year allows that peat to become dry and to decompose aerobically, or at least reduces plant growth in such places. The shape of two small Scottish raised mires does seem to be hemi-elliptical in section (Fig. 6) as equation (1) implies. For one of them, Dun Moss, there is reasonable agreement between U^*/K inferred from the shape and the values of K and U^* measured as the driest hydrological year in ten, as Ingram[17] has shown. The question 'what is the best period for measurement of U^*?' has not yet been

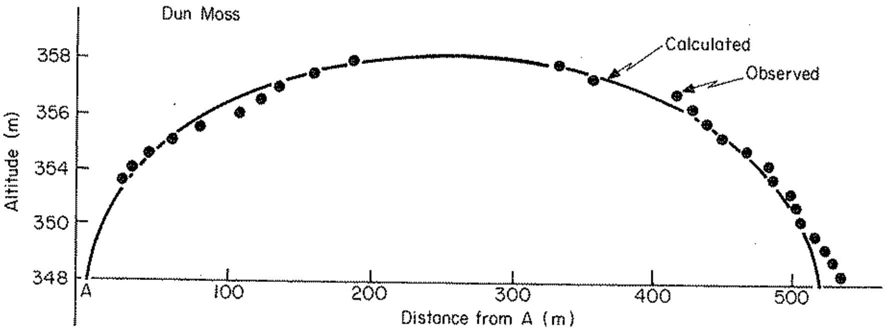

Fig. 6. Section across Dun Moss, Scotland (from Ingram[17]). The points are measured values of the water table in hollows. The continuous line is equation (1) with $a = 1$, measured H (the maximum value of h), and an independent estimate of U^*/K (see text for explanation).

answered satisfactorily, and there are very few sites where sufficiently detailed records have been kept for long enough.

If this mechanism does indeed determine the overall shape of raised mires then it follows that the maximum height, H, of the dome is given by

$$\frac{U^*}{K} = \frac{aH^2}{L^2} \qquad (2)$$

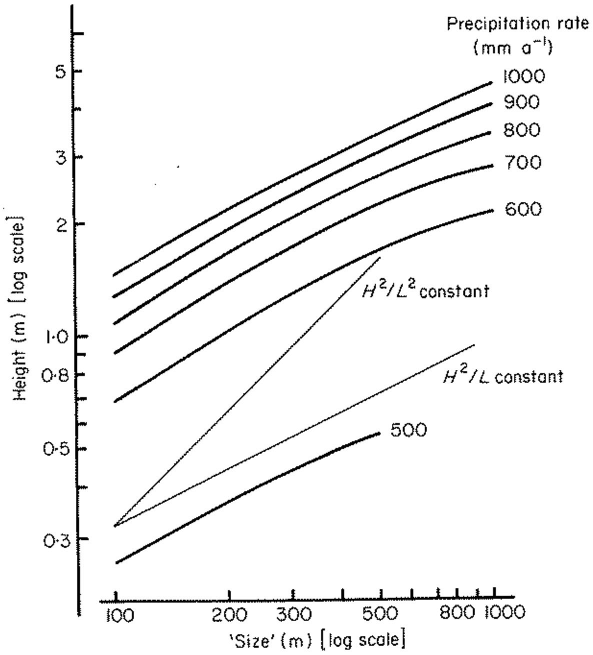

Fig. 7. Diameter and height of the dome of raised bogs in various climates in southern Sweden, redrawn from Granlund.[15] If equation (2) were a correct description the lines would be straight and of slope 1.0.

Granlund's curves are shown on log scales in Fig. 7, which should give straight lines if (2) is true. The value of U^*/K for 250 m radius and 1000 mm precipitation is about 0.4×10^{-3} compared with 1.2×10^{-3} for Dun Moss, which is of similar size. The lines in Fig. 7 should have a slope of 1.0 if equation (2) is a good description. In fact the slopes are about 0.5. We do not know whether it is Granlund's freehand limiting curves or equation (2) which will need modification. One may suspect that both will.

It is obvious that equation (2) sets no limit to the size a raised bog may reach: all it does is specify a relation between height and breadth. Is there then any limit other than that set by the area of land in a suitable climate? It seems that there is. In the acrotelm of a growing mire new organic matter is added by plant growth mainly at or above the surface but organic matter is also lost by aerobic decay throughout the acrotelm. The essential feature of a mire is that, on average, the rate of addition exceeds the integrated loss at all depths in the acrotelm. The acrotelm gradually rises around a particular piece of organic matter and eventually the catotelm engulfs it but the acrotelm maintains an approximately constant thickness. The zone, defined by the *processes*, moves up past the *material*. About 90% of the original mass has by this time been lost by decay. About 10% survives and passes into the catotelm. Here the same process is repeated, though much more slowly. It used to be thought that the rate of decay in the catotelm was either zero or negligible. But the concentration of carbon dioxide and methane (both products of decay) increases the deeper one samples in the peat. Clymo[3] has shown that this profile is consistent with continued decay and upward movement of gases by diffusion. There is no plausible explanation that does not involve continued decay. The rates of decay are low—about 10^{-4} yr^{-1}—but are they negligible? We now have a picture of the catotelm which is fed at the top at a rate, p, by what has passed through the acrotelm, but in which decay continues at the rate α at all depths. Formally, $dm/dt = p - \alpha m$, and hence $m = (p/\alpha)(1 - e^{-\alpha t})$ where m is the accumulated mass on a unit area basis at time t. When the peat first begins accumulating the rate of addition to the catotelm is much greater than the integrated rate of loss. But as the catotelm thickens so the integrated rate of loss increases until, in the limit, a steady state is reached. This asymptotic maximum depth is p/α. If decay continues at all then there *must* be a limit to the depth of peat as Fig. 8 illustrates. At this point the surface is still healthy and growing as fast as it ever has done, but there is no longer any *net* accumulation of peat.

One consequence of these processes may be seen at the right of Fig. 8: the age versus depth profile should be concave not linear (as had always been tacitly assumed). Clymo[3] has examined suitable sets of data and found that most are indeed concave. From the slope and concavity the rate of addition to the catotelm and the rate of decay can be calculated. The rate of decay is approximately 10^{-3} to 10^{-4} yr^{-1}. The rate of addition differs enormously. In Fennoscandia it is fairly constant at about 50 g m^{-2} yr^{-1} but on Beauchêne Island in a 13 m deep peat formed from the grass *Poa flabellata* it is about 650 g m^{-2} yr^{-1}.

Can the hydrological shape-determinants be combined with this view of an asymptotically approached maximum depth of peat? They can if one supposes that p is constant in time at no more than one point on the bog. (It need not be constant, and in the short term certainly is not, even at one point.) Elsewhere it adjusts to the accumulated depth of peat and to the hydrologic constraints. There are no tests yet of the predictions of the combined theory.

The early belief, quoted by Gorham,[14] 'that peat was a living vegetable, *sui generis*, the surface vegetation merely growing on the dead outer crust', did recognize that the

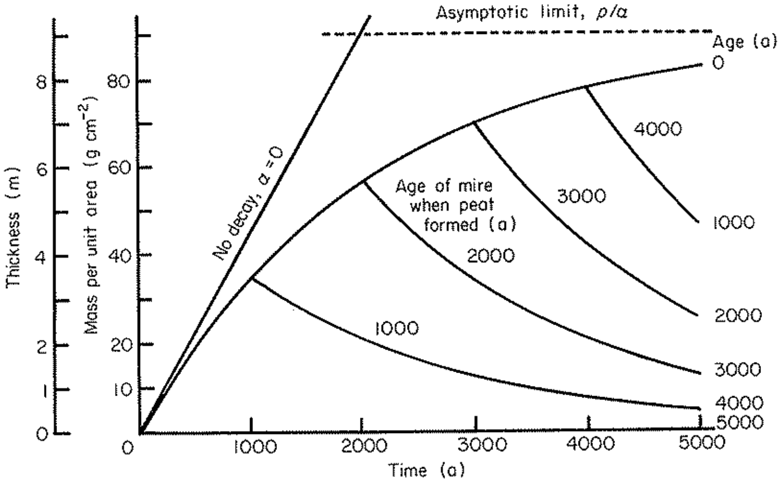

Fig. 8. Accumulation of matter in the catotelm if there is a constant rate of addition, p, at the top and constant proportional rate of decay, α, throughout. The limiting depth is p/α. The depth scale assumes that the dry bulk density is 0.1 g cm^{-3}. The family of concave curves show the fate of peat formed at 1000-year intervals. The age versus depth profile at the right is non-linear. (From Clymo.[3])

peat itself was not 'dead'. To that extent peat is more important to a mire than heartwood is to a tree. But this early view failed to recognize the essential organic connection between the surface vegetation and the peat below.

Growth of plants on peat bogs

The most important plant on many bogs is *Sphagnum* (bog-moss) whose physiology and ecology are reviewed by Clymo & Hayward.[6] All species contribute to acidification of the rain which falls on them, so that the pH of water in hummocks in summer is often below 3.2. The process depends on continued growth of the plants so, with heavy rain and little growth in autumn, the acid water washes into pools and then out of the bog altogether.

Another important feature of *Sphagnum* is its low concentration of nitrogen and consequent low rate of decay. This is a very important cause of peat accummulation.

The species of *Sphagnum* have distinctive habitats. For example *S. fuscum* and *S. capillifolium* occur on hummocks, *S. papillosum* on lawns, and *S. lindbergii* and *S. cuspidatam* in hollows and pools. These are not necessarily the conditions in which the species grow best: *S. capillifolium* grows better in pool conditions (in experiments) than it does on hummocks. But the habitat in the field is where the species grows better than other species do. Part of the explanation seems to be in the ability of smallleaved species to transport water to a greater height above the water table than can large-leaved species. But the occasional plant of a hollow-species is found high on a hummock. Rydin[24] suggests that it is relying on its neighbours to transport water.

Most of the field measurements of *Sphagnum* growth show that the rate, as dry mass/(area × time), is lower in pools than elsewhere mainly because the plant cover in pools is patchy. This may be important in controlling the development of surface features.

In many cases *Sphagnum* acts as the matrix in which rooted plants grow. Some surprising discoveries have recently been made by Wallén[28] working on a subarctic peat bog: the dwarf shrubs *Andromeda polifolia* (bog rosemary), *Empetrum hermaphroditum* (crowberry) and *Rubus chamaemorus* (cloudberry) had 90–98% of their mass below 'ground'—in this case the tops of *Sphagnum fuscum*—and produced about 95% of new growth below ground. The main roots of *Rubus chamaemorus* and of *Eriophorum angustifolium* may grow down to 70 cm deep or more. These roots have large intercellular gas spaces and probably exist aerobically in the predominantly anoxic peat.

The growth of *Sphagnum* can interact with that of dwarf shrubs (and other plants). *Calluna vulgaris* (ling) grows on a variety of mineral soils in which it often has a fixed life-span of perhaps 30 yr. It grows on peat bog hummocks too but not in wetter places. If the *Calluna* stand is open then *Sphagnum* grows up around the 'base' of the stems which are stimulated to produce new roots. This seems to keep the *Calluna* young and such mixed stands appear to be potentially immortal.

Surface pattern on peat bogs

The patterns of hummocks, lawns, hollows and pools have been briefly described. Some of their characteristics are easily explained. Elongate pools follow contours because if they did anything else they would drain and cease to be pools. But are pools a normal feature of bogs, and how do the strings and flarks of aapa mire originate and survive? There is no clear answer to such questions.

That pools have been a feature of bog surfaces for some time can be seen in the sequence of macro- and micro-fossils in a peat core. Different species of *Sphagnum* are characteristic of hummocks and hollows. So too are amoeba-like Rhizopods which construct 'tests'—houses of form and size characteristic of the species—which survive after the animal dies. Single sequences are difficult to interpret however; faces exposed during peat cutting are more informative. Walker & Walker[27] found that in the top 1–2 m of eight Irish bogs hollows or pools had formed erratically, persisted for a time, then disappeared. There was no sign of a regular cycle of hummock and hollow—a hypothesis popular at one time but with most of the evidence now firmly against it. There do seem to have been times when hollows or pools formed over large parts of a bog at the same time, and this is plausibly attributed to a generally wetter climate. At greater depths, however, the evidence for hollows or pools is usually sparse. It is difficult to tell whether this is because the evidence has decayed or that there really were fewer hollows and pools in the early stages of peat accumulation. Foster *et al.*[11] have produced evidence about the growth of pools in peat bogs in North America. Some pools seem to be hollows in which peat accumulation has not kept pace with the surrounding hummocks partly because the rate of addition of plant matter is low and partly because decomposition is more rapid in the oxygenated warm pool water. Once such pools become more than 5–10 cm deep they may lose most of their plants except sparse *Menyanthes trifoliata* (bog-bean) and scattered patches of *Sphagnum cuspidatum*. Such pools give the impression of being permanent features which can only enlarge (by erosion) unless they develop an outlet and drain. They may then become foci for destructive erosion or become revegetated.

The integration of ideas about pool formation with those about hydrology has scarcely begun outside the U.S.S.R. For example, a moderate number of hollows or pools could exist on a bog surface without invalidating the hydrological needs already considered. But many or large pools would begin to affect the overall shape of the whole bog. This sort of interaction *has* been considered by Ivanov,[19] however. His treatment is, unfortunately, too complex to be easily summarized here.

Mire erosion

The theoretical limits to peat bog growth have been described, but in practice peat erosion is common, particularly on blanket mires, because they often exist on slopes and in very humid climates. There are numerous accounts of catastrophic mire flows, slides or bursts. Usually they happen during or just after prolonged heavy rain, and failure occurs (or extends back to) a break in the slope of the underlying rock. Large tabular blocks of peat slide on a sole lubricated by water and underlying clay. What we know is inferred from observations after the event: rarity, remote location and awful weather have so far combined to prevent eye-witness accounts of the start of these episodes.

Erosion may begin in a less spectacular way, usually at the margins of the peat mass. Gullies ('groughs') cut back into the mire, often following the line of pools. Eventually the mire is reduced to isolated tabular blocks ('haggs').

The most careful studies of the early stages of erosion have been those of Tallis[25,26] who used pollen and macrofossil counts to establish the botanical composition and (by cross-reference to C-14 dated events) the rate of growth of peat at numerous points within 1 km^2 on single peat bogs in the southern Pennines. This detailed work showed that erosion began 1000–1200 years ago as a natural phenomenon before the onset of burning or sheep grazing. The immediate cause seems to have been the rapid accumulation of a layer of relatively unhumified *Sphagnum* peat over a more humified peat. Topography prevented lateral spread and it was this loose peat which triggered marginal slides and gully erosion. Some of these gullies were recolonized by

Sphagnum, but about 200–300 years ago the *Sphagnum* was killed by polluted air. This, coupled with burning and grazing, restarted vigorous erosion.

Water chemistry

There is an approximately inverse relationship between the concentration of H^+ and that of Ca^{2+} in mire waters, reflecting the degree of influence of mineral-soil water. The majority of samples fall toward one end or the other of this gradient. This may mean that the conditions causing fen and bog tend to persist, or that the plant succession from minerotrophic fen to ombrotrophic bog is rapid when it does occur, or some combination of both.

The chemistry of water in *Sphagnum*-dominated bog, described by Clymo,[5] is complicated. In the initial stage rain falls on the plants, which contain polyuronic acids in the H^+ form. Cation exchange results in a drop in the pH around the plants. At this stage the counter anions are mostly Cl^- and SO_4^{2-}. If dry weather follows rain then the concentration of both cations and anions in the water increases because of evaporation. Water samples from lower down, and those in water which is displaced from hummocks in the autumn contain a relatively high concentration of yellow or brown organic acid anions: in effect inorganic counter anions have been replaced by organic ones. The process by which this occurs is obscure. Painter[23] showed that *Sphagnum* itself contained a fairly large proportion of a very unusual uronic acid: 5-keto-D-mannuronic acid. By acid catalysed dehydration and partial decarboxylation this forms soluble yellow-brown aromatic acids isolateable from bog water by the procedures used to separate 'humic acids'. There is no role for microorganisms in this change, though microorganisms are active in this region.

Inorganic chemistry of surface bog peats

The surface layers of ombrotrophic peat have potential for recording the historic influx of atmospheric particles, particularly metals, without the contamination unavoidable in lakes and fens. The techniques of atomic absorption spectrophotometry and, more recently, inductively coupled plasma spectrometry have made it practicable to make analyses of many elements on the same samples. Measurements of magnetic variables supplement purely chemical ones as they may help to identify the type of particle. Coleman[7] has reviewed recent work.

Concentration profiles differ from element to element and from site to site (Fig. 9). In general, potassium and sodium have maxima at the surface, probably in live plants. Aluminium and titanium (probably from soil dust) peak at the mean water table. So do iron, phosphorus, lead, zinc, copper strontium, barium and others including magnetic variables. Calcium and magnesium typically fluctuate with no clear trend, and managanese is idiosyncratic, sometimes fluctuating and sometimes falling steadily from the surface.

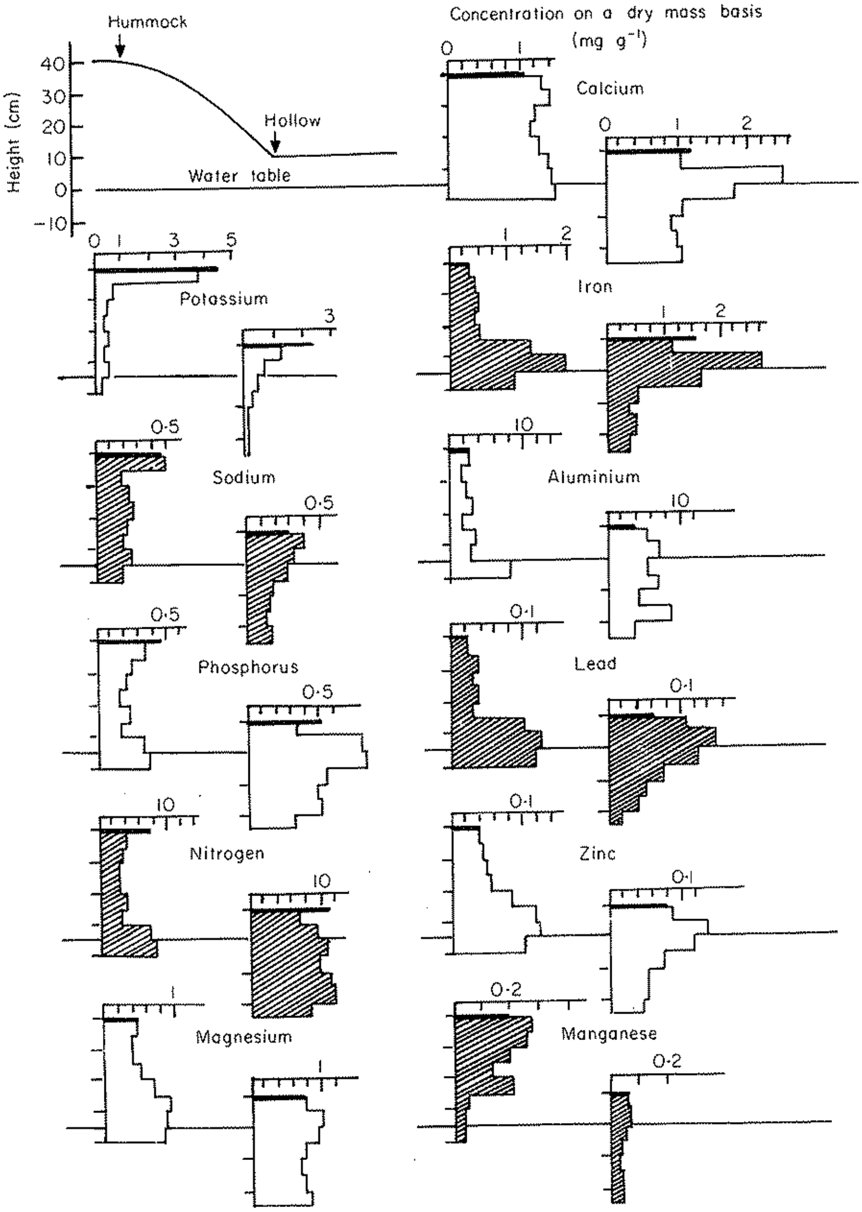

Fig. 9. Concentration profiles of eleven elements in the surface of a hummock and an adjacent hollow on Storemosse, southern Sweden (after Damman,[10] with correction of some scales). Peaks in concentration are often associated with the water table.

Influx rates have been calculated, but there are great difficulties in the interpretation of profiles. A few of these are discussed below.

(1) As Oldfield *et al.*[22] have shown, the influx to hummocks may be 10 times that to hollows or pools.

(2) The peak concentration of elements such as iron and lead seems to be associated with the position of the water table (Fig. 9). The same is true of magnetic variables. That suggests that in hummocks at least there may be substantial vertical movement, especially downwards.

(3) Flux calculations require accurate dates. A number of techniques have been used but none is really satisfactory. Some methods give a continuous and absolute timescale; others give a relative timescale, which must be anchored at two points at least; the rest give spot values suitable for anchoring.

(a) The 'moss-increment' technique resembles tree-ring counting in that it relies on annual periodicity of moss growth. Recognition of periodicity is subjective and can be used only in favourable cases: it is of no use in hollows, for example. The increments of growth in associated species such as *Scirpus cespitosus* (deer sedge), *Drosera* spp. (sundews), and the root whorls of *Calluna vulgaris* (ling) have all been used but take one back no more than 20 years or so.

(b) The relative concentration of C-14 in the air has fluctuated during the last 600 years. The pattern of fluctuations is well-known from dated tree rings and may be matchable with the fluctuations in peat ('wiggle matching'). The method is very expensive because it requires numerous accurate determinations, but it may become the ultimate standard.

Any substance which is added at constant rate and is thereafter immobile can be used to provide a relative timescale.

(c) Pb-210, derived from Ra-226 via Rn-222, is increasingly used, after allowing for its radioactive decay and for any innate Pb-210 'supported' by Ra-226 (usually very little in peat). At first it was isolated chemically and alpha emissions counted, but nowadays direct γ-counting is possible and much simpler. The assumption of immobility in hummocks is dubious, as Malmer & Holm[20] showed, probably because Pb-210 behaves as ordinary Pb does (Fig. 9), but hollow peats may be more suitable. The diffusion of Ra-226 gas further complicates interpretation.

(d) Conceptually very similar is the use of dry matter itself. Here immobility is assured but the rate of addition and the rate of decay may both vary.

(e) 'Ash' (the unburnable fraction of peat) has been used. It may be satisfactory in some places, but many peats show erratic profiles of 'ash' concentration, sometimes associated with accumulations of the siliceous walls of diatoms.

(f) Nitrogen, calcium and magnesium have all been tried. None is reliable.

Spot measurements, useful by themselves or for calibrating relative measurements, are of two main sorts.

(g) Pollen analysis may allow the identification of horizons which can be correlated with local changes in vegetation. The abandonment of *Cannabis* (hemp) cultivation and afforestation with conifers are often recognizable in Britain. Tallis[24] gives excellent examples of what may be possible.

(h) Aerial testing of nuclear bombs in 1963, just before the U.S.A.–U.S.S.R. moratorium, produced worldwide fallout of many radionuclides. Of these Cs-137, with a half-life of 30 years, is a suitable marker and has been widely used. It is easily measured by direct γ-counting, but is mobile—probably more so than Pb-210. There is a possibility that H-3 (tritium) produced in 1963 may have been incorporated into plant organic matter, but the method is untested as yet. The recent accident at Chernobyl has given what one hopes is a never-to-be-repeated opportunity to follow the dispersal of Cs-137 (and other tracers). The Chernobyl material will be identifiable for perhaps 10 years because it was accompanied by Cs-134, which the 1963 bomb tests were not. The immediate concentrations in the top few centimetres of the acrotelm were up to 700 pCi g^{-1} (compared with about 30 pCi g^{-1} in 1963) but only in the worst affected places.

In summary, it is still not easy to get accurate estimates of age in the acrotelm and top of the catotelm for peat younger than 400 years or so. It is more difficult still to convince others that the dates are accurate.

Conclusion

I have tried to show how our present understanding of the ecology of peatlands has required studies at different scales in space and time and from seemingly disparate disciplines. The massive accumulations of organic matter in peatlands result from an unusual balance of productivity and decomposition—unusual but not different in kind from those in other systems.

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INTERACTIONS OF SPHAGNUM WITH WATER AND AIR

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ABSTRACT

Peat-accumulating wetlands occupy 2-3% of the Earth's land surface. Sphagnum, an important constituent of much of the peatland vegetation, is responsible for initiating acid conditions in ombrotrophic bogs and, because it decays disproportionately slowly, becomes over-represented in peat. Several features of Sphagnum physiology are important: (1) the plant produces polyuronic acids which, by cation exchange, release H^+ into the bog water; (2) it is sensitive to the combination of high pH and high Ca^{2+} concentration together, though not to each separately; (3) it is sensitive to even moderate concentrations of o-phosphate, NO_3^- and NH_4^+; and (4) it is sensitive to moderate concentrations of HSO_3^-.

Cation exchange may be an important source of acidity in some bogs but is probably less important generally than was once thought. The role of coloured organic acids as primary sources of acid is not clear. Acid rain sensu stricto has not been shown to affect Sphagnum, but atmospheric pollution in the wide sense is responsible for its disappearance from badly polluted areas of the southern Pennines.

Since the last glaciation, peatlands have been a 'sink' for atmospheric carbon, but some bogs in Europe, at least, are becoming less effective as they approach the natural limit to their growth. Death of their vegetation, where it occurs, and mining of peat both contribute to increasing atmospheric CO_2 concentration, the extent of which can only be guessed. Nor do we know how peatlands would respond to increased concentrations of CO_2 in the atmosphere.

INTRODUCTION

Estimates of the area covered by peat-accumulating systems have tended to increase. A recent one (Kivinen and Pakarinen 1981) of 420 Mha - about 3% of the Earth's land surface - was obtained by summing national estimates by other authors who used a variety of criteria. Olson et al. (1983) used similar methods and recorded 90 Mha of bog and mire, and 380 of low-arctic tundra. Their central estimate of phytomass carbon in these two components was 2.0 and 3.8 Gt in a world non-ocean total of 560 Gt. Estimates of the phytomass of forests, which cover 4000 Mha, include that in trunks and branches of trees. However, the estimates for peatlands ignore the peat, which has almost as important a role in these ecosystems as trunks and branches do in forests. A crude estimate of peat mass can be made. Assuming that the mean bulk density of dry matter in peat, taken to be of average composition CH_2O, is 0.1 $g.cm^{-3}$ and that the mean depth of peat is 1 m, then the total carbon in peat and its surface vegetation

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(using cm for calculation) is about $420 \times 10^{14} \times 0.1 \times 100 \times (12/30) / 10^{15} = 170$ Gt. The value of 1 m for peat depth is little better than a guess, but it seems possible that perhaps 1/4 to 1/3 of readily accessible vegetable carbon is in peatlands. These ecosystems have usually been considered as a sink for carbon, so a substantial change in the rate at which peat is accumulating might have noticeable effects of the concentration of CO_2 in the air.

Among peat-forming plants, one of the most important is *Sphagnum* - the bog moss. A general account of its ecology and physiology is given by Clymo and Hayward (1982). Of the 200-300 species about twenty are quantitatively important. Each species has its own range of tolerance of water supply and solute concentrations, but all are able to make their environment unusually acidic by cation exchange, and most have an unusually low rate of decay. Most *Sphagnum*-dominated peatlands are ombrotrophic, even if they rely to some extent on focussed drainage from a larger catchment to keep them in hydrological balance in dry periods. Two factors contribute to the vulnerability of peatlands to atmospheric pollutants when compared with many mineral sites: (1) the dependence of peatlands on precipitation, and (2) the sensitivity of *Sphagnum* to atmospheric pollutants because of its one-cell thick, uncuticularized leaves. The vulnerability of peatlands to inorganic compounds of S and N in areas with relatively high pollution has been convincingly shown; the evidence is reviewed by Lee *et al.* (this volume). They also give reasons for suspecting that there may be sub-lethal effects in less heavily polluted areas.

In this article I consider some general interactions between *Sphagnum* and water chemistry, and some possible effects on the peat-accumulation process.

EFFECTS OF *SPHAGNUM* ON WATER CHEMISTRY

One of the most obvious effects of *Sphagnum* plants is that they make the surrounding water acidic. Some, and probably most, of the initial effect is a consequence of cation exchange. Up to about 30% of the plant dry mass is uronic acid residues in long polymers. There seem to be two uronic acids in about equal amounts: galacturonic acid and 5-keto-D-mannuronic = D-lyxo-5-hexosulopyranuronic acid (Painter 1983a). The latter is unusual among naturally occurring sugars in its ability to crosslink glycan chains. The cation-exchange capacity of *Sphagnum* is close to that predicted from the measured polyuronic acid concentration (Clymo 1963; Spearing 1972). Both are related to the dryness of the microhabitat; hummock species have values about twice those of pool species. The same tendency is found among individuals of the same species in different microhabitats. Not all plant species of oligotrophic acid habitats have a large cation-exchange capacity. Roots of *Eriophorum angustifolium*, for example, have a capacity about 1/10 that of *Sphagnum*. There is no obvious explanation for these trends and differences.

Sphagnum is extraordinarily efficient at producing dry mass, which consists mostly of polysaccharides, with a small investment in cytoplasm. Most of the uronic acid is in the holocellulose fraction, and cation-exchange properties persist after death. It is likely, therefore, that most of the exchange capacity is in the cell walls. The whole plant may be considered as if it were in a cation exchange phase, which would come, if left for a short time into equilibrium with the surrounding solution. This does indeed occur (Fig. 1), showing that in the live Sphagnum plant most, if not all, the uronic acids are manufactured in the free acid form, i.e., as $-COOH$ (or $-COO^- H^+$) rather than as $-COO^- R^+$, where R^+ represents some cation other than H^+.

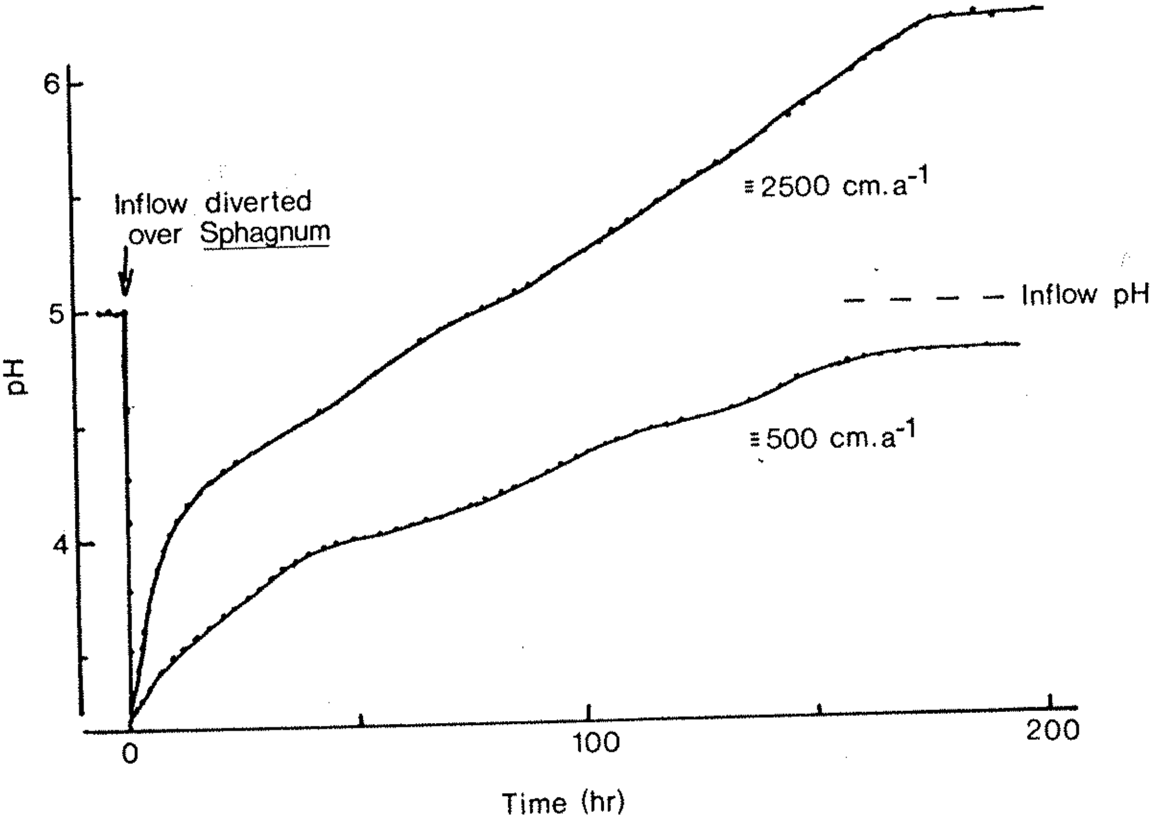

Fig. 1. pH of simulated rain flowing over Sphagnum recurvum at two rates. Both are much greater than normal precipitation averaged over a few days. The plants were in continuous light. At the arrow at t = 0, the solution, which had been bypassing the plants, was diverted over them.

The formation of a uronic acid rather than a sugar may be considered overall as:

$$-CH_2OH + O_2 \rightarrow -COOH + H_2O.$$

Given the presence of O_2, it is not necessary that H^+ be involved in this reaction. It is apparent from Fig. 1 that in the higher flow-rate the pH of the effluent rises as the H^+ on the exchange sites is slowly leached away. Eventually the pH of the outflow exceeds that of the inflow, perhaps as a consequence of photosynthesis (though curious results are found when light and dark alternate). The higher flow-rate, equivalent to 2500 $cm.y^{-1}$, is very much greater than natural rates of precipitation averaged over periods of more than a day or so. Even though the plants are living and, one assumes, producing new -COOH groups, they cannot produce them fast enough to keep up with the monsoon conditions of this part of the experiment. At the lower rate of inflow (Fig. 1) the plants are able to maintain their pH below that of the inflow. This steady-state pH clearly depends on the plant growth rate and on the solution (precipitation) flow-rate. It also depends on the concentration of solutes. A simple theory (Clymo 1967) shows that with measured growth rates, effective precipitation and solute concentrations, a mean pH of about 4.2 could be maintained in an unpolluted atmosphere. An extension of the theory (Clymo 1984b) allows the effects of acidified rain, evaporation, rain composition and temporal and spatial variations of *Sphagnum* growth to be calculated. At Moor House (575 m altitude in the northern Pennines of England), during the year in which detailed measurements of growth and rain chemistry were available, *Sphagnum* contributed about half of the measured acidity. The rest came in the rain, which had a volume-weighted mean pH of 4.1.

The pH of *Sphagnum* hummocks at the Moor House site in the period 1968-70 showed autumn and spring values of from 4.2-4.5, with a summer pH depression to 3.4, but with a sharp return to higher values with the heavy autumn rains. At that time the pools became, for a short time, more acid than the hummocks. The values of pH calculated for the hummocks from the measured properties of precipitation and from measured plant growth rates agreed fairly well with the measured values except during drought. This is assuming cation exchange to be the only process contributing to further acidification of the bog water.

The concentration of other ions in the water around the plants was also measured. During the summer, there were strong correlations in hummock samples within the group H^+, Na^+, K^+, Ca^{2+}, Mg^{2+}, Al^{3+}, Cl^- and SO_4^{2-}, implying that evaporative concentration may have been important. On the assumption that Cl^- is relatively biologically inert, Cl^- concentration was used to assess the extent of this process. The result was that the solution around the plants had, in the extreme cases, been concentrated 7.9-fold. Theoretically, a pH of 2.9 would be predicted while the measured value was actually 3.4. Some of this discrepancy can be accounted for if it is allowed that the last rain before the drought probably drained down the plants first, equilibrating with them as it did so, and then moved up again as evaporation began. This was simulated as a 'batch' of rain (Fig. 2) moving down through ten layers of *Sphagnum* then back up again, equilibrating with each layer as it moved. The simulation used measured values of ion concentration in the rain and measured values of *Sphagnum* growth. The immediate effect of the 'last' rain, which had a lower concentration of cations than that in the previous 3 months, was to allow the pH to rise by about 0.1 unit. After evaporation to the point at which the sum of cation concentrations in the top layer was 7.9 times that in the 'last' rain, and after replacement of solution from below, there was a very steep concentration gradient at the surface. This sort of thing occurs naturally as well; after long dry periods one may find the surface of Sphagnum encrusted with brown tarry concentrates of what was once dissolved organic matter, or even (although rarely) with crystalline salts. The surface layer is very different from all the others, but the volume-weighted mean pH is 3.5, compared with the measured 3.4. (The choice of 10 layers was arbitrary, but the number of layers has only a tiny effect on the result because the 'last' rain is distributed among as many layers as are chosen.) This simulation is crude, but it does serve to show the sort and magnitude of effects that Sphagnum may have on the water around it. It is this water, of course, that eventually runs off into the surrounding streams.

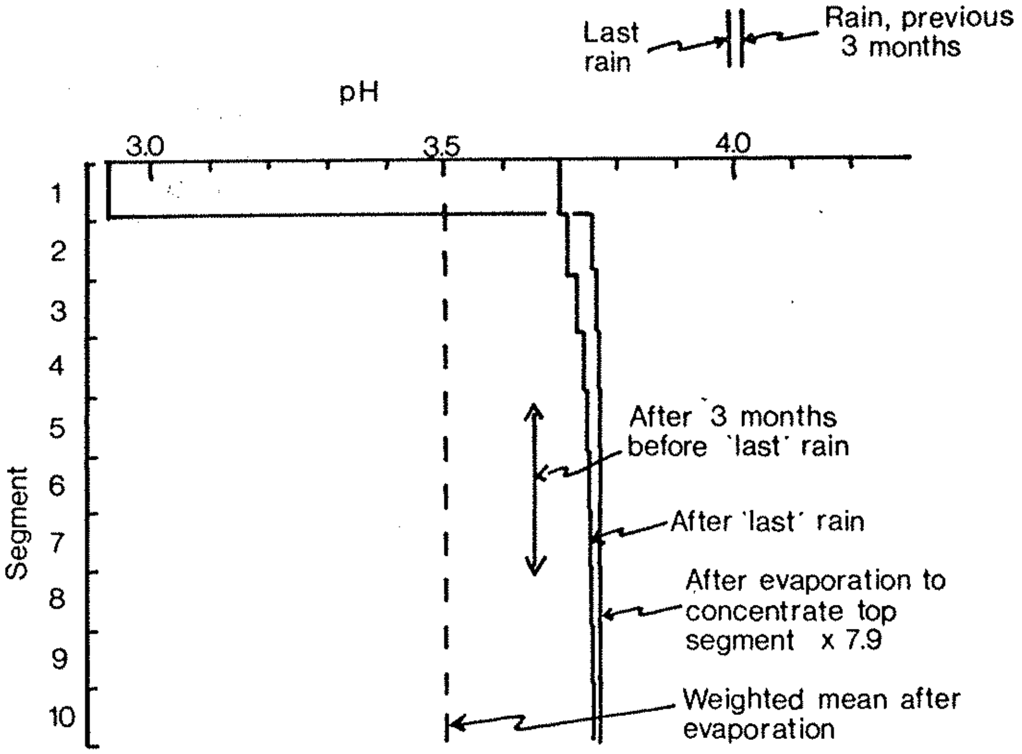

Fig. 2. Simulation of the consequences of cation exchange in a Sphagnum hummock. During April - June, the plants produced 2.4 g.dm^{-2}. This has been arbitrarily allocated to segments 2 - 9 and equilibrated with the measured 330 mm of rain of volume-weighted pH 4.01 and concentration of mono-, di- and tri-valent metallic cations 0.07, 0.16 and 0.04 mmol.L^{-1}. In the next three weeks, plants grew 0.27 g.dm^{-2} (segment 1) and received 39 mm of rain, pH 3.94, and cation concentrations 0.03, 0.06 and 0.5 mmol.L^{-1}. This rain was first assumed to flow down, displacing solution from the segment below and reaching a new equilibrium, in 10 equal aliquots. The following drought, which resulted in a 7.9-fold increase in the Cl^{-} concentration, was simulated by allowing the solution to move upwards in aliquots, equilibrating at each stage with each segment. This, of course, produces a steep concentration gradient at the surface because solutes accumulate there.

While the concentrations of most ions in the solution around hummock-Sphagnum were strongly correlated with each other (and much more so than in rain) they were almost uncorrelated with those of NH_4^+ and NO_x^- (NO_3^- + NO_2^-), which were themselves correlated at r = 0.74, n = 38. The quotient NH_4^+/NO_x^- was 0.9 in rain, 7 in pools, and 9 in hummocks. It seems clear that there must be rapid and extensive interconversions of nitrogen-containing compounds - a conclusion supported by detailed studies reported i.a., by Hemond (1983). That these may be directly attributed to Sphagnum or to its associated microflora is shown by the work reviewed by Lee *et al*. (this volume).

Cation exchange is not the only possible cause of acidity in the surface water of Sphagnum bogs or, perhaps more importantly, in the runoff from them. From time to time it is claimed that high concentrations of CO_2 are found in bog water, and that these may cause the pH to fall to less than 4.0 (e.g., Villeret 1951). If CO_2 is bubbled through bog water the pH falls; conversely, for some samples, if the CO_2 is flushed out by bubbling N_2 gas through the sample then the pH rises to values of about 6.0. In only 5 of 29 samples of water around live Sphagnum from Moor House did the pH rise by more than 0.5 unit when treated in this way - a result similar to that recorded by Gorham (1956a). These five samples were all from places in which the water was probably static and may have been effectively subsurface drainage. They were the only samples that were visibly coloured yellow or brown. It may very well be that microbial activity in peat produces substantial amounts of CO_2; the concentration in peat 1-4 m below the surface was 1-10 $mmol.L^{-1}$ (Claricoates, pers. comm.). This could contribute to the observed pH of about 4.0. But a peat-accumulating system must, on balance, be a sink for CO_2. If there are high concentrations in the catotelm (Ingram 1978) then there cannot also be high concentrations in the surface acrotelm. The CO_2 in the catotelm is thus a secondary, not a primary, source of acidity.

Another possible source of acidity is related to the supply and interconversion of S- and N-containing compounds. In Sphagnum bogs there are few of the neutralization reactions that exist in calcareous fen peat and mineral soils. Therefore, after the modifications imposed by cation exchange, most of the H^+ in precipitation contributes directly to the observed acidity. The anions may, however, undergo conversions which also affect the acidity. One example, simplistically:

$$2H^+ + SO_4^{2-} \text{ (anaerobic) } \rightarrow \leftarrow \text{ (aerobic) } H_2S + 2O_2,$$

is probably microbiologically mediated. Gorham (1956b) was the first to suggest that the reverse reaction might account for the observed approximately four-fold higher concentration of SO_4^{2-} in bog pools during dry weather. At the same time, the pH fell to below 4.0. The method used for analyses of SO_4^{2-} included organic anions (Gorham, pers. comm.). The concentration of other ions was also higher after dry weather: Na^+ and Cl^- by about two-fold; Ca^{2+} and Mg^{2+} by about four-fold. Evaporation may, therefore, have been partly responsible in the way already discussed. The mechanism of sulphide oxidation itself remains plausible. Hemond (1980, 1983) and Urban et al. (this volume) have made the most detailed attempts yet recorded to calculate the effects on acidity of assimilation of S and N into organic combination. In effect, when N in NH_4^+ is incorporated into neutral organic molecules, there is a concomitant acidification. The reverse is true of NO_3^- and SO_4^{2-}.

The last primary source of acidity may be loosely called excreted free organic acids. Ramaut (1955) extracted small amounts of an acid from Sphagnum recurvum and identified it as succinic acid or one of its polymers. He thought it might be excreted and might be at least partly responsible for the acidity of bog water. It is easy enough to identify a variety of organic acids in Sphagnum by chromatography, but in the only reported experiments in which C-14 was supplied to Sphagnum the rate of appearance of organic compounds in the water was tiny; over 1 day less than 0.1% of the C-14 fixed by the plants in soluble organic form appeared in the water, and most of that was in sugars (Clymo 1967). The rate of release of organic compounds is notoriously dependent on the environmental conditions, however, so perhaps this possibility should not be dismissed. More interesting is the recent demonstration (Hemond 1980; Gorham et al. 1985; Urban et al., this volume) that a very wide geographic range of North American bog waters contained organic anions at concentrations of 0.05-0.3 $mmol.L^{-1}$ - a result foreshadowed by Malmer (1963). This may be represented as pA 4.3-3.5 to allow comparison with pH. The concentration was strongly correlated with that of dissolved organic carbon and with the absorbance at 320 nm. On photo-oxidation the pH, in most cases, rose to 6.0 or above. This is a convincing demonstration that some of the H^+ is associated with these yellow or brown 'humic' or 'fulvic' acids of unknown chemical constitution. Painter (1983b) has recently shown that the coloured organic anions in one sample of peat water are probably derived from carbohydrates rather than from lignins. But whether or not these are the source of H^+ is a much more difficult question to answer. The dissolved organic anions are probably products of breakdown. Some might be colourless chunks of original plant material liberated from polymers in pieces small enough to be soluble. Small carbohydrates of this kind are usually rapidly attacked by microorganisms. Most of the yellow and brown anions are probably new productions by microorganisms. In the first case, the associated H^+ is scarcely new: the 'source' is the original plant. In the second case, it may be 'new', but one still has to account for the original H^+, both that in the water and that left in the exchange phase. This requires a clear model of the structure and processes in the surface layers - approximately the top 30-50 cm - of a peat bog.

Suppose the surface of a bog is Sphagnum-dominated. New material is added to the top few centimetres, while aerobic decay occurs down to the water table at perhaps 2-30 cm depth. Because the rate of diffusion of O_2 in water is only 10^{-4} that in air, the peat below the water table becomes anoxic as long as microorganisms are active, and the rate of decay then drops by several orders of magnitude. Aerobic decay in the acrotelm, and the accumulation of mass, eventually cause macroscopic structure at the base of the acrotelm to collapse. (The first snows of winter, at a time when the surface is not frozen solid, may be particularly important.) After collapse, the spaces between elements are very much smaller; therefore, hydraulic conductivity decreases by several orders of magnitude. Most excess water, therefore, flows laterally rather than through the newly collapsed structure and all that lies beneath it. It is this process that is the main cause of the high water table in bogs. Capillary forces are of secondary importance (Ingram 1983). This model is not universally applicable of course, but it will serve to direct attention to the fate of the organic matter.

Any particular piece of organic matter has to wait in aerobic conditions, during which the rate of decay is relatively great, until it collapses and passes into the catotelm. During this time perhaps 90% of the dry matter is lost (Clymo 1984a). Carboxylic acids may disappear by reactions that have the overall effect: $4COOH + O_2 \rightarrow 4CO_2 + 2H_2O$. There is an implied change in the concentration of H^+ insofar as the concentration of COOH was itself buffering H^+. But the acids associated with a metal cation, $-COO^-R^+$, cannot simply abandon the R^+ without a counter-ion. Their charge might be balanced if microorganisms use the $-COO^-$ as a substrate and release in its place equivalent amounts of alternative (yellow or brown) acid anions. Organic acids might also be produced using neutral plant carbohydrates (just as uronic acids are produced by plants). These would be new acids. The main possibilities are summarised in Fig. 3.

There appear to be differences in the bogs of England and those of North America with respect to organic anions. Hemond (1980), Gorham et al. (1984), and Urban et al. (this volume) all report substantial concentrations of yellow or brown organic anions in summer samples of bog water from North America. Hemond's samples were probably from the catotelm but the others were above or just below the water table. However, in similar midwinter samples from bogs in England Gorham et al. (1985) and Urban et al. (this volume) found no more than a very low concentration of organic anions perhaps because these pools had been flushed by recent rain (Gorham, pers. comm.). Clymo (1984b) reported that the concentration of cations and inorganic anions in an English blanket bog were close to equilibrium. The balance was maintained even in summer. It may be that the relatively high concentration of marine and pollution solutes masked the organic anions and that the relatively great excess of precipitation over evaporation prevented summer concentration of the organic anions in pools to the extent found in North America (Gorham, pers. comm.).

As Gorham et al. (1985) point out, the higher concentrations of organic anions are generally found in those areas in which precipitation is little more than evaporation, and perhaps below it in summer when the samples were collected. Not only is the lateral flux of water small, but solution around the lower part of *Sphagnum* plants may be drawn up to the apices by evaporation and concentrated there to the surprising extent already mentioned.

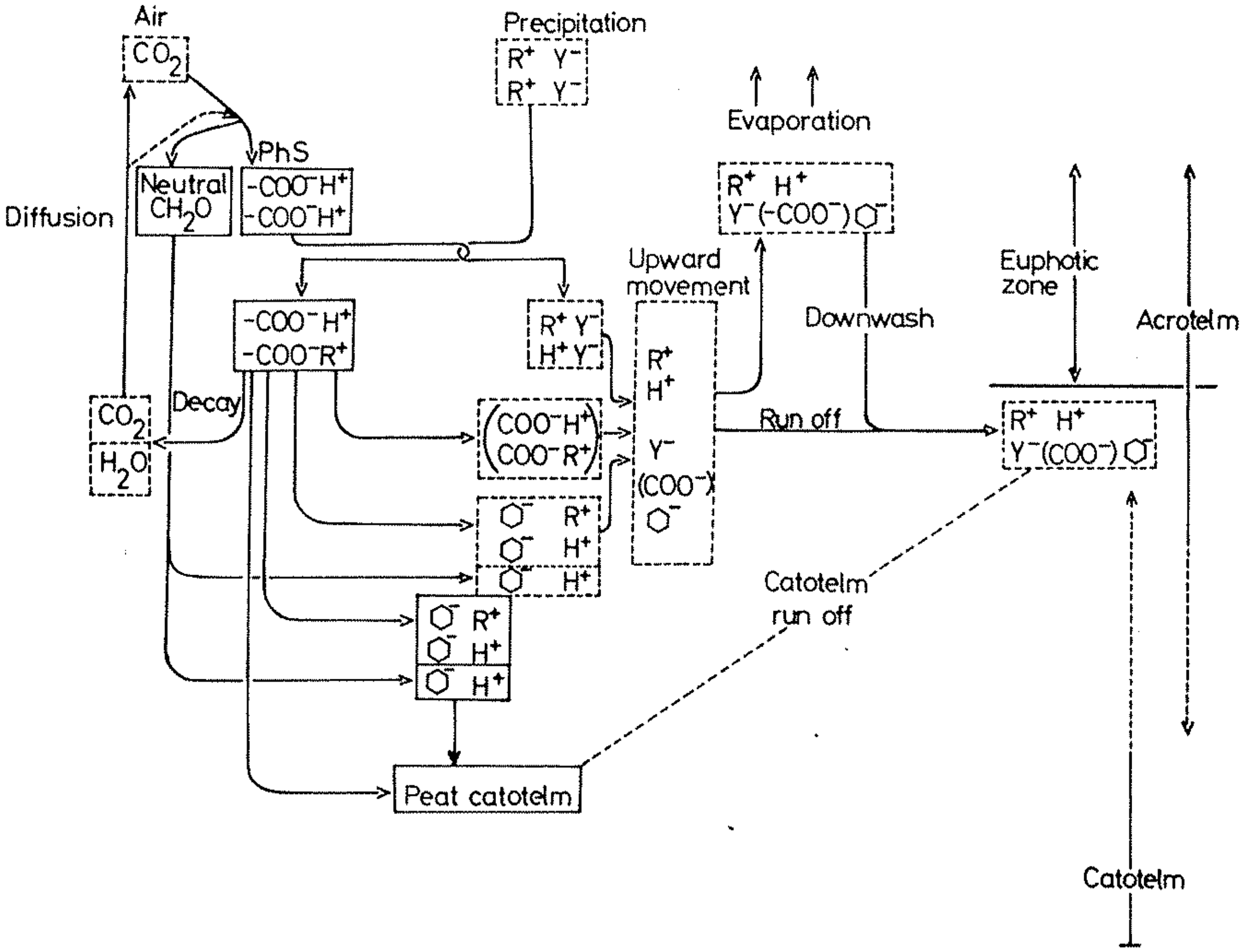

Fig. 3. Some of the processes involved in acid production in bog waters around Sphagnum. The effects of CO_2, of direct acid precipitation, of some forms of cation and anion uptake into plants, and of the interconversion of the various forms of N and S are omitted. Soluble forms are surrounded by broken lines, insoluble ones by a continous box. The symbol R^+ indicates a cation other than H^+; $Y^-$is an inorganic anion; $-COO^-$ represents uronic acid; ⬡$^-$ represents yellow or brown coloured 'fulvic' or 'humic' acid, perhaps aromatic, but perhaps derived from carbohydrate (Painter 1983b) and shown in parentheses. Some of the CO_2 produced during decay may be taken up again at the plant apex without escaping to the air. Decay does continue in the catotelm and some water does flow through it. These three processes are shown by broken lines.

The existence of high concentrations of coloured organic anions serves to buffer the pH of the water at about 4.0, but it does not *per se* tell us about the *primary* origin of the H^+. We need to know to what extent these coloured anions are chemically equivalent to the $-COO^-R^+$ that have been destroyed, and to what extent they are new products in the H^+ form.

An approximate calculation of the chemical nature of the coloured anions can be made. Suppose *Sphagnum* productivity is 300 $g.m^{-2}.y^{-1}$ with 20% of dry mass as polyuronic acid. Suppose also that 50% of the H^+ is exchanged for other cations. This proportion will be greater the larger the value of P - E (precipitation - evaporation) and the greater the concentration of non-H^+ cations in the precipitation. Suppose further that 90% of the plant mass is lost during passage through the acrotelm (Clymo 1984a). The molecular mass of a uronic acid residue is 176; therefore the rate of destruction of those $-COO^-$ associated with non-H^+ cations is 300 x 0.2 x 0.9 x 0.5 / 176 = 150 $mmol.m^{-2}.y^{-1}$. For dissolved 'fulvic' and 'humic' acids the mean negative charge density, on a carbon basis, of many samples was 10 $mmol.g^{-1}$ (Oliver *et al.* 1983). If the lost non-H^+ uronic acids were all replaced by coloured organic anions in solution in this way then the mean concentrations would be:

P - E	($cm.y^{-1}$)	1	10	100
Coloured anions	($mmol.L^{-1}$)	15	1.5	0.15
Coloured anions as DOC	($mg.L^{-1}$)	1500	150	15

Most of the recorded concentrations lie toward the right hand side. On the other hand, as Gorham and Urban (pers. comm.) point out, for 14 samples in a transect across North America (Gorham *et al.* 1985) the mean concentration of H^+ was 107 $\mu mol.L^{-1}$, of other cations was 75, of $Cl^- + SO_4^{2-}$ was 21, (and of the anion deficit, probably mostly coloured organic anions, was 157 $\mu mol.L^{-1}$). This indicates a minimum of (107 - 21) / (107 - 75) = 0.47 $\mu mol.L^{-1}$ of 'new' coloured organic acids. However, this makes no allowance for undissociated acids.

In short, it is possible that the coloured organic anions are no more than microbially-produced replacements for non-N^+ associated carboxyl groups originally formed by the plants as polyuronic acids. One calculation indicates that they *may* all be replacements, but another indicates that half or more *may* be 'new'. We need more studies of the chemistry and microbiology of peat-forming ecosystems.

EFFECTS OF WATER CHEMISTRY ON *SPHAGNUM*

Most species of *Sphagnum* are unable to survive prolonged submergence in most, and particularly calcareous, groundwaters. From observations of their field behaviour as colonists in fens, it would seem that a few species, have a greater tolerance than most (e.g., *S. squarrosum*, *S. fimbriatum*). Is it the high ionic strength, more specifically Ca^{++}, or the pH to which the plants respond? Wilcox (1984) showed that *S. recurvum* continued to grow in NaCl at 40 mmol.L^{-1}, although at a reduced rate, and Paul (1908), recorded by Skene (1915), showed that several species of *Sphagnum* were able to grow in $CaSO_4$ solutions as concentrated as 15 mmol.L^{-1}, equivalent to a 1/2 Ca of 30 mmol.L^{-1}. Experimental work is bedevilled by the high cation-exchange capacity of the plants: any attempt to change the ambient concentration of cations is 'resisted' by the plants. It is necessary to flush them with large volumes of solution if approximate control concentrations in the solution are to be imposed. When this was done (Clymo 1973), it became clear that pH and Ca^{2+} concentration had independent effects, but also interacted. It was the *combination* of pH 7.5 and 1/2 Ca^{2+} concentration of 5 mmol.L^{-1} that *reduced* most species to bare survival. Two groups of species emerged in these experiments. The more tolerant were *Sphagnum inundatum*, *S. squarrosum*, *S. subnitens*, and *S. recurvum*. Less tolerant were the 'high moor' species *S. papillosum*, *S. capillifolium*, *S. magellanicum*, and *S. cuspidatum*.

Concentration gradients in the field can sometimes be very steep. For example, at Sunbiggin Tarn in northern England (National Grid reference NY 6808) 60-cm tall hummocks of *S. fuscum* rise apparently directly from mineral soil flushed by water so calcareous that tufa forms. The pH in water around the plants falls in adjacent 4-cm thick samples from 7.3 at the base to 4.1. The 1/2 Ca^{2+} concentration falls from 1.45 to 0.07 mmol.L^{-1} at the same time (Bellamy and Rieley 1966).

Rate of supply may be just as important as concentration (Pearsall 1950). Species such as *Sphagnum inundatum* and particularly *S. recurvum* may grow extremely rapidly (more than 50 cm.y^{-1}) in the flushed habitats of slow flowing ditches or drainage lines on hillsides. Flushing at rates up to the equivalent of precipitation at 30 cm.day^{-1} (3 L.dm^{-2}) increased growth by up to 15% (Clymo 1973). This increase is probably much less than that produced by favourable conditions in the field.

This comparison of rate and concentration was further investigated in an experiment with *S. papillosum*. Single plants, initially 4.0 cm long, were supported in a test tube with the capitulum top about 1 cm above the level of 17 mL of solution. The solution was either left in position and topped up with distilled water as necessary to compensate for loss by evaporation, or replaced (equivalent to flushing) every 2 or 3 days. The solutions contained one or more of $NaNO_3$, NH_4Cl, and NaH_2PO_4. No attempt was made to control the pH, but it was measured and varied between 4.1 and 5.2, tending to be lower in the unreplaced solutions. The most concentrated solutions of the two forms of N were 30 mmol.L^{-1}, and of ortho-P 6 mmol.L^{-1}. These were calculated to supply, in 17 ml, about 100 times the amount initially in the plants (i.e., x100 treatment). Dilutions to supply x50, x20, x10, x1, x0.1 and '0' (distilled water) were also used. Each treatment was duplicated and the tubes were randomized in racks, protected from rain, and put on a north-facing windowsill of a building in the relatively unpolluted Hampstead area of northwest London. The experiment ran from January to June 1981. As expected all plants in the x100 and x50 treatments of all three solutes died within 2-3 weeks. Results for the rest are shown in Fig. 4. Separate '0' treatments were included for all three single-solute series, but these are in fact all the same treatment. The results of all six agreed well, as did most of the duplicates throughout the experiment. The results showed the following:

(1) In the unreplaced series all the treatments reduced growth, compared with the nominal '0', except perhaps that which was most dilute in NH_4^+.

(2) Replacing distilled water - the nominal '0' - increased growth, although in three of the six cases the plants died shortly before the end of the experiment in mid-summer. It may be that N and P had been removed to such an extent that the plants could not survive during active growth.

(3) Most of the other results are consistent with the hypothesis that, within the range of concentrations and rates of supply used, a higher supply reduces growth, although there may have been an initial stimulation, followed in spring by death.

(4) The x0.1 treatment with unreplaced NH_4^+ was less inhibitory than the similar one with NO_3^-.

(5) The mixtures of solutes allowed the plants to survive better than might have been predicted from the single-solute results, but the plants still grew poorly.

These results are consistent with field observations that dilute solutions of inorganic N and P compounds kill Sphagnum - at least those species in the 'high moor' group. But all these experiments lasted for a relatively short time. It is interesting, therefore, that the same effect is seen on hummocks where owls or grouse have perched and defecated: Sphagnum in the immediate vicinity dies, but that a little distance away may grow faster. A similar chance observation of increased growth of Sphagnum around ground rock phosphate applied in a fertilizer trial was made by McVean (1959). These two field observations extend the time scale over which effects may occur. Lastly, the growth of S. fuscum in the field is stimulated by balanced fertilization with N and P (Gardetto, pers. comm.).

The lowest concentrations supplied deliberately in the present experiments were 30, 30 and 6 $\mu mol.L^{-1}$ for NO_3^-, NH_4^+, and otho-P, respectively. The N concentrations are similar to those in rain in the UK and southern Norway (Barrett et al. 1983). No attempt was made to exclude gaseous dry deposition, although particulate deposition must have been much reduced if not completely prevented by the transparent covers. Even so, if unintended supplies had been important then one might not have expected the lowest deliberate rates of supply to have had such a depressing effect as did, for example, NO_3^-.

It seems clear that the growth of at least the 'high moor' species of Sphagnum is affected by concentrations or rates of supply of inorganic N that are commonly found nowadays in precipitation. Even present supplies may be beyond the nutrient and neutral ranges and into the toxic one. The results reported by Lee et al. (this volume) differ in detail but lead to similar conclusions.

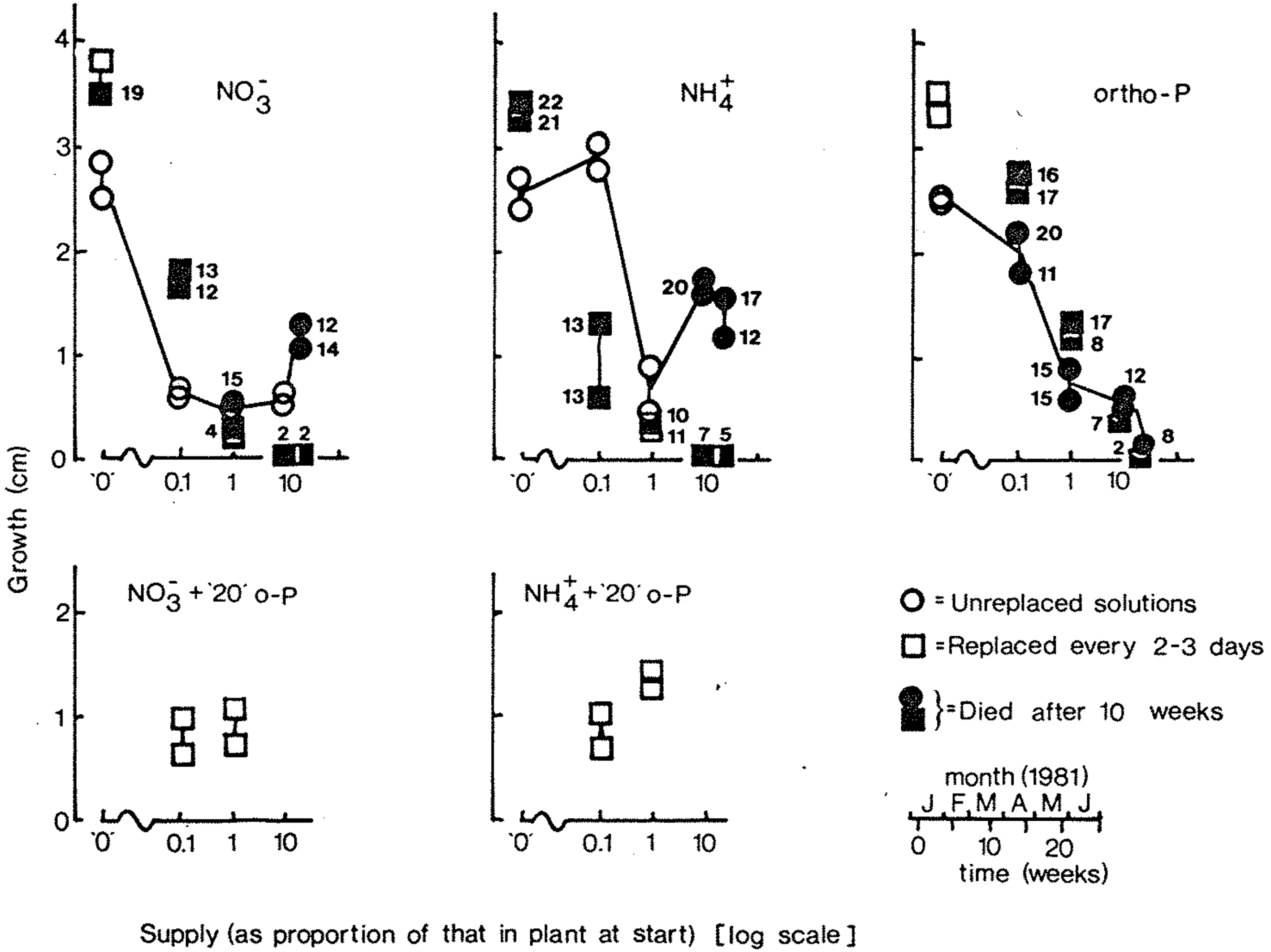

Fig. 4. Survival and growth of Sphagnum papillosum plants in relation to supply of NH_4^+, NO_3^-, ortho-P, or a mixture. 'Concentration' is in units of the amount in the plants at the start of the experiment. In the replacement series (squares) the solution was replaced every 2 or 3 days. Filled symbols indicate plants that died after the number of weeks shown adjacent to the symbol. Other details are given in the text.

There is one curious exception to this. Boatman and Lark (1971) showed that the protonema of *Sphagnum* flourished in, and perhaps needed, concentrations of P of about 1 $mmol.L^{-1}$. In the field protonema is almost unknown, but it has recently been discovered (Clymo and Duckett, in press) that peat below *Sphagnum* contains abundant spores which can easily be stimulated to germinate and eventually to produce mature gametophytes, which are the plants one normally sees, *in situ* in low concentrations of solutes. High concentrations are not necessary.

This discussion has been selective, concentrating on pH, Ca, N and P. Other compounds, such as those containing S, have as great or greater effects (Lee *et al.*, this volume.). Yet other compounds, such as those containing Pb and Cd, or AsO_4 and F have effects on the ultrastructure and growth of *Sphagnum* if the concentration is sufficiently high (Simola 1977). Doubtless others do too. Their importance in nature remains to be determined.

It is of some interest to know the cytoplasmic pH of *Sphagnum*. If it is similar to that of the environment in which the plants normally grow, then either it is unusually low or the proton gradient across the plasmalemma is unusually great. Preliminary results (Clymo and Hawkes, unpub.) with NMR spectroscopy of the ortho-P peak allow one to infer that the cytoplasmic pH of *S. cuspidatum* growing in a pool of pH 5.5 was also 5.5. This *is* an improbably low value for cytoplasm, and is being checked by an independent method. The value proved to be strongly 'buffered'; a change of pH of the solution by 2 units in either direction produced a change in the cytoplasm of no more than 0.1 - 0.2 units. These differences were maintained for several days at least, without impairing the ability to grow normally when returned to water of pH 5.5.

Change of pH in the water *per se* may be of much less importance to *Sphagnum* than quite small changes in the rate of supply of some inorganic compounds.

SPHAGNUM AND THE PEAT-ACCUMULATION PROCESS

The process by which *Sphagnum* formed at the surface is submerged by the rising acrotelm and eventually engulfed by the anoxic catotelm has been described. If the acrotelm maintains the same general character then it injects matter into the catotelm at an approximately constant rate, about 1/10 that at which matter is being added to the acrotelm by plant primary production. If this continues without change and decay ceases altogether in the catotelm then peat will accumulate without limit. But if decay continues, however slowly, then as time passes the integrated loss by decay throughout the growing peat column approaches more and more closely the (constant) rate at which it is injected into the top of the catotelm. The true rate of accumulation slows asymptotically towards zero *even though* the acrotelm surface is healthy and assimilating matter at the same rate that it always has done. There are two reasons for believing that this account is broadly correct. First, the age *vs* depth relation is curvilinear in many, but not all, European cases. This implies continued decay (or steadily accelerating productivity). Secondly, the concentrations of CH_4 and CO_2 in the peat increase steadily downwards (Claricoates, pers. comm.) to the base of the peat several metres deep. This is consistent only with continued production of CH_4, and hence of decay. The whole problem is considered in detail by Clymo (1984a). In the present context it is important because some, and perhaps many, peat-forming systems may be reaching the stage at which the true accumulation rate has become very small, so that they are no longer acting as effective sinks for atmospheric carbon. (In most North American bogs for which sufficient data are known (Gorham, pers. comm.) there seems to be, however, little evidence of a curvilinear age *vs* depth relation). Peat mining ('harvesting' is a euphemism) for burning or horticulture will make peat-bogs sources of atmospheric carbon. Draining may have the same effect as peat mining because it increases the effective depth of the acrotelm and hence the total mass exposed to aerobic decay.

Destruction of *Sphagnum*, or decrease in its growth rate caused by atmospheric pollution, may have complex effects. *Sphagnum* itself decays relatively slowly, probably as a direct result of its low N concentration (Coulson & Butterfield 1978). Not only does proportionally more of it survive into the catotelm, but it enables the catotelm to rise faster and hence it increases the fraction of other species that survive into the catotelm too. On the other hand, *Sphagnum* itself, excepting the aquatic species, usually forms a fairly thick acrotelm while a surface dominated by *Eriophorum vaginatum*, for example, may have a shallow acrotelm. Whether or not damage to a *Sphagnum* carpet, or its replacement by vascular plants, would turn peat bogs from sinks to sources of carbon cannot be confidently predicted at present.

The consequences of an increase in the concentration of CO_2 in the atmosphere are also unpredictable. Billings *et al.* (1983) showed that the direct increase of the rate of carbon storage in tundra was much smaller than the decreases, as a consequence of postulated increase in the temperature and lowering of the water table.

The links between those aspects of atmospheric pollution that most concern us now and those that seem likely to be occupying us by the end of the next decade remain unquantified. *Sphagnum*-dominated peat bogs may be useful systems on which to begin this task.

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