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Profiles of water content and pore size in *Sphagnum* and peat, and their relation to peat bog ecology

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The bog mosses, *Sphagnum*, form a significant part of the total mass of plants in the world. Their rate of growth depends to a considerable extent on the supply of water to them, and different species occupy characteristic habitats which differ in their ability to supply water. We used the profiles of water content in almost undisturbed cores of two species to infer the size and distribution of spaces around the plants in an attempt to account for the observation that *S. papillosum* is usually found not far above the water table, while *S. capillifolium* is usually found on hummocks well above the water table.

Profiles of water content were recorded non-destructively from 30 cm diameter cores of *Sphagnum* and underlying peat, with use of the absorbance of the soft gamma radiation of ^{241}Am. The distribution of water-fillable spaces of different size was inferred from profiles with the water table at different distances, to a maximum of 150 cm, below the surface.

The larger spaces, which are the main path of water transport, are outside the plant cell walls: between leaves and between pendent branches and stems. The mean radius of such spaces around the hummock species *S. capillifolium* is smaller than that around *S. papillosum*. For a given depth of water table the water content of the apical tuft of branches, where growth occurs, is greater in the hummock species than it is in the lawn species. Of ecological importance is that, for a given water content in the apex, the water table is at a greater depth below the hummock species than it is below the lawn species.

As the water table rises and falls, so the water content of both species shows hysteresis as large as the difference between them. The ecological significance of this and the need for measurements while water is flowing are discussed.

INTRODUCTION

Peat covers 1–2% of the Earth's land surface (Kivinen 1981) and individual peatlands can be large. A single peat bog complex in Russia, for example, occupies an area approximately 1800 km × 800 km (Walter 1977). The bog moss *Sphagnum* is one of the most abundant species in the surface vegetation of such peat-forming communities. Because it decays so slowly, *Sphagnum* becomes over-represented in the peat itself (Coulson & Butterfield 1978; Clymo 1982) so that *Sphagnum* is, if

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measured by amount, perhaps the only important bryophyte, and there may be more carbon incorporated in *Sphagnum*, dead and alive, than in any other single genus of plants anywhere (Clymo & Hayward 1982). This, in itself, justifies a study of *Sphagnum*.

An individual *Sphagnum* plant produces leaf and branch primordia at the apex, which is protected by an overarching head (capitulum) of crowded leaves and growing branches. The branches are in groups (fascicles). In a fascicle, some branches are spreading and, in most species, some are pendent. The plants have no control of their rate of water loss and are not very tolerant of prolonged desiccation (Green 1968; Clymo 1973); so their growth depends on an assured water supply. It has long been known that in dry periods water reaches the capitulum from below through capillary films. The driving force is the low humidity of the air, and this causes evaporation. In most species of *Sphagnum* the water is drawn up through an extremely effective system of capillary spaces formed by the pendent branches which hang down against the stem and overlap each other. As Cavers (1911) observed: 'If the tufts of branches be removed from the end of the stem, which is then dipped into water, the plant remains dry, hence the stem-tissue does not serve a conducting function'. Our own experiments (Clymo & Hayward 1982) confirm this observation.

Carpets of *Sphagnum*, i.e. large groups of individuals with touching or overlapping branches, are often composed predominantly of only one species and grow at a height above the average water table characteristic of the species (Ratcliffe & Walker 1958; Clymo & Hayward 1982). Some species, *S. cuspidatum*† for example, are usually restricted to pools, while others, such as *S. papillosum*, are usually found in extensive green carpets, here termed lawns, at, or not far above, the water table. Other species, such as *S. capillifolium*, usually grow on hummocks 10 cm or more above the water table (figure 1).

The submerged species, *S. cuspidatum*, grows less rapidly when transplanted to lawns or hummocks than it does in pools, but *S. capillifolium* although it is usually found on hummocks will, when transplanted in clumps, grow more rapidly in lawns than it does on hummocks, and more rapidly still in pools (Clymo & Reddaway 1971). From the ecological viewpoint, what is important is that *S. capillifolium* on hummocks grows more rapidly *than do the other species* when transplanted there. These three species differ in many respects, but one feature that may perhaps account for the observed natural dominance of *S. capillifolium* on hummocks is the structure of the plants. *Sphagnum capillifolium* is smaller in all its parts than are the other two species and may therefore be able to maintain external capillary films at heights above the water table at which the films in the other species have broken. Without such capillary films, a *Sphagnum* plant ceases to conduct water, with consequent desiccation of the capitulum in periods of dry weather. *Sphagnum cuspidatum* lacks pendent branches and this may restrict it to pools.

The purpose of the work reported here was to raise and lower the water table beneath several species of *Sphagnum*, and to measure the resulting profiles of water content in the plants. In particular we hoped to discover how the water content

† Nomenclature follows that of Hill (1978).

of the capitulum (where growth occurs) in different species depends on the depth of the water table.

Structure of *Sphagnum* and the state of water in it

Structure of a Sphagnum carpet

A *Sphagnum* carpet has a diffuse, ordered but heterogeneous, very porous structure. The bulk density of dry matter is surprisingly low: about 0.02 g cm^{-3} at the surface, increasing to perhaps 0.12 g cm^{-3} at 30 cm depth (Clymo 1978, 1982). The structural elements of which the carpet is composed may be considered

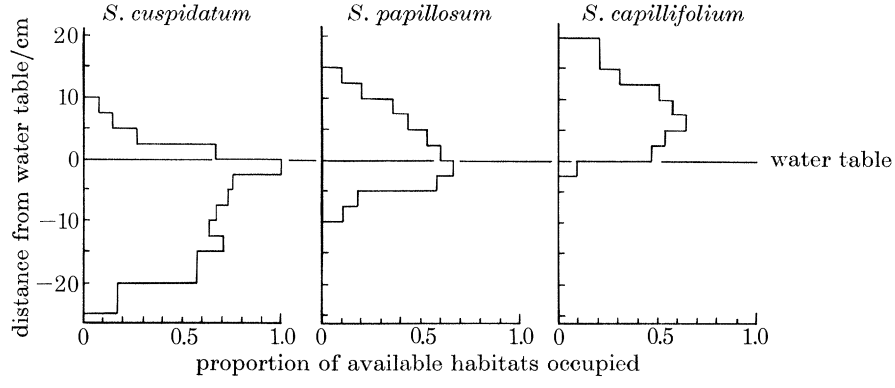

Figure 1. Proportion of 1 m^2 quadrats containing three species of *Sphagnum* at various heights in relation to the water table on the Silver Flowe, Kirkcudbright. (Calculated from Ratcliffe & Walker (1958).)

at three scales: macroscopic, microscopic and submicroscopic. It is convenient to consider the microscopic scale first. The most important features are the porose cells. These occur in the leaf, and also envelop the branches and, in some species, the stem. The leaves themselves are one cell thick and consist of the well known beautiful arrangement of an elongated network of sinuous parallelograms of narrow chlorophyllose cells. Each parallelogram bounds a single large hyaline cell. Mature hyaline cells have no living contents. Their walls have ribs of thickening and one or both the upper and lower walls have pores that allow free mass flow of water (and of algae and small animals) into and out from the cell. The size and shape of these cells, and the number, size and position of pores in them, are characteristic both of the individual species and of the region of the leaf (table 1). An 'average' hyaline cell would be about 200 μm × 30 μm × 30 μm, with pores of radius 4–8 μm. At the submicroscopic scale are the interfibrillar spaces of radius perhaps 0.01 μm. At the macroscopic scale there is also characteristic structure: the leaves are imbricate on the branches, but the space between leaves differs considerably in character in the different species. At one extreme is *S. papillosum* with large, broad leaves, convex along both length and breadth. The gap between leaves is about 0.1–1.0 mm; this gives the branches a large water-holding capacity. As water is removed the radius of interfoliar menisci decreases. The hydrostatic

pressure between the leaves therefore decreases and generates a force that tends to suck the leaves together. The menisci soon break, however, because the leaves are dome-shaped and have a broad curved attachment to the stem, and therefore cannot move far. The leaves of *S. capillifolium* are smaller (about one-sixth the mass of *S. papillosum* leaves) and less domed, and have a narrower attachment to the stem. The branches of this species therefore have a smaller water-holding

TABLE 1. HABITAT AND STRUCTURAL CHARACTERS OF THREE COMMON SPECIES OF *SPHAGNUM*, LARGELY FROM HILL (1978)

	S. cuspidatum	*S. papillosum*	*S. capillifolium*
habitat	pools	lawns	hummocks
general appearance	large, but firmly made	robust	rather delicate
stem			
diameter/mm	0.4–0.8	0.7–1.0	0.4–0.6
pores in outer layer (per cell)	none	1–5	none
branches			
number (per fascicle)	3–5	3–4	3–4
spreading: pendent	no distinction	2:1–2	2:1–2
length/mm	8–25	7–24	5–20
branch leaves			
shape	lanceolate	ovate, hooded	narrowly ovate
size/mm	1.5–3.5 × 0.3–0.7	1.5–2.5 × 1.3–1.9	0.8–1.4 × 0.4–0.6
†thickness/μm	14–35	27–48	15–29
†hyaline cell length/μm	90–300	70–250	50–150
†pores, dorsal:ventral (per cell)	0–1:4–10	3–10:none	4–7:none
†pore radius/μm, dorsal:ventral	1–3:2–4	7–11:none	4–12:none

† In mid-leaf.

capacity at first, and the leaves are more easily sucked together as the plant dries. Species differ in the length and number of their pendent branches: each fascicle of *S. capillifolium* has three or four short branches of which one or two are pendent, but *S. cuspidatum* has no definitely pendent branches.

For a species growing above the water table, the carpet as a whole consists of a relatively dense porose roof (the capitula) supported on vertical stems which do not themselves conduct water to any extent but which are clothed in pendent branches which constitute a wick of various and variable size spaces. The branches form innumerable horizontal wicks, and where they touch one another they allow lateral flow of water (Clymo & Hayward 1982). Water may thus move fairly easily either vertically or horizontally, but it is channelled around the stems and branches.

The state of water in a Sphagnum carpet

Table 2 shows the potential of water in equilibrium with menisci of given mean radius of curvature, the height to which water in a wettable capillary of that radius would rise, and the vapour pressure reduction (expressed as relative humidity) over the concave meniscus. If the water table were 30 cm below the surface of a *Sphagnum* carpet and in equilibrium, with no water movement either upward or

TABLE 2. WATER POTENTIAL AND THE EQUIVALENT RELATIVE HUMIDITY, HEIGHT OF WATER COLUMN THAT COULD, IN THEORY, BE SUPPORTED, RADIUS OF CURVATURE OF A WATER MENISCUS, AND THEIR RELATION TO STRUCTURAL FEATURES OF *SPHAGNUM*

water potential, ψ (log. intervals)	relative humidity at 20 °C (log.–log. intervals)	equilibrium height of water column, h (log. intervals)	pF†	mean‡ curvature of meniscus, r_m (log. intervals)	position of water in, and corresponding structural features of, *Sphagnum*	proportion of total§ volume (%)
−100 Pa	nearly 1.0	1 cm	0	1.5 mm	external 'capillary' water: affected by changes in level of water table	about 90
−1 kPa	nearly 1.0	10 cm	1	150 μm		
−10 kPa	0.99993	1 m	2	15 μm	water inside the hyaline cells; radius of pores in *Sphagnum* hyaline cells	about 10
−100 kPa (= −1 bar ≈ −1 atm)	0.99931	10 m	3	1.5 μm	water mainly within chlorophyllose cells	< 1
−1 MPa	0.9931	100 m	4	150 nm		
−10 MPa	0.933	1 km	5	15 nm	relatively immobile water in interfibrillar and intermicellar spaces	< 0.1
−100 MPa	0.50	10 km	6	1.5 nm		
−1 GPa	0.1	100 km	7	0.15 nm	moisture in 'oven-dry' material	

† $pF = \log_{10}(h/cm)$ (Schofield 1935).

‡ $2/r_m = 1/r_a + 1/r_b$, where r_a and r_b are the principal radii of curvature. For a hemispherical meniscus, $r_m = r_a = r_b$; for parallel plates $2r_a$ apart r_b is infinitely large and $r_m = 2r_a$ = the distance apart of the plates.

§ Total water at field capacity.

downward, the water potential (ψ) in the capitula would be about -3 kPa and menisci in spaces larger than about 0.1 mm would break or retreat into spaces of this mean radius. Hyaline cells would remain full: the water table would have to fall to the improbable depth of 1–10 m ($\psi = -10$ to -100 kPa) before they emptied. But a water table at 10 m depth would be in equilibrium with air of relative humidity 0.999, which is indistinguishably drier than saturated air. For long periods in natural conditions the air is, therefore, potentially capable of emptying the hyaline cells. If the cells do not empty then it is only because water is moving upwards through the capillary films around the plant. As the water table is lowered so the water films become longer and, which is more important, thinner, and the hydraulic conductance of the carpet becomes smaller. The depth of the water table still has an important influence, therefore, on the control of water content of the capitula in dynamic conditions. If the supply of water from below cannot keep pace with loss by evaporation however, then ψ is likely to fall rapidly because a relative humidity of 0.5 (corresponding to $\psi = -100$ MPa, and sufficient to start emptying interfibrillar spaces) is quite common in dry weather. Hyaline cells empty at a ψ of about -100 kPa, and the plants then look white and papery. Some capitula may survive for several weeks at potentials down to about -2 MPa (relative humidity 0.98 (Clymo 1973)), at which potential water may perhaps be retained by osmotic forces, but no capitulum survives so long in experiments with $\psi = -100$ MPa (0.5 relative humidity). The water content per unit volume of plant (ϕ_v) is about 0.04 from -1 GPa to about 20 MPa, and then increases sharply to about 1.5 at -2 MPa (Clymo & Hayward 1982). Thereafter it continues to rise. A plot of log ϕ_v against log ψ is roughly linear over nine orders of magnitude of ψ, but with local disturbances. The results given in this paper show that about 90 % of all the water in a *Sphagnum* carpet is associated with spaces with mean radius or width, r_m, of 15 μm and larger, corresponding to $\psi = -10$ kPa and a water table less than 1 m deep.

There are no obvious boundaries in this continuum of states of water but it is convenient, nevertheless, to recognize three categories of water. We follow Romanov (1968), who was considering water in peat, and recognize adsorbed, intracellular and capillary water. Adsorbed water we consider to be that retained at ψ no greater than about -20 MPa. Intracellular water was described by Romanov (in translation) as 'water retained in the internal cells of undecomposed plant residues or living plants'. He defined it as water that could be removed from the surface by applying a suction equivalent to a water table at 30–40 cm below the surface of undecomposed peat i.e. at $\psi \approx -3.5$ kPa. We found, however, that there were still substantial changes in water content as the water table was lowered below 40 cm depth. When it reached 100 cm depth ($\psi = -10$ kPa), however, the changes became very small. We therefore chose this potential to define intracellular water, including water in the hyaline cells, and use the term to include adsorbed water too. The third category is capillary water, which Romanov described rather misleadingly (in translation at least) as 'water retained by capillary forces in the peat soil pores at a specific height above the level of free water'. We use it for water held in any part of the *Sphagnum* or peat at a potential greater than about -10 kPa.

Methods

The previously used methods of measuring water content profiles in *Sphagnum* canopies are destructive. Individual plants can be removed, cut into segments, weighed, dried and weighed again (Clymo 1973). Even when the plants are handled carefully and kept vertical until sectioning is complete it is inevitable that capillary spaces and films of water will be disturbed, so that although the measurements are easily made and the results are reproducible (i.e. precise) they are not necessarily, and not demonstrably, accurate (i.e. give the true values). Moreover the method cannot be used on plants that have lost their structural integrity. A better method is to remove a core and to cut it into horizontal slices. If the core is frozen before it is sliced, then further movement of water is prevented. The resolution of this method is about 1 cm, which is too large for our purposes. Moreover, the variability among nominally replicate cores is so large that several samples are necessary, and it is impracticable, and too destructive of bog vegetation, to investigate the effects of changing the water table at one site.

For these reasons we sought a method that had greater precision, greater resolution and demonstrable accuracy, was non-destructive and would allow replicate measurements and experiments to be made, all on the same core. In addition we wanted to be able to measure the profile of water content with the water table lowered to at least 1 m below the surface. Our early attempts to use electrical resistance and capacitance as measures of water content gave unpromising results (though resistance may be worth pursuing where the distribution of bottlenecks limiting water movement is important). The method that we finally developed was to irradiate a cylindrical core of *Sphagnum* or peat with a collimated beam of gamma radiation, and to measure the attenuation of the beam in conditions in which Beer's Law could be applied. The mass of plant material and water in the path of the beam could then be calculated. The mass absorption coefficient of dry *Sphagnum* is about 1.2 times that of water (see appendix), but in normal conditions the water content per unit (dry) mass of *Sphagnum* rarely falls below 10 g g^{-1} and is usually greater, sometimes much greater, than 20 g g^{-1}. Consequently the absorbance of gamma radiation can be used as a direct measure of the mass of water through which the beam passes. For accurate work the absorbance attributable to the plant material itself can be subtracted.

The principle of this method is not new: Gurr (1962) used it on soils and Unger (1968) used it to measure plant productivity. Indeed it was the conspicuous diel rhythm of reported 'biomass' that first drew our attention to the usefulness of the technique for measurements of water content.

The apparatus (see appendix) contained a 30.5 cm diameter core of *Sphagnum* inside a Perspex cylinder. The core was 8–20 cm deep and the lower parts might equally well be termed peat. The base of the core was separated from a water-filled compartment below it by a membrane filter. The lower compartment had a flexible outlet tube, also water-filled, the end of which could be moved up and down. If the end of this tube was placed *above* the level of the membrane filter and a volume of water poured rapidly into the Perspex cylinder then water flowed rapidly through the core and filter and out from the end of the tube until the level of water

inside the Perspex cylinder fell to that of the end of the outlet tube. If the end of this tube was now lowered to a level *below* the membrane filter then water at first flowed out but only until the level of water in the cylinder reached the membrane filter. Then it stopped because the hydrostatic force was insufficient to pull the capillary films through the pores in the membrane filter. Capillary films in the plants, continuous with those in the filter, were now at the same water potential as they would have been had the free-water table been at the depth of the end of the outlet tube. The end of the outlet tube could be moved up and down below the membrane filter to simulate a water table at different depths: 150 cm below the *Sphagnum* apices could be reached without difficulty. The principle of this method of controlling the water potential is not new: it was used by Collis-George & Sands (1959) and by Harper & Benton (1966).

The apparatus allowed the *Sphagnum* core to be rotated in the beam of gamma rays, and to be scanned vertically. It was self-controlling and produced a paper-tape record which, in conjunction with a computer program, produced a profile of water content, on various bases, with attendant estimates of precision. The precision decreased logarithmically with absorbance and was least (i.e. the mean value was most uncertain) when the core was completely full of water. In these conditions absorbance was 6.24 and a 20 s count gave a standard error of 0.12, about 2 % of the absorbance.

Results

It seemed best to investigate equilibrium states before considering dynamic states. The results shown here are all for equilibrium states. Overbeck & Happach (1956) allowed 30 min for equilibrium to be reached after a change of water table, but some of their results showed that changes were still continuing even after 24 h. In our experiments the change of water level was often small and the relatively undecomposed *Sphagnum* had a low resistance to water movement. In these circumstances equilibrium was reached within a few hours. As a precaution, however, no more than one change of water level was made in any one day and no profile was recorded before the day following the change. A typical experiment commonly took a month or more to complete.

Equilibrium profiles with successively lower water tables

In the first experiment, with *S. capillifolium*, the water table was first moved to the surface of the carpet of plants and then lowered successively to 2, 4, 6, 9, 16, 30, 50 and 120 cm below the surface. The last three depths were below the membrane filter. At each depth the absorbance profile was measured. (Profiles obtained when the water level was raised are considered later.) After the completion of this and subsequent experiments the core was allowed to dry for 21 days and the absorbance profile of the dry plants was then measured. Finally the core was cut by hand into 2 cm thick slices which were then weighed. The agreement between measured slice dry mass and that calculated from absorbance is shown in figure 2. The calculated profiles of water content are shown in figure 3. The scanned depth of core was 15 cm; so the depth to the lowest water table (120 cm below the surface) ranged from 120 cm (below the carpet surface) to 105 cm

(below the base of the core). The potential of water at the surface and base of the core was therefore −12 and −10.5 kPa respectively; so it seems valid to consider the whole 15 cm profile made with the water table at 120 cm depth as being that of intracellular water. The capillary water profile is shown as an addition to that of intracellular water with the water table at different depths. The bulk density

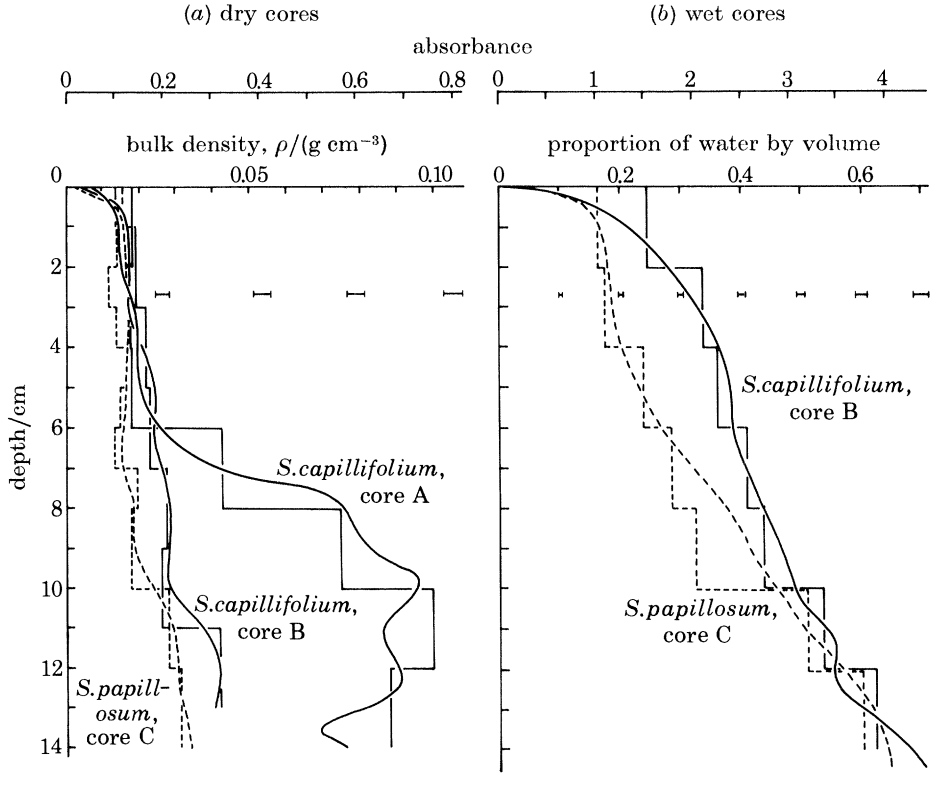

FIGURE 2. Profiles of (*a*) bulk density of dry matter and (*b*) water content, with water table at 30 cm depth, of *Sphagnum capillifolium* (two cores), A and B (solid lines), and of *S. papillosum*, C (broken lines). The curves are those produced by the automatic apparatus; histograms show measurements on slices cut subsequently from the cores. The curves are not 'fitted' to the histograms; they are calculated from totally different measurements. The absorbance scales for the curves allow comparison between graphs in (*a*) and (*b*). Note that the scale in (*a*) is much larger than that in (*b*). The horizontal bars show 95 % confidence limits for representative values of absorbance. The precision is inversely related to the value.

The patterns of bulk density exemplified by the A and B curves of *S. capillifolium* are both common.

(profile shown in detail in figure 2) is about 0.02 g cm^{-3} to 6 cm depth, the plant substance occupying about 0.015 cm^3 cm^{-3}. Further down, the bulk density increases and reaches about 0.08 g cm^{-3} at 8 cm depth. This change correlates with a loss of structural integrity: the stems of the plants have collapsed but the leaf and branch structures remain little altered. Such an abrupt change in bulk density

is quite commonly found but a more gradual change (figure 2) is equally common. It is rather surprising to see that the amount of intracellular water is almost independent of the mass of plant material. Even if non-porose stem and branch cells had all broken down they could hardly account for so small an increase with a fourfold change in plant mass. The space occupied by capillary water decreases

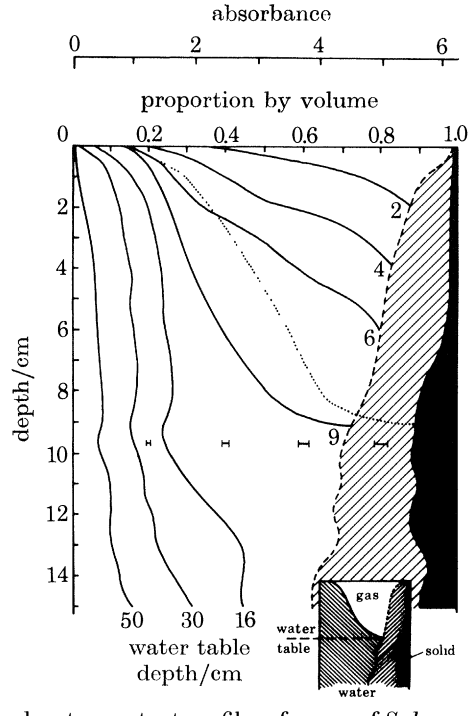

FIGURE 3. Dry matter and water content profiles of a core of *Sphagnum capillifolium* (A of figure 2*a*) with water table lowered to 2, 4, 6, 9, 16, 30 and 50 cm below the surface. The horizontal axis represents the total volume of the whole carpet. At the right are the dry matter (solid) and intracellular water (that retained at a water table depth of 120 cm; hatched). The other profiles show capillary water additional to this intracellular water. The triangular space between represents gas, as shown in the inset scheme. For the 9 cm depth the dotted line shows the sum of intracellular and capillary water, and may be compared with the curves in figure 4. The horizontal bars show 95% confidence limits.

steadily with distance above the water table. It is obvious that statements such as '*Sphagnum* holds twenty times its own mass of water' (or ten or forty or any other factor) are arbitrary: the amount held depends on several factors, including distance to the water table, packing, and bulk density.

The change in capillary water content is not the same at all depths: if it were, the lines branching off to the left from the intracellular water curve would be parallel to one another. In fact, when the water table is at 9, 6, 4 and 2 cm depth, the 2 cm section immediately above the water table holds, as capillary water, 0.29, 0.22, 0.27 and 0.53 of the whole carpet volume in the 2 cm section. The height of section needed above the four named levels to include 0.5 of the carpet volume

as capillary water is 80, 45, 36 and 18 mm respectively. These differences probably result from the capitulum and just below it having a greater volume of capillary spaces, in the appropriate ranges, than do the lower parts of the core. It may be that in the upper parts of the core the leaves and branches are still fairly stiff and are rigidly attached to branches or stems, while in the lower parts they have become

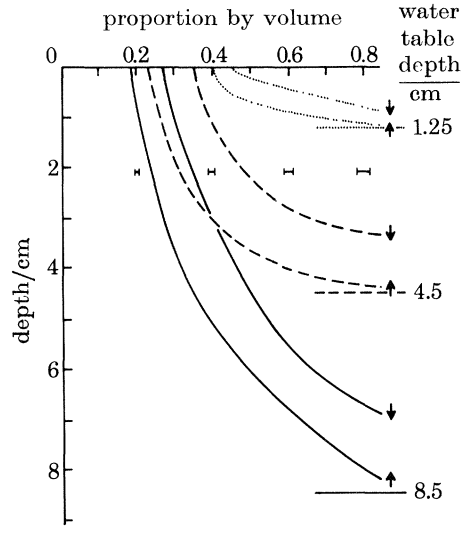

FIGURE 4. Water content profiles in a 30 cm diameter core of *Sphagnum papillosum* with water table at 1.25, 4.5 and 8.5 cm depth. Arrows indicate the direction from which the water table approached each depth. The profile is of the sum of intracellular and capillary water. The horizontal bars show 95% confidence limits.

more flexible as decay begins. The modest reduction in hydrostatic pressure inside the capillary films will then be sufficient to suck together the more flexible leaves in the lower part of the core, thus reducing the water content.

Similar results were obtained with other cores of *S. capillifolium* and with cores of some other species. *Sphagnum cuspidatum* could not be used because its stems were too weak to support a 30 cm diameter carpet out of water.

Hysteresis

Romanov (1968) points out that the moisture capacity of peat that has drained from saturation is rarely, if ever, the same as that of a sample that has absorbed water upwards through its lower surface. Therefore we expected, and found, that the results obtained in cores when the water table was raised by stages were not the same as when it was lowered in the same core. But the size of this hystersis effect was surprising. The general effect for *S. papillosum* is illustrated in figure 4. The hysteresis, in terms of proportion of carpet volume at a given depth, is rarely less than 0.1 and in some cases exceeds 0.3. The details of hysteresis in water content of carpets of *Sphagnum* proved complex; so water behaviour in a simpler model, plastic sponge, was also studied. The main effects are most clearly shown (figure 5) in measurements on a cylinder of plastic sponge 8 cm thick and 25 cm

in diameter. The sponge had a three-dimensional trabecular structure, each arm about 0.4 mm long, and a bulk density of 0.04 g cm^{-3}, similar to that of *Sphagnum* (figure 2). The sponge proved to be homogeneous, unlike the *Sphagnum* carpet. At a (figure 5) the cylinder was completely water-filled. By the time the water table had reached 30 cm below the surface (b) about 93 % of the water had drained out. When the water table returned to the surface (g–c), the water content was only

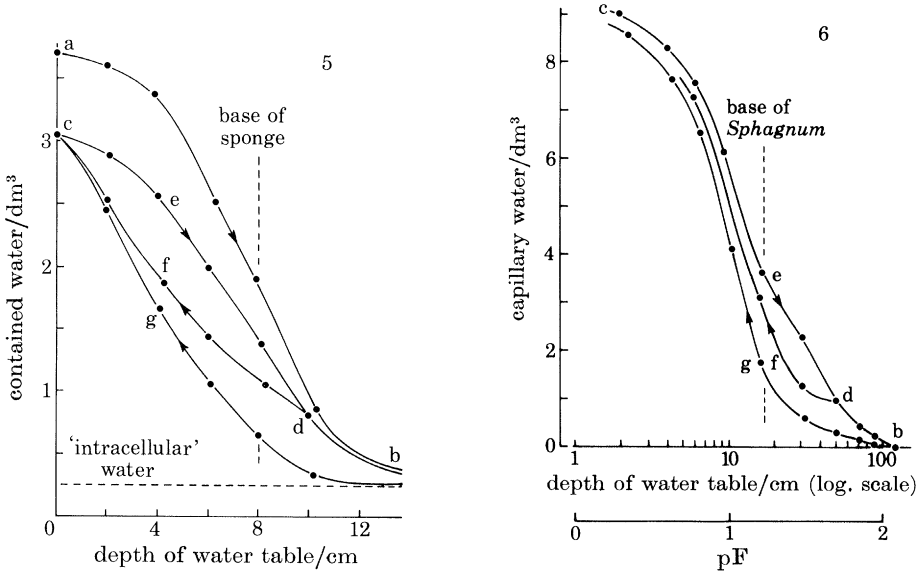

FIGURE 5. Total water content of an 8 cm deep, 25 cm diameter cylinder of plastic sponge. The cylinder was saturated with water by boiling under vacuum at room temperature (a). The water table was lowered by stages to 30 cm depth (b), then raised again (g–c). The c–e–b–g–c loop was repeated several times, giving nearly identical results. If the downward movement was stopped at 10 cm depth then the curve d–f–c was followed.

FIGURE 6. Capillary water of a 16 cm deep, 30 cm diameter core of *Sphagnum capillifolium*. The water table followed c–e–b–g–c. It was lowered again to d and then raised through f to c. The letters correspond to those in figure 5, but the depth scale is logarithmic.

82 % of the initial value. The other 18 % of the volume must have been filled by air. Subsequent cycles c–e–b–g–c gave consistently reproducible results, and are shown as the primary curve, similar to that found for a thin layer of ballotini (glass) beads by Poulovassilis (1962). Secondary curves, from subsidiary cycles such as d–f–c, are contained within the primary envelope and results for these were reproducible too. They were obtained by starting from somewhere other than the extremes of the primary curve. Presumably there would be tertiary and higher-order curves, but we did not seek them. They are probably the normal curves for natural carpets of *Sphagnum*, which are only rarely either completely flooded or entirely dried. It is worth noting that Poulovassilis's layer of beads was thin and the water in it could be considered as being at a single potential. The sponge cylinder, and the *Sphagnum* cores, were much thicker and contained water at a range of values of potential.

Results similar to those from the sponge cylinder were obtained with cores of

Sphagnum: figure 6 shows an example, the letters indicating points corresponding to those in figure 5. The vertical axis in figure 6 shows capillary water alone, and the horizontal axis is logarithmic; this allows comparison with conventional soil wetting and drying curves. The comparison is misleading above about 40 cm however, because the water potential derived from the water table depth is that

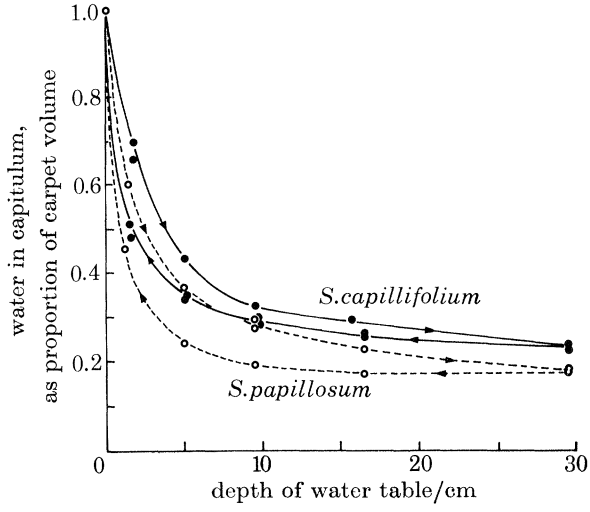

FIGURE 7. Total water content of the capitulum (defined as the section between 0.5 and 1.5 cm below the surface of a 30 cm diameter core) as a proportion of the whole carpet volume, for the hummock species *Sphagnum capillifolium* and the lawn species *S. papillosum* as the water table is raised and lowered by stages.

of the core *surface* only, and the core is 16 cm deep. The results were again reproducible along c–e–b–g–c and secondary curves can be shown as before, for example that from d.

Capitulum water content

The results presented thus far have been concerned with whole cores. The capitulum is the part of the core in which water potential is lowest; it is also where most of the cell division occurs. Ecological differences between species may well be determined to a great extent by the relative ability of each species to maintain water in its capitulum, and it is this property that we now examine. The behaviour of the lawn species *S. papillosum* and of the hummock species *S. capillifolium* is shown in figure 7. Both species show hysteresis, and the water content on either arm of the hysteresis loop is always higher for *S. capillifolium*. If the water table is more than 7 cm below the surface the whole of the *S. capillifolium* loop is above that of *S. papillosum*. The reservoir of water in the capitulum of *S. capillifolium* is larger than that in *S. papillosum*. The hysteresis in water content in each species is as large as the difference between species when on the same branch of the hysteresis loop.

Discussion

Physically equivalent models

The *Sphagnum* carpet contains a complex set of interlinked spaces. It is helpful to simplify it to an equivalent physical model that gives the same profiles of water content as, for example, those shown in figure 3. The simplest such model is a glass block drilled with a large number of parallel, vertical, circular capillary holes of different radii. The height, h, of a water column in one tube of radius r is given by

$$h = 2S \cos \theta/(rpg),$$

where S is the surface tension of water, θ is the contact angle, ρ the density of the liquid, and g the weight per unit mass. For water in contact with a completely wettable surface $\theta = 0$, and $h \approx 15/r$ (units: mm). For any given water table in figure 3 the depth axis can therefore be rescaled upwards as an inverse radius axis, and the proportion of water retained at that radius can be read from the graph.

A more realistic model is that of two flat plates. If the plates are parallel then the same equation holds except that r is now the distance between the plates (see footnote to table 2). Suppose that two plane plates are clipped together at one side but separated at the other side (for example by wire 1 mm in diameter), thus enclosing a wedge-shaped space. If the plates are held vertically and dipped into water then the water rises to the top at the clipped side, but ascends only a few millimetres at the open wider side. Within the space between the plates it forms a rectangular hyperbolic curve. If one of the plates was curved in the horizontal plane, but the plates were still parallel everywhere in the vertical plane, then the curve described by the water surface would not be so simple. By a suitable choice of shape of plate the curve could be made to reproduce one of those in figure 3. By removing the restriction that the plates be parallel in the vertical plane then a model could be made that could reproduce all the curves in figure 3. The cumulative volume in spaces of different radius in such a model is shown in figure 8. The data of figure 3 are replotted to give figure 8*a* in which the radius depends on the depth in the carpet. Figure 8*b* shows the same surface marked by lines of equal mean radius as well as equal depth. A greater proportion (up to 0.1) of the capillary water occurs in spaces of radius less than 30 μm at the base of the core than does so at the top, but the reverse is true of the range 30–60 μm. Apart from the capitulum, about 0.2 of the total volume of spaces at all depths have radii of 60 μm or less. These differences may reflect differences in the integrity of the hyaline cells at different depths. Spaces of radius 0.2 mm and less occupy about 0.35 of the volume at 14 cm depth but only 0.23 at 2 cm depth. There is a notably larger volume of spaces with radii in the 0.6–2 mm range at 3–5 cm depth than at other depths: at this depth they constitute 0.63 of the carpet volume. Spaces of this range of size (0.6–2 mm) probably occur between adjacent pendent branches in plants that are live, or scarcely decomposed, and are still fairly stiffly held. Such a supposition is supported by the fact that the bulk density of dry matter (figure 2*a*) at this depth is only 0.02 g cm^{-3}, indicating that the main plant structure is largely intact.

The distribution of spaces in cores of *S. capillifolium* of different degree of

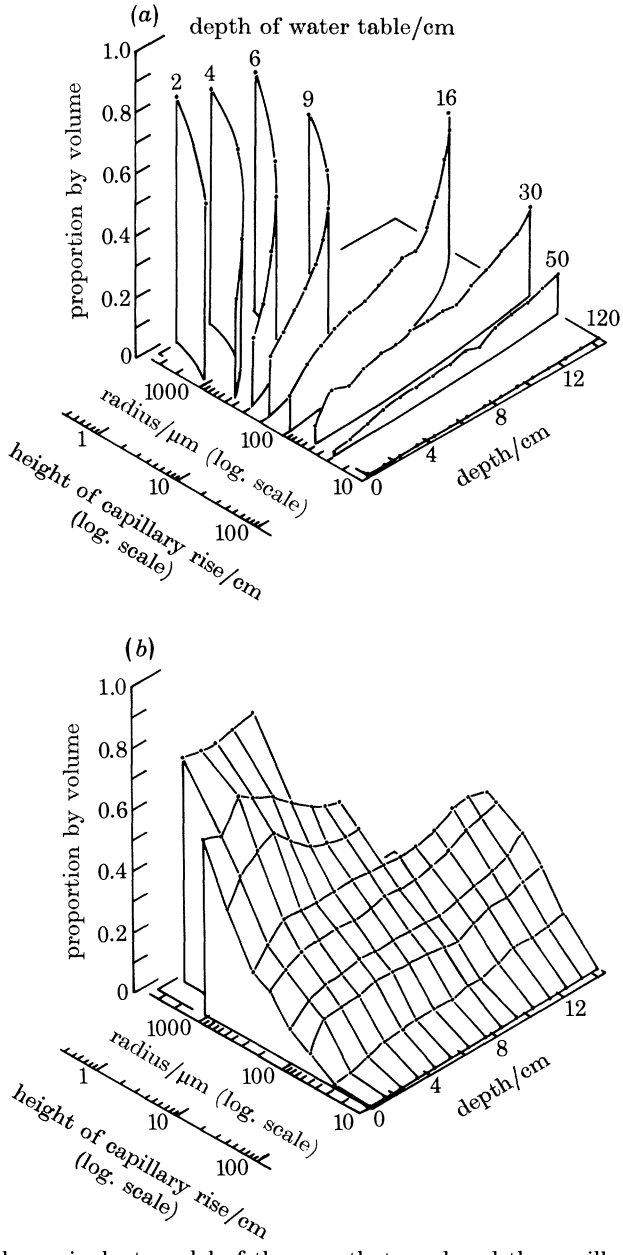

FIGURE 8. Physically equivalent model of the core that produced the capillary water results shown in figure 3. The depth axis shows the depth below the surface of the core. The radius axis shows the radius of circular capillaries, or the distance between parallel plates, that would have produced the same profiles as those in figure 3. The height that water could rise to in such capillaries is also shown. The vertical axis shows the cumulative volume within *all spaces up to* a particular radius. (*a*) Measured profiles, from figure 3. (*b*) Surface of (*a*) with lines of equal radius and equal depth.

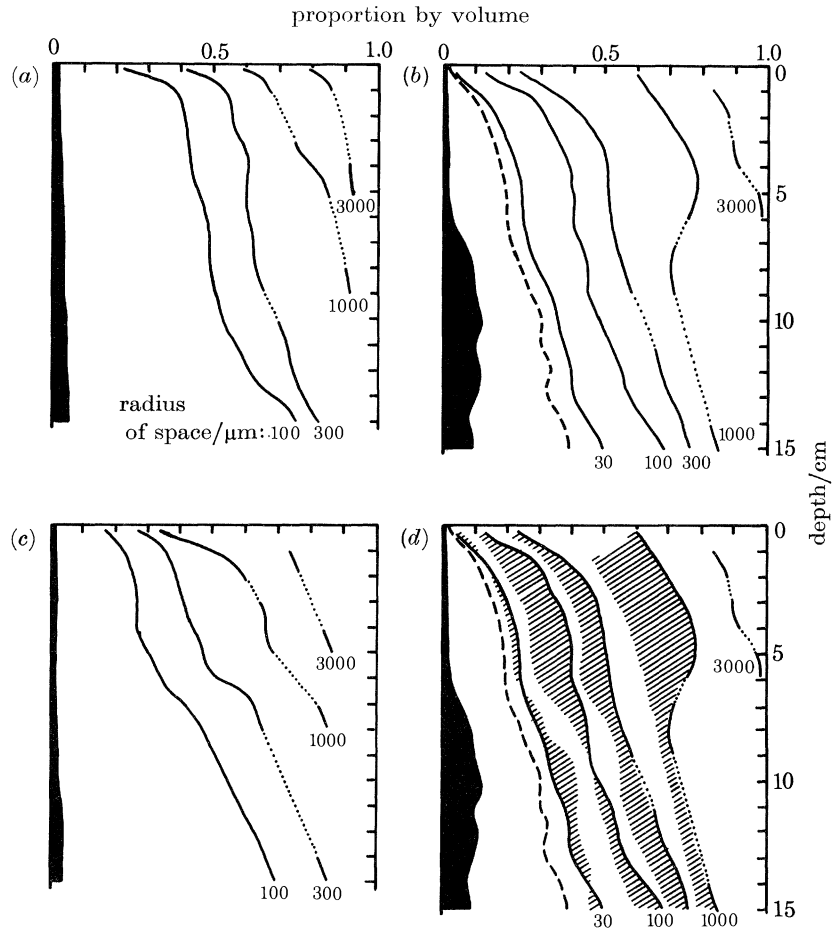

FIGURE 9. Profiles of the proportion of carpet volume occupied by spaces of specified radius or smaller. Solid area represents space occupied by plant matter. Broken lines in (*b*) and (*d*) show the limit of intracellular water (not determined for (*a*) and (*c*)). Dotted lines are interpolated in regions where no measurements were available. (*a–c*) From measurements with the water table lowered by stages: (*a*) *Sphagnum capillifolium*, unhumified; (*b*) *S. capillifolium*, lower part humified; (*c*) *S. papillosum*. (*d*) The same core as (*b*) but with the water table raised by stages too, thus showing hysteresis (hatching).

humification, and in *S. papillosum*, is summarized in figure 9. The spaces in *S. papillosum* are generally larger (or there is a smaller volume of spaces of up to a given size) at all depths. There are considerable differences too between different cores of *S. capillifolium*. Such differences may well affect the *rate* of water transport to the capitulum, and thus could be ecologically important, particularly if a fourth power law similar to Poiseulle's law is found to apply.

Hysteresis

The effects of hysteresis on the apparent distribution of spaces of different radius is shown in figure 9*d* for a single core of *S. capillifolium*. These results are typical. Hysteresis is largest in the upper layers where the plant structure is still intact,

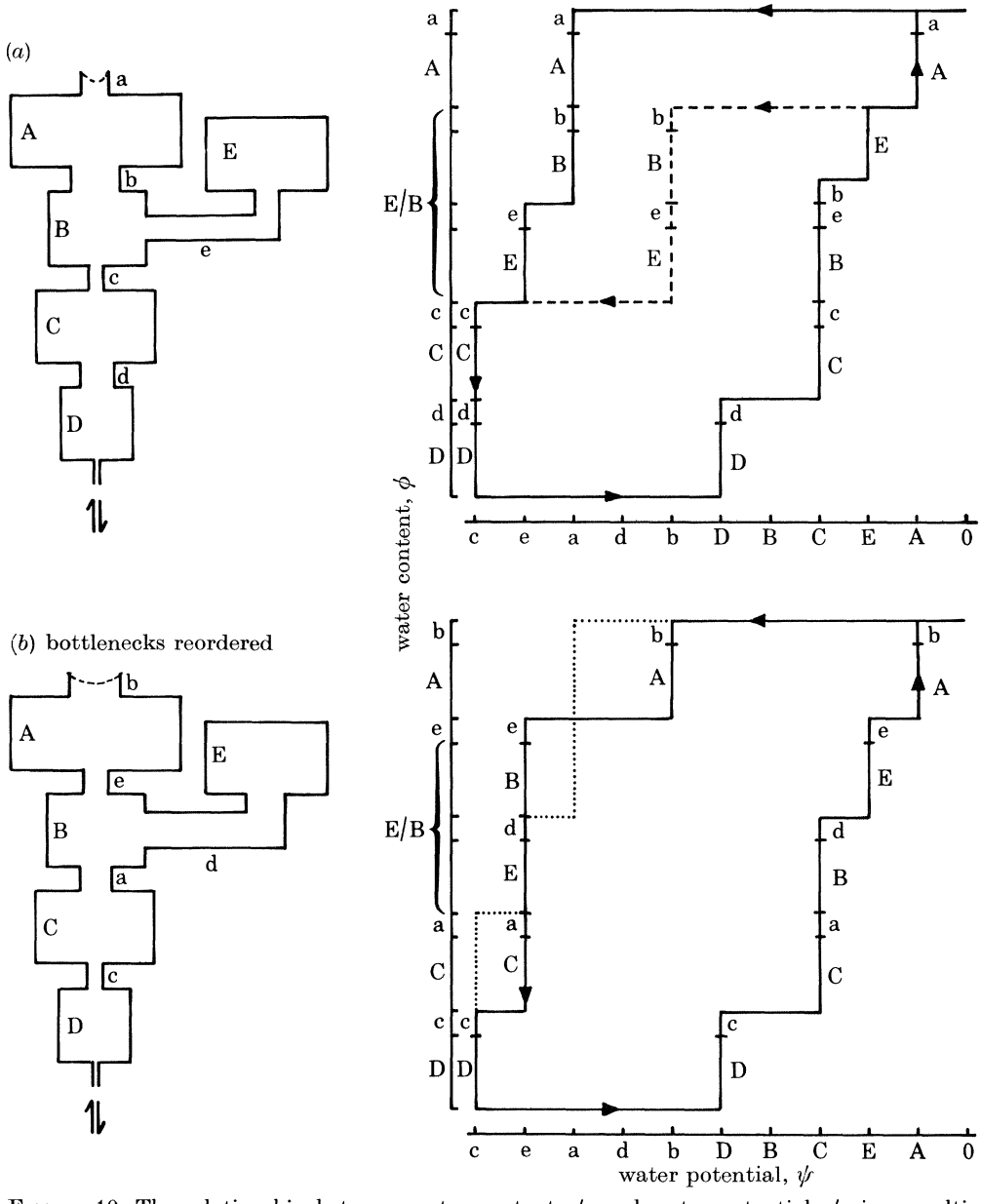

FIGURE 10. The relationship between water content, ϕ, and water potential, ψ, in a multi-chambered system of capillary 'caverns' linked by bottlenecks. The wall of cavern E is supposed to be completely permeable to gas but impermeable to liquid water. The system starts full of water and suction is applied at the bottom. The water potential axis shows the bottlenecks and caverns in rank order of diameter; the water content axis shows the caverns in order, as far as possible, but B and the side cavern E empty in the reverse order to that in which they fill. The upper example (*a*) shows a secondary line (broken). The lower example (*b*) contains the same elements as (*a*) but the bottlenecks are arranged in a different order. The filling line is unchanged, but the emptying line is changed from that of (*a*), which is repeated as a dotted line for comparison.

and may be 0.2 or more of the whole carpet volume. It is largest around spaces of 0.1 and 1 mm radius, and perhaps rather less between, but the difference is not great.

There is a simple explanation for hysteresis in a system of interlinked caverns that may be bridged by capillary films. The behaviour of a very simple model of vertical cyclindrical capillary caverns linked by cylindrical bottlenecks is shown in figure 10*a*. Suppose that the caverns start full of water and that suction of increasing strength is applied at the bottom. The meniscus at a will gradually become more concave until its radius of curvature is that of a itself. A slight increase in suction (decrease in water potential) will be sufficient to empty a and then the cavern A, followed at once by the bottleneck b (which is larger than a) and the cavern B. Further increase in suction will eventually empty e and E, and so on until D empties. The potential at which caverns will *empty* is governed by the radius of the bottleneck. But the potential at which they will *fill* is governed by the radius of the caverns. If the water potential is now increased, no caverns will fill until the potential rises to that of a meniscus able to span D, at which point D and d fill, and so on. The presence of side caverns may complicate the simple order of emptying and filling: B will empty before E but will also fill before it. Secondary and higher-order curves will also occur.

A similar system which contains the same caverns and bottlenecks as before, but with the position of bottlenecks changed, is shown in figure 10*b*. Such changes affect the emptying sequence, but not the filling sequence.

This model is, of course, very much simpler than the real system of spaces around *Sphagnum* plants, but it does draw attention to three important common features. The first is the fact that the emptying (or drying) curve is controlled by the constrictions and the filling (or wetting) curve by the aneurisms. Secondly the sequence of emptying and filling is not necessarily constant if there are side caverns. Thirdly, because the rate of flow through the system, when full, is determined to a large extent by the number, radius and length of bottlenecks, then in a straight series of caverns the lowest part of the emptying (drying) curve is of greatest significance for water transport, as it is this that provides information about the smallest bottlenecks.

In normal conditions about 0.1 of the water around and within the capitulum of a *Sphagnum* plant is contained in hyaline cells, which can be regarded as side caverns. Much more water is probably present in a continuous highly convoluted and branched sheet of very variable thickness. There is some evidence that significant amounts of water can move laterally through the canopy, particularly if the vertical path around the stem is interrupted (Clymo & Hayward 1982), but it seems likely that the crucial feature determining the vertical supply of water to the capitulum is the abundance of films of water of about 0.01–0.1 mm radius at 2–4 cm below the surface of the carpet.

Ecological significance

At present we know that, for a given water table and in conditions with no flow of water, *S. capillifolium* holds more water in its capitulum than does *S. papillosum*. We also know that at 2–4 cm below the surface *S. capillifolium* has a larger

proportion of its space in the 0.03–0.1 mm range than does *S. papillosum*. Of more importance is that if the capitulum, where growth occurs, has the same water content in *S. capillifolium* and *S. papillosum* at equilibrium then the water table will be considerably deeper below *S. capillifolium* (the hummock species) than it is below *S. papillosum*. The water content of capitula of plants in the field after several weeks without rain is often about 0.1 $cm^3\ g^{-1}$, equivalent to about 0.25 of the canopy by volume (Clymo 1973). This is just the point at which the net rate of photosynthesis begins to decline (Clymo & Hayward 1982) and corresponds to a water table that has fallen at equilibrium to a depth of about 30 cm below *S. capillifolium* or 15 cm below *S. papillosum*. These values for the depth of the water table are not inconsistent with those observed in the field. But it is clear from figure 7 that hysteresis is important. If, in the field, the rate of evaporation exceeds the rate at which water can move up the plants then the capitula will dry out. This is the equivalent of moving to the other branch of the primary hysteresis curve. When the rate of evaporation declines (at night for example) some of the spaces will not refill with water even if the depth of the water table has not changed, and the capitulum may then remain dry until wetted again by rain. Thus the effect of an initially small difference in water content of two species may become catastrophic, in both the technical and the general senses, if it allows the capitulum of one species to cross to the other branch of the hysteresis loop. There is some indication that this does happen in the field: towards the end of the occasional drought (perhaps once in 5–20 years) it is common to find places where *S. papillosum* has dried to the point where the plants appear white and papery, a sign that the hyaline cells are empty of water, but immediately adjacent patches of *S. capillifolium*, with the same depth to the water table, are still wet.

The kinetics of water content – of how the profile of water content changes with rate of evaporation – can be investigated with the same apparatus used in this work.

Appendix

We consider: first, the design of the apparatus; secondly, the construction of a profile of water content from a series of counts of radioactivity; and thirdly, the errors in such a profile.

The design of the apparatus

The core of *Sphagnum* was contained in a Perspex cylinder and separated from a water-filled space below by a membrane filter. This allowed a tension equivalent to that of a water table as much as 150 cm below the surface of the *Sphagnum* to be applied. The core was rotated, raised and lowered in a beam of soft gamma radiation, the attenuation of which gave a measure of water content.

We first chose the core diameter to be as large as practicable so that edge effects and heterogeneity would be minimized. This diameter was 30.5 cm (12 inches, determined by the availability of Perspex tube) and gave an areal density of *Sphagnum* (or peat) plus water across the diameter of 3–30 g cm^{-2}, depending on water content. This in turn determined the choice of radioactive isotope: we wanted absorbance to be in the range 1–6 and so a soft gamma emitter of long

half life was needed. The isotope ^{241}Am (americium), 0.06 MeV, half life 458 years, in a sealed source proved satisfactory. Precision depends on total count: the more active the source the more quickly a given precision is reached. The minimum activity for an acceptable scanning speed (and the maximum that we could afford) was 14 mCi.

The centre of the apparatus (figure 11) was a 23 cm tall Perspex cylinder, of internal diameter 30.5 cm, with a Tufnol base. This cylindrical space was divided into a lower, 3 cm deep, water-filled compartment and an upper compartment in which the *Sphagnum* core was placed. The cores were collected by means of a cylindrical stainless steel cutter, and the base of the core was trimmed in the laboratory, usually to a depth of about 15 cm. The membrane filter rested on a fibreglass filter over a 0.2 mm mesh stainless steel gauze which in turn rested on a multiperforate Tufnol plate.

It was essential to have excellent contact between the capillary films in the plants and those in the filter. This was achieved by injecting a 2–3 mm thick layer of Kieselguhr among the cut bases of the moss stems immediately over the membrane filter.

The pores in the membrane filter were nominally of diameter 40 nm, which is theoretically small enough to support a water table at a depth of about 300 m. We had no difficulty with gas flowing through larger pores or with decay of the filters, but gas did diffuse through the membrane filter and then came out of solution, at about 1 ml per day, at the reduced pressure below the membrane. The gas was sucked out every month or so through a system of fine tubes in the lower compartment.

The sealed radioactive source, 14 mCi of ^{241}Am, was mounted in a brass collimating tube placed to one side of the Perspex cylinder so that the beam, 10 mm wide and 2 mm deep, passed radially through the core to a NaI crystal detector covered by a collimating mask (figure 11). The detector was mounted on a photomultiplier tube that sent pulses to an amplifier, analyser and scaler (modified to be controlled externally), and thence through an interface to a teletype that produced a record on punched paper tape.

The apparatus was intended to produce profiles; so it was necessary for it to scan the core vertically. We chose to move the core (rather than the source and detector) because the construction problems seemed simpler: we were not trying to reinvent computerized axial tomography. To achieve this end, the Perspex cylinder containing the core was mounted on a hollow polyvinylchloride cylinder that floated in water inside a larger plastic cylinder. As more water was added to the annular space between the cylinders the floating inner cylinder rose and the core moved up and through the fixed beam of gamma radiation.

A *Sphagnum* core is not homogeneous, and to sample as much of it as possible the floating cylinder and core were rotated by a synchronous motor. The central 10 mm part of the core was rotating in the beam the whole time, but the main part of the core was sampled at a rate approximately inversely proportional to the distance from the centre; so, for example, the time spent sampling the *whole* annulus from 14 to 15 cm from the centre was about the same as that spent on the whole annulus from 7 to 8 cm from the centre. One of two diametrically

opposite projections from the floating cylinder interrupted an infrared beam every half revolution and initiated a new count. The speed of rotation was constant from day to day to about $\pm 3\%$ but no better; so the counter was set to terminate the count after a more precisely controllable time which was about four-fifths of that needed for a half revolution. Each timed count was thus followed by a shorter

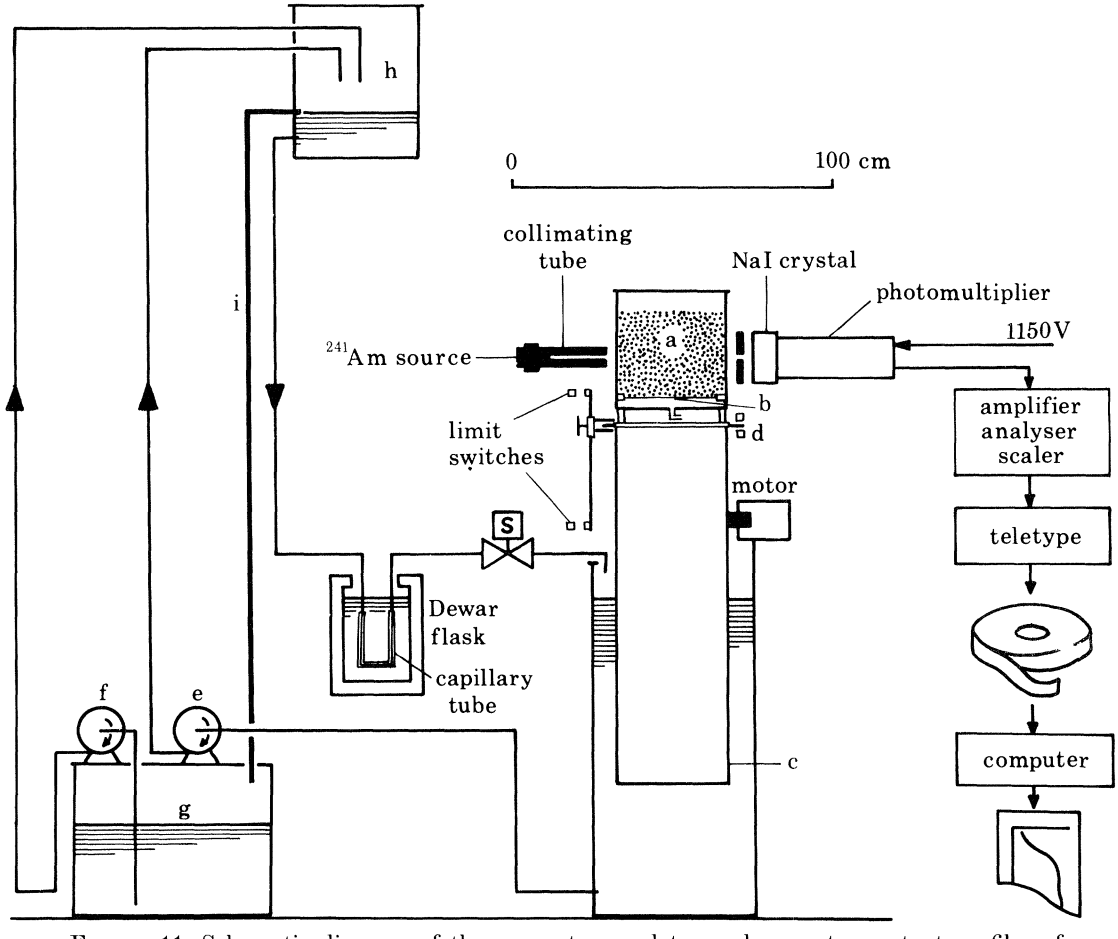

FIGURE 11. Schematic diagram of the apparatus used to produce water-content profiles of *Sphagnum* and peat. The hydraulic system causing vertical movement is at the left. The motor produces radial scanning. The parts of the apparatus that control the water table depth below the surface of the *Sphagnum* are not shown. Symbols: a, *Sphagnum*/peat; b, membrane filter; c, floating cylinder; d, rotation detector; e, emptying pump; f, filling pump; g, reservoir; h, header tank; i, overflow; s, solenoid valve. The scale is approximate and not all parts are to scale.

untimed count, and any marked change in the quotient of these two counts indicated inaccuracy in the short-term control of rotation.

If the vertical scanning rate is to be constant then the water must be added to the outer cylinder at a constant rate. We managed this by allowing water to flow in from a constant height (figure 11) through a glass capillary kept at constant

('room') temperature in a water-filled Dewar flask. No significant change in flow rate during a scan was ever detected. Small differences did occur between scans, but the actual rate of scan was measured by including a strip of lead at the top of the Perspex cylinder in the untimed sector. This, and the basal brass filter holder produced a near-zero count and enabled the rate of scan to be calculated. A typical vertical scan of 10 cm needed 100 half revolutions and took 50 min.

The requisite constant head of water was maintained by pumping water from

TABLE 3. MASS ABSORPTION COEFFICIENTS, μ, FOR 0.06 MeV GAMMA PHOTONS FOR A VARIETY OF MATERIALS

(Value shown is the mean of n measurements.)

material	n	μ / $cm^2\ g^{-1}$	material	n	μ / $cm^2\ g^{-1}$
copper	10	1.619	wood of *Araucaria araucana*	4	0.196
polyvinylchloride sheet	4	0.494	Perspex	3	0.196
aluminium	5	0.309	(un)punched computer card	30	0.189
plate glass	1	0.271	plastic sponge	3	0.189
dry *Sphagnum*	3	0.249			
Tufnol	3	0.226			
water	10	0.204			

a reservoir into a header tank, the overflow from which returned to the reservoir. At the end of a scan, detected by an infrared limit switch (figure 11), a solenoid valve closed the water supply to the outer cylinder and a second pump returned water quickly from the outer cylinder to the reservoir (via the header tank to avoid siphoning) until a lower limit switch was closed. Counting was suppressed during this operation but zeros were still recorded. At the next radial interrupt the solenoid valve opened and counting resumed.

The whole sequence of operations was automatic, and a number of safety features were included: high and low water level detectors, overrun detectors etc. A full account is given by Hayward (1980).

Discrimination within profiles could be adjusted by changing the counting time (linked to the rate of rotation) and the rate at which the cylinder rose.

Constructing the profile

For the collimated narrow beam of gamma photons in this apparatus the analogue of Beer's law should apply:

$$\ln (I_0/I) = \mu x = A,$$

where I [physical dimensions T^{-1}] is the transmitted photon flux, I_0 [T^{-1}] is the incident flux, x [$M L^{-2}$] is the areal density of absorbing matter, μ [L^2M^{-1}] is the mass absorption coefficient of the absorbing matter, and A is the absorbance. This relation was shown to be closely followed with characteristic values of μ, by the materials listed in table 3. The coefficient of variation was no more than 0.01.

The absorbance was calculated from

$$A = \ln\{(I_0 - I_b)/(I - I_b)\},$$

where I_b [T^{-1}] is the background flux.

We turn now to the calculation of the mass of water (figure 12). Let r [L] be

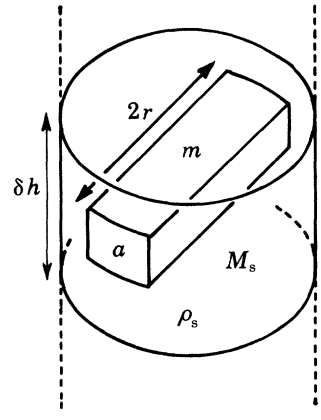

FIGURE 12. Meaning of symbols used in deriving water content profile from gamma photon flux.

the radius of the core, δh [L] the thickness of the slice exposed to radiation, ρ_s [ML^{-3}] the bulk density of water in the slice, M_s [M] the mass of water in the slice, M_c [M] the total mass of water in the core, m [M] the mass of water through which the beam passes, and a [L^2] the cross-section area of the beam. Then

$$\rho_s = M_s/\pi r^2\,\delta h \approx m/2ra.$$

If the part of the slice probed by the beam is representative of the whole, and as $x = m/a$, it follows that in the limit, as $\delta h \to 0$,

$$M_c = \frac{\pi r}{2\mu}\int_{h_1}^{h_2}(A - A')\,dh,$$

where A' is the absorbance of dry plant matter. The value of A' was always less than 0.1 A, and often less than 0.01 A. The value of μ for dry *Sphagnum* is only about 1.2 times that of water; so in practice there is a negligible error in M_c if an average value of A' is assumed for the whole core.

The integration may be approximated in two ways (figure 13). The simplest is the trapezium method (figure 13*a*). In this

$$\int_{h_1}^{h_2} A\,dh \approx \left\{\sum_{i=2}^{n-1} A_i + \tfrac{1}{2}(A_1 + A_n)\right\}\delta h,$$

where $\delta h = (h_2 - h_1)/n$. This method is applicable when 'spot' measurements are made at equidistant heights. The automatic scan however produces an average value for A over a slice of thickness δh. For this case (figure 13*b*, complete block method),

$$\int_{h_1}^{h_2} A\,dh \approx \sum_{i=1}^{n} A_i\,\delta h = \left\{\sum_{i=2}^{n-1} A_i + A_1 + A_n\right\}\delta h.$$

In practice, however, the apparatus made an accurately timed count for a large proportion, p, of each slice but then an untimed count for the remaining $1-p$ of the slice (figure 13*c*, incomplete block method). For this case it can be shown that

$$\int_{h_1}^{h_2} A\,\mathrm{d}h \approx \left\{\sum_{i=2}^{n-1} A_i + \tfrac{1}{2}A_1(1+p) + \tfrac{1}{2}A_{n-1}(p-1) + A_n(2-p)\right\}\delta h.$$

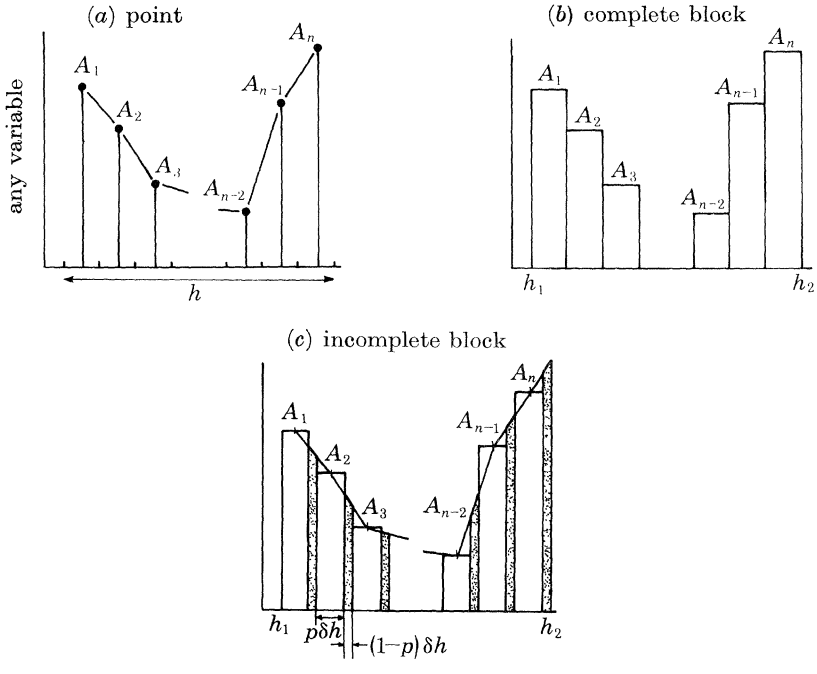

FIGURE 13. Integrating absorbance by three methods. The absorbance is unknown in stippled areas. See text for details.

When $p = 1$ this expression becomes the same as that for the complete block. The methods differ only in the way in which they deal with the leading and trailing terms, and as long as n is large, or $\mathrm{d}A/\mathrm{d}h$ is small at the start and end, they give very similar results. As the complete block method (figure 13*b*) gave a much simpler equation it was used in the calculation of precision.

Errors in the profile

It is convenient to consider three sorts of error: mistakes, systematic error (associated with the ideas of bias, accuracy, and distance from the true value), and random error (associated with the ideas of precision and reproducibility).

Mistakes did occur (the counting equipment and teletype were old and the interface was built as a student project) at a rate of about 4 % of all counts. Conspicuous mistakes such as zeros, or counts that were about ten times too large or too small, were the commonest, but there were some subtle mistakes. These could often be detected as an erratic change in the quotient of the timed and untimed

counts. All these sorts of mistake were sifted out by the computer program. Some smaller mistakes probably remain and may be confounded with systematic and random errors.

Systematic errors are potentially the most dangerous of the three types because even large ones may not be self-evident. They were sought by making measurements by two methods based on totally different principles. For example, the speed at which the profile was scanned was controlled by the head of water in the top tank and the resistance in the capillary tube in the Dewar flask. The rate of scan was measured manually, and also recorded automatically by a lead strip and a brass ring which gave a near zero count on the untimed sector of the core container. Any marked change in rate was investigated. Any consistent change in the quotient of timed and untimed counts, apart from those caused by the metal strips, was an indication of systematic error.

The most important checks were made by comparing the profile of water content produced by the computer program from the automatic apparatus with that obtained by subsequent hand-clipping and weighing a core. The results of two such checks, one on dry plants, the other on wet ones, are shown in figure 2. The total amount of dry matter or of water estimated by the two methods differed by 6 % or less, and the general shapes of the profiles agreed, though that from the automatic apparatus was of course much more detailed.

The rapid change in the top 5 mm probably results partly from the imperfectly level surface of the 30 cm diameter core. But a carefully levelled cylinder of plastic sponge showed a similar rapid change in the top 1 cm; so part of the explanation must be that this represents the change from penumbral to umbral conditions. It gives some indication of the resolution of the method.

Random errors could have been measured by making large numbers of replicate profiles, but this would have taken an inordinate time and been unacceptably destructive of bog vegetation. An analysis of the measurements made allows the precision of the value of water content in each slice and in the whole core to be estimated however. In those cases where replicate profiles were recorded on the same core, the spread of results was nearly always within the limits calculated.

In general, if $z = f(u, v, w \ldots)$ and s represents error and is not more than about 5 % of the value of the variable, then

$$s_z^2 = \left(\frac{\partial z}{\partial u} s_u\right)^2 + \left(\frac{\partial z}{\partial v} s_v\right)^2 + \left(\frac{\partial z}{\partial w} s_w\right)^2 + \ldots .$$

In our particular case let N represent count and t time, and subscripts 0 and b incident and background as before, then $I = N/t$, $I_0 = N/t_0$, $I_b = N_b/t_b$ and

$$A = \ln \frac{(N_0/t_0 - N_b/t_b)}{(N/t - N_b/t_b)}.$$

The standard error in a count, s_N, is $\sqrt{N}$ and that in the times is negligible. Assembling the partial differentials and errors then gives

$$s_A^2 = \frac{N}{(N - tI_b)^2} + \frac{N_0}{(N_0 - t_0 I_b)^2} + N_b \left\{\frac{I_0 - I}{t_b (I - I_b)(I_0 - I_b)}\right\}^2,$$

where the three terms are respectively the contributions from the count for the particular slice, the incident count (with no peat) and the background count. These values were used to decide for how long the different components should be counted.

The error in the value for the total mass of water, $\overline{M}$, between h_1 and h_2 in the core can be calculated in a similar way. For convenience let Δh represent $h_2 - h_1$ and ΣA represent $\Sigma_{i=1}^{n} (A_i - A')$ i.e. the complete block method (figure 13*b*). Then it can be shown that

$$s^2_{\overline{M}} = \left(\frac{\pi r \Delta h}{2n\mu}\right)^2 \left\{\left(\frac{\Sigma A}{\Delta h}\right)^2 (s^2_{i=1} + s^2_{i=n}) + \left(\frac{\Sigma A}{r} s_r\right)^2 + \left(\frac{\Sigma A}{\mu} s_\mu\right)^2 + (n s_{A'})^2 + \left(\sum_{i=1}^{n} s^2_{A_i}\right)\right\}.$$

This expression was also used to reveal the importance of the contributions of error from various sources. It was used to calculate the error in the mass of water for parts, or the whole, of the core by appropriate choice of h_1 and h_2.

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