Chapter 8

The Ecology of *Sphagnum*

R.S. CLYMO AND P.M. HAYWARD

> *I held it truth with him who sings . . .,*
> *That men may rise on stepping stones*
> *Of their dead selves to higher things.*
>
> *Tennyson* In Memoriam A.H.H.

8.1 INTRODUCTION

It may be true of men; it is certainly true of *Sphagnum*. The plants grow at the apex, as do most other mosses. The apex produces initials which develop into branches of determinate growth, though in a few cases (*S. cuspidatum* var. *plumosum* for example), the branches may themselves branch. Whilst the branches are increasing in length the internodes of the main stem do not elongate. This results in the branches and attendant leaves forming a compact hemispherical head – the coma or capitulum. Later, after branch growth has finished, the internodes do elongate; it then becomes obvious that the branches are borne in groups (fascicles) on the central stem. Each branch bears 30 to 150 spirally arranged imbricate leaves. These leaves are one cell thick, with the unique and well known differentiation into porose hyaline cells with thickened hoops, and enclosed or chlorophyllose cells. The branches may be spreading or pendent and clasping the stem (Fig. 8.1). The individual leaves live for a year or two, but by that time the growth of branches above has put them into dense shade and they die. The only parts left alive at this distance below the apex seem to be the axillary buds. These usually remain inactive, and eventually die, but if the apex is destroyed, either artificially (for example, by cutting if off) or accidentally (for example, by drought) then one or more lateral buds may begin to grow again from as far as 10 cm below the apex. These buds can survive for at least 18 months in a refrigerator (dark, about 2°C). The shoots formed from such buds are very thin at first but reach full width

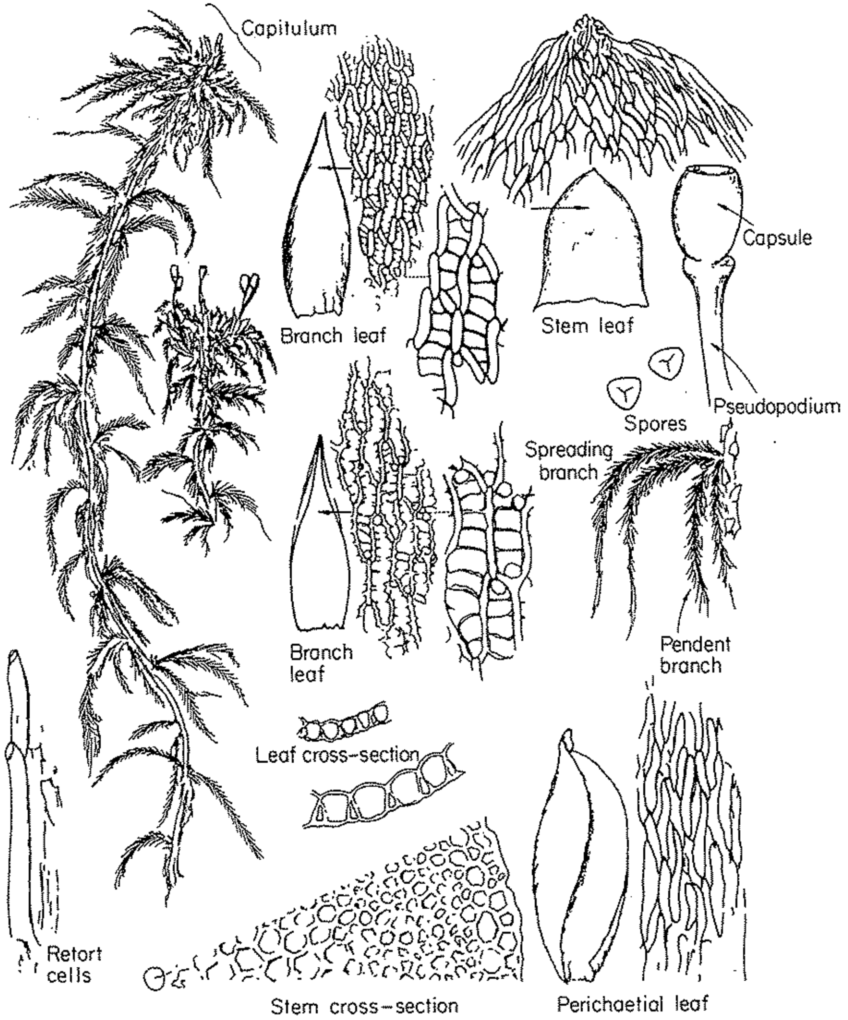

Fig. 8.1 The structure of a *Sphagnum* plant, *S. recurvum (S. fallax)*. Imbricate leaves on branches which are either spreading or pendent are shown. The hyaline cells of the leaf have thickened hoops, and the walls are perforated by pores. Branches are invested with a sheath containing retort cells, which have a single large apical pore (lower left). From Nyholm (1969).

within a year or two. This suppression of lateral buds is similar to that seen in vascular plants in which it is controlled by hormones from the apex itself, and suggests that there may be more vertical transport in *Sphagnum* plants than is commonly supposed. The apex of a *Sphagnum* plant may sometimes be replaced by two smaller ones. Whether this results from direct division of the original apex or from development of an axillary bud prematurely released from subjugation is not clear.

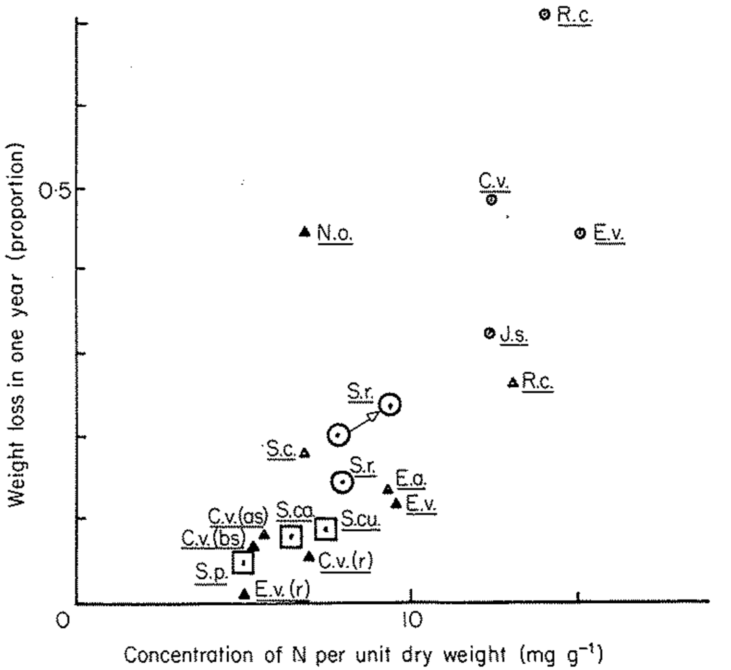

Fig. 8.2 Decay rate just below the surface of blanket bog at Moor House of *Sphagnum* and of other plant materials in relation to concentration of nitrogen. *Sphagnum: S.ca, S. capillifolium; S.cu, S. cuspidatum; S.p., S. papillosum; S.r., S. recurvum*. Other plants: *C.v.*, *Calluna vulgaris* shoots; *C.v.* (as), *C. vulgaris* above-ground stems; *C.v.* (b.s.), *C. vulgaris* below-ground stems, *C.v.* (r), *C. vulgaris* roots; *E.a.*, *Eriophorum angustifolium* leaves; *E.v.*(r), *E. vaginatum* roots; *J.s.*, *Juncus squarrosus; N.o.*, *Narthecium ossifragum* leaves; *R.c.*, *Rubus chamaemorus* leaves; *S.c.*, *Scirpus cespitosus* shoots. Symbols: ⊡, Clymo (1965); ◬, Heal *et al.* (1978); ⊙, Coulson and Butterfield (1978). Larger size symbols are *Sphagnum*. The arrow shows the effect of experimental enrichment with nitrogen.

Much the same growth pattern is shown by many other species of moss. What makes *Sphagnum* peculiar is that the rate of decay of the dead material of the commonest species is unusually slow so that the dead plants accumulate as peat (Fig. 8.2). There are several reasons for this. One is the unusually low concentration of nitrogen in the plants – usually less that 1% of dry mass. Not only is there a positive correlation between decay rate and nitrogen concentration, but increasing the nitrogen concentration of the plants by fertilizing the live plants increases the rate of decay when the plants die (Coulson and Butterfield, 1978). This is a specific effect of nitrogen enrichment, and does not occur when the plants are enriched in phosphorus. A second reason may be the acid conditions which are produced by the *Sphagnum* itself (Skene, 1915; Clymo, 1963). The third reason for slow decay is associated with the generally wet environment which most species of *Sphagnum* require. Not far below the apices – perhaps 2 to 20 cm down – the peat is water-saturated. There is a continuum of water potential but it is convenient to recognize three points in the continuum. First, water may be present as free liquid: a hole dug in the surface may fill to give a free water surface. Secondly, the water may be held in capillary spaces, roughly 1 μm to 1 mm across. Thirdly, the water may be present in smaller spaces, as it is in a jelly. A hole in the jelly will not spontaneously fill with water but the jelly is water-saturated nevertheless.

Micro-organisms living on the plants just at and below the level of water-saturation use the molecular oxygen in solution. They are mainly aerobic or facultatively anaerobic fungi and bacteria. Oxygen does diffuse down from the air, but the rate is very slow, being only 1/10000th of the rate of diffusion in air. There is probably very little convective or other mass (non-diffusive) movement in the water. Anaerobic conditions prevail, therefore, and the rate of decay in such conditions is much slower than it is in aerobic conditions, though why this is so is not clear. The water and the associated anaerobic, low decay-rate conditions, are not static. They fluctuate over the course of minutes to days as rainfall, run-off, evaporation and temperature determine. But in the long term the level of water-saturation rises steadily too, because at some point below the living surface the stems of the dead *Sphagnum* have decayed to such an extent that they lose their mechanical strength and the plant its integrity, so that the whole open plant structure collapses. The bulk density increases from about 0.01 to about 0.1 g cm^{-3}. The leaves retain their structure but pack down more tightly; the lateral hydraulic conductance falls, and the water table rises when it rains. Thus, as the plants grow at the apex so the water-saturated level follows them upwards. This concept of an aerobic layer above and an anaerobic layer below is too simple though (Fig. 8.3). The upper layer (acrotelm of Ingram, 1978) contains some anaerobic spots. These become more frequent, and probably larger and more anaerobic, nearer to the water-saturated layer (catotelm). Even here the roots of vascular plants, such as *Eriophorum* spp., create local aerobic channels (Armstrong, 1964). Nevertheless, the general effect is that the *Sphagnum* branch dies and decays predominantly aerobically until its structure collapses and thereby raises the water-saturated layer to cover it. From that point onward decay is predominantly anaerobic. It is clear that the rate at which dead material enters the relative safety of the anaerobic zone depends partly on the rate at which new plant material is produced and partly on the proportion of that material which is lost whilst running the gauntlet of the dangerous aerobic zone. Calculations show how the initial advantage of a relatively slow rate of aerobic decomposition of *Sphagnum* can lead to its considerable over-representation in peat (Clymo, 1982). There are differences between species of *Sphagnum* too: the proportional loss, in one year, of newly dead *S. cuspidatum*, *S. papillosum*, and *S. capillifolium* placed in the top layer of a valley bog in Southern England was 0.16, 0.06 and 0.11 respectively (Clymo, 1965).

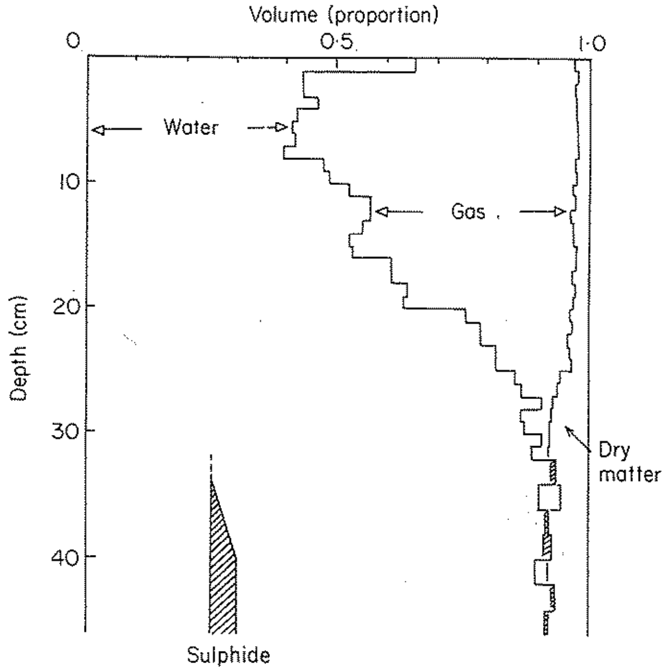

Fig. 8.3 The proportion of dry matter, water and gas at different depths in a carpet of *S. fuscum* at Nordmjele, Andøya, Norway. A 20-cm diameter core was collected in a tube which was then sealed to prevent loss of water. The core was stood vertical for 24 h and then ejected vertically and sliced in 1 cm steps. Clymo (unpublished).

The extensive carpet-like growth and the slow rate of decay are two of the reasons why *Sphagnum* is such an important bryophyte genus: there is an enormous amount of it, and more dead than alive. Peatlands cover about 150×10^6 ha, which is between 1 and 2% of the earth's land surface (Tibbetts, 1968). Many of them – perhaps most – have *Sphagnum* as a major component. The depth of peat can exceed 15 m, but 1–5 m is more usual. If one assumes a mean depth of 2 m and bulk density of 0.1 g cm^{-3}, then the mass of dead plant material is about 300×10^9 t. This may be compared with an estimate for terrestrial productivity of 72×10^9 t year^{-1} (Woodwell *et al.*, 1978). If only half this peat is *Sphagnum* then there is more carbon locked up in *Sphagnum*, alive and dead, than is fixed by all terrestrial vegetation in one year. It is interesting to speculate that there may be more carbon in *Sphagnum* than in any other genus of plants, vascular or non-vascular. The comparison is rather artificial because the *Sphagnum* genus is so taxonomically isolated that the comparison ought perhaps to be at the level of the family, or higher. But it seems clear that no other bryophyte can approach the general success of *Sphagnum*, though some (*Polytrichum commune*, *Racomitrium lanuginosum*) may have higher productivity over small areas.

8.2 GENERAL ECOLOGY

The distribution and rate of growth of *Sphagnum* plants and the performance of one species relative to another are determined primarily by the supply of water and by the concentration of solutes, particularly of Ca^{2+} and H^+. The general requirements are an assured water supply with a relatively low concentration of Ca^{2+}.

In many places these conditions are provided by relatively high-rainfall, equitably distributed throughout the year, with no long periods when evaporation exceeds precipitation. Labrador and Ireland (both oceanic coastal islands) are examples. In such climates *Sphagnum*-dominated vegetation may blanket the whole countryside on slopes up to 20°. In regions with summer drought, *Sphagnum* may be more localized in basins where the accumulated peat is sufficient to insulate the plants from the ground-water and to provide a reservoir (which shrinks during summer) allowing *Sphagnum* to survive. In a few places, a carpet of *Sphagnum* or sedges (or both) grows out over a deep pool. Here again the surface may in time become insulated from the water below and float up and down on it (Green and Pearson, 1968). The same continuity of water supply may be found in some valleys but these are suitable for extensive *Sphagnum* growth only if the water has flowed through solute-poor rocks with soils such as the Bagshot sand of southern England or the erosion-resistant rocks of the Canadian Shield.

These four cases are recognized types of mire: blanket bog, raised-bog, schwingmoor and valley-bog respectively. There are many other types of mire, and seemingly no end to the schemes classifying them (Moore and Bellamy, 1974; Kivinen *et al.*, 1979) but they need not be considered further here.

The taxonomy of the genus *Sphagnum* is still in flux. The main sections are generally agreed and in most cases the taxa in these sections share a distinctive anatomy and ecology. Thus, species of the sections *Cuspidata* and *Subsecunda* are often found with the capitulum at or slightly above or below the free water surface. *Sphagnum cuspidatum* and *S. subsecundum* themselves may be found in pools and, when growing in slowly flowing water in ditches, may grow in length by 50 cm or more during the summer months of one year (Overbeck and Happach, 1956). Species of the section *Sphagnum*, including *S. papillosum* and *S. magellanicum*, are robust and often form carpets or low hummocks, whilst several species of the section

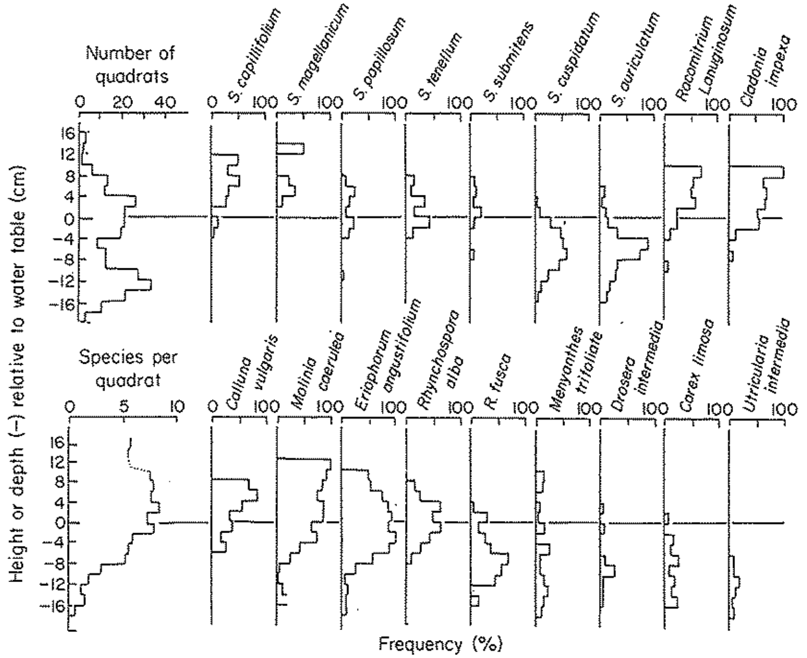

Fig. 8.4 Frequency of species (in 25×25 cm quadrats) in relation to the water-table on the patterned mire at Kentra, north-west Scotland. The observations were made during a short time in September 1979 during which the water-table may have been unusually high. The number of quadrats, and the total number of species per quadrat, are shown too. Unpublished results of the following members of the Mires Research Group: A.D.Q. Agnew, S. Agnew, O. Bragg, A. Coupar, H.A.P. Ingram, M.C.F. Proctor. Similar observations were made by Ratcliffe and Walker (1958).

Acutifolia, including *S. capillifolium* and *S. fuscum*, usually grow on hummocks some way above the water table. Some of these tendencies are shown in Fig. 8.4.

Within the sections, however, the taxonomy is in dispute. *S. acutifolium*, *S. rubellum*, *S. capillaceum* and *S. capillifolium* may be nearly synonymous: *S. recurvum* has been variously renamed and subdivided in the *S. flexuosum* aggregate. More important is the plasticity of form: *S. recurvum* grown submerged may be difficult to distinguish from *S. cuspidatum* grown in unusually dry conditions, though they are clearly distinct when grown together in the same conditions. Similarly, the 'species' of *S. subsecundum* of some authors may be interconverted by changing the growing conditions. Because of these and other problems the nomenclature of Hill (1978) is used in this account.

There are perhaps 300 species of *Sphagnum* world-wide. The greatest bulk of *Sphagnum* (probably of fewer than 30 species) grows in the North

Temperate and Boreal zones. At other latitudes *Sphagnum* does grow, but usually at high altitudes, for example in the Snowy Mountains of Australia, in the Chilean Andes, and near the top of the high equatorial African mountains. An example of a single species with a disjunct distribution of this kind is *S. junghuhnianum* ssp. *junghuhnianum* growing on mountains in Malaysia, China, Taiwan and Japan (Johnson, 1960).

Small amounts of *Sphagnum* of many species may sometimes be found in the most unlikely habitats. For example, Lange (1973) describes 15 species, with *S. teres* and *S. subnitens* the commonest, around hot springs in many parts of Iceland. The pH of water in the springs ranged from 2 to 9 (though that amongst the plants was not measured) and the temperature of the water amongst the plants was in some cases more than 40°C, the plants growing adjacent to water at 90°C or more.

8.3 INTER-RELATION OF *SPHAGNUM* AND SOLUTES

8.3.1 Effects of solutes on plant growth

Most species of *Sphagnum* cannot survive in water which has flowed through calcareous rocks or soil. There are a few exceptions: *S. squarrosum, S. teres* and *S. fimbriatum* are usually found in places where the water supply is moderately calcareous – perhaps reaching a concentration of $\frac{1}{2}Ca^{2+}$ of 1 mmol dm^{-3}. In experiments, *S. squarrosum* grew almost as much when supplied with solutions containing a concentration of $\frac{1}{2}Ca^{2+}$ of 0.5 and 5.0 mmol dm^{-3} as they did in 0.05 mmol dm^{-3}, whilst seven other species grew much less well (Fig. 8.5). Water with a high calcium concentration usually has a high pH too, and this may be inimical to the growth of most species of *Sphagnum* (Olsen, 1923). It is not easy, however, to achieve and maintain a high pH in *dilute* solutions around *Sphagnum* plants. When this is done it becomes apparent that high concentrations of Ca^{2+} alone or high pH alone are not sufficient to reduce the growth rate of most species significantly (Fig. 8.6). It is the combination which is lethal. Amongst the major peat-forming species, hummock species such as *S. capillifolium* seem to be particularly sensitive to combined high Ca concentration and high pH whilst immersed species are less so.

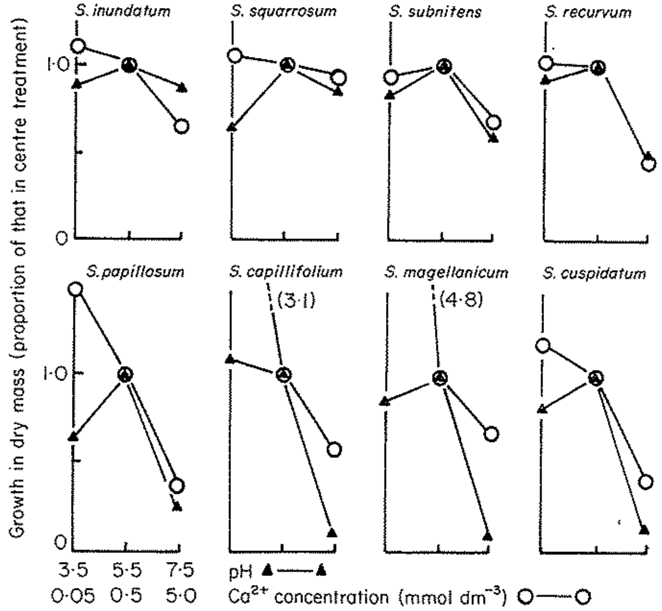

Fig. 8.5 The Relative growth in mass of eight species of *Sphagnum* in relation to pH (△-△) and concentration of Ca^{2+} (O–O) in the water. Results scaled to the value 1.0 for the central treatment: pH 5.5 and $\frac{1}{2}Ca^{2+}$ concentration 0.5 mmol l^{-1} respectively. Redrawn from Clymo (1973).

The growth rate of *Sphagnum* plants is affected not only by concentration but also by the rate of supply of solutes – what might be called the rate of flushing (Fig. 8.7). Increasing the rate of flow of solution to eight species of *Sphagnum* from zero to about 20 cm day^{-1} caused an increase in

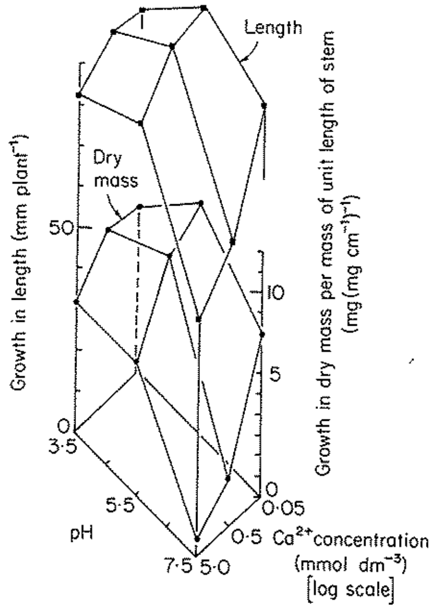

Fig. 8.6 Mean growth in mass (●) and in length (□) of eight Species of *Sphagnum* in an experiment with factorial combinations of pH and of Ca^{2+} concentration in the water. The growth in mass is expressed per mass of unit length of stem, so that the effect of specific plant size is minimized. Redrawn from Clymo (1973).

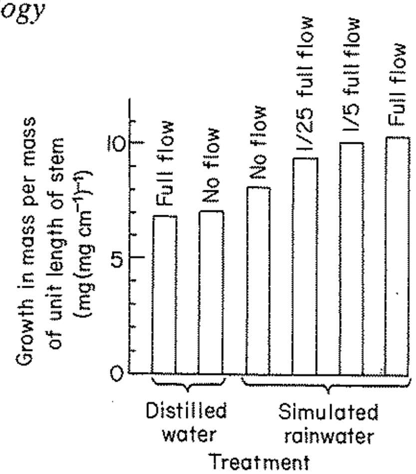

Fig. 8.7 Mean growth in mass of eight species of *Sphagnum* in relation to rate of flow of a solution simulating rainwater, and of distilled water. The full rate of flow was at a velocity of about 20 cm day^{-1}. Redrawn from Clymo (1973).

growth rate of about 30%. This experiment was made outdoors, but with artificial solutions. Much the same result was found by Sonesson *et al.* (1980) who grew *S. riparium* in open-topped cylinders placed in a wet, flushed area in which the species usually grows. Some cylinders were closed at the base; but the base of most were covered by a nylon net. The cylinder walls were perforated, so that water could move in and out. The closed cylinders contained eight times the volume of water that the perforated ones did. The concentration in the water of PO_4, Cl, SO_4, Fe, Zn, Mn, Mg, Ca, K, Na and NO_3 and NH_4 was measured at weekly intervals. In the perforated cylinders no concentration (except Fe) changed by more than two-fold during the 12-week growing season. In the closed cylinder, however, the concentration of PO_4 dropped from 0.6 to <0.04 μmol dm^{-3} within a week. The concentration of chloride fell from 47 to 2 μmol dm^{-3} over four weeks; that of Mg was halved within a week but then remained steady; Fe fell from 15 to 2 μmol dm^{-3} over a month (but rose steadily in the perforated containers to 126 μmol dm^{-3} after nine weeks). The concentration of total N in the closed container fell to about a fifth that in the perforated ones after six weeks. These differences were paralleled by the differences in the amount of growth: plants in the perforated containers made about twice the growth that those in the closed containers did.

Although some species – *S. squarrosum* for example – are almost always found in habitats with a relatively high concentration of solutes, or a high rate of flushing, the behaviour of other species is less consistent. At Cranesmoor (southern England) *S. papillosum* occupies the more oligotrophic lawns and *S. magellanicum* the flushed areas (Newbould, 1960),

but at the Åkhult mire (southern Sweden) the reverse tends to be true (Malmer, 1962a).

The concentration of nitrate, ammonium, and of phosphate in water squeezed from around *Sphagnum* is very low; Gorham (1956), for example, records that at Moor House, northern England, the concentration of ½Ca^{2+}, NO_3–N, and PO_4–P amongst *S. cuspidatum* and *S. auriculatum* was about 50, <3, and <0.1 μmol dm^{-3}.

The growth rate of adult plants of *Sphagnum* may be limited by the supply of phosphate: when ground rock-phosphate was applied to a bog surface then the growth rate of *S. compactum*, *S. auriculatum*, *S. cuspidatum*, and *S. tenellum* appeared to increase, and the plants became apple green (McVean, 1959). Grouse droppings and sheep dung usually kill the adjacent plants, but are later covered by bright green, robust, and apparently fast-growing plants which invade from the side. The same effect on grass-growth is seen around cow-pats. Certainly *S. papillosum* is able to

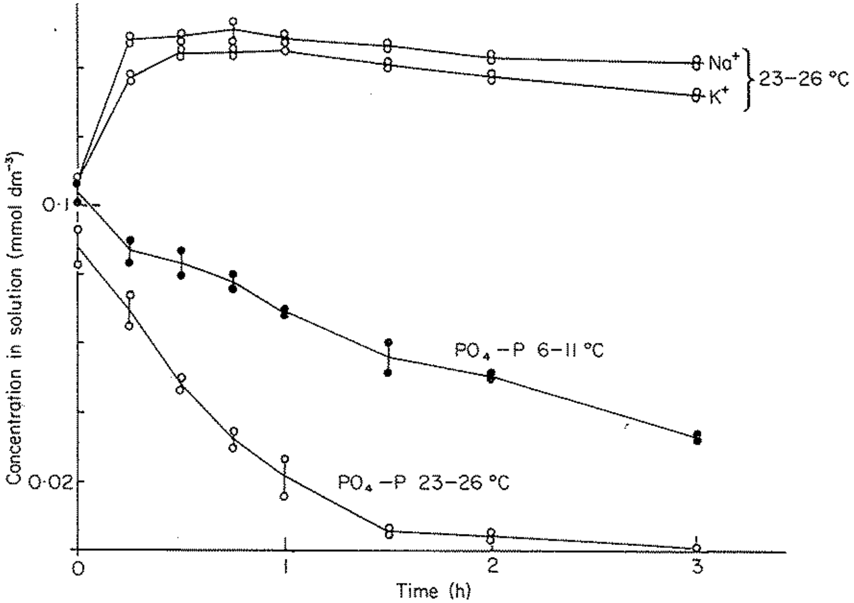

Fig. 8.8 Course of accumulation of phosphate from a carpet of *S. papillosum* at different temperatures. The carpet was 5 cm deep and 25 cm diameter. A total volume of 2.5 l of solution was sprayed on the plants at 78 ml min^{-1}, and then recycled. The initial increase in concentration of Na^+ and K^+ results from cation exchange, and change in concentration of cations in the solution by subsequent accumulation in the cells would be small because of the buffering action of the exchange sites. Clymo (unpublished).

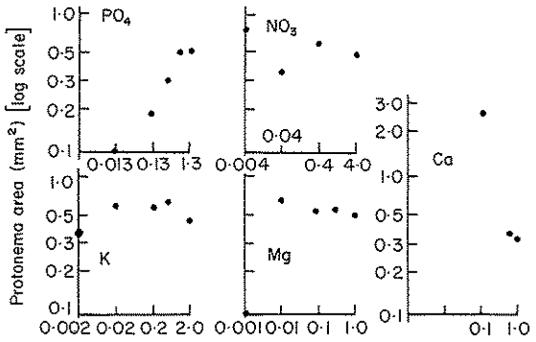

Fig. 8.9 Growth in area of the protonema of *S. papillosum* in relation to concentration of five ions. In these conditions phosphate is a nutrient, calcium a toxin, and the plants are indifferent to nitrate, potassium, and magnesium. Redrawn from Boatman and Lark (1971).

take up phosphate fairly rapidly from solution (Fig. 8.8) just as most other plants can.

It is surprising to find that the response of the protonema of *Sphagnum* to solutes is different from that of the adult haploid plants. The protonema seems to thrive on solutions of relatively high concentration of solutes; it grows better on agar made with full strength Moore's medium which contains concentrations of Ca^{2+}, NO_3–N, and PO_4–P of 0.7, 12.5 and 1.5 mmol dm^{-3}, than it does on any lower concentration (Clymo, unpublished). Of these solutes it seems that phosphate is the most important to *S. cuspidatum* and to *S. papillosum* (Fig. 8.9): a concentration of PO_4–P of about 1 mmol dm^{-3} seems to be necessary if the morphological transitions from filamentous to plate growth, and from plate growth to shoots are to be made. The concentration of PO_4 in bog water is about 10000 times smaller. How new plants establish from spores in the field is a mystery. Perhaps they do so only in very exceptional circumstances, though the rapidity with which *Sphagnum* re-invades suitably wet habitats argues against such an explanation.

8.3.2 Effects of plants on solute concentrations

That most *Sphagnum* plants grow in unusually acid conditions and that the *Sphagnum* plants contribute to the production of these very conditions has been known for a long time (Paul, 1908; Skene, 1915). The process of acidification was recognized as one of cation exchange by Williams with Thompson (1936) and Anschutz and Gessner (1954), and this approach has been extended to allow quantitative predictions (Clymo, 1963, 1967).

The cation exchange sites are probably the carboxyl (COO^-) groups on long-chain polymers containing uronic acids (Theander, 1954). A uronic acid may be visualized as a sugar in which the CH_2OH side chain at C6 has been replaced by COOH. There is a very close correlation of the concentration of uronic acid residues in polymers with the cation exchange capacity, and the regression of exchange capacity on uronic acid concentration is almost exactly the calculated one (Clymo, 1963; Spearing, 1972). Uronic acids constitute approximately 10% of the dry mass of immersed *S. cuspidatum* and up to about 30% of *S. fuscum* growing on hummocks. This is reflected in the exchange ability of the different species, and of plants of the same species growing in different habitats (Table 8.1). Any one species tends to have a higher exchange ability the further above the water table that it is growing, and at a given height above the water table those species which commonly occur in the higher habitats have a greater exchange ability than those usually found at lower levels. It is possible to suggest hypotheses to account for this striking pattern, but none is easily testable.

Table 8.1 Cation exchange ability (Ca^{2+} 7.4 mmol dm^{-3}, pH 6.0) of species of *Sphagnum* growing at various heights above the water table (-w-). For each of the ten sites the heights are ranked, but the vertical intervals are not the same either at one site or between sites. From Clymo (1963). *S. cus, S. cuspidatum; S. pul, S. pulchrum; S. sub, S. subnitens; S. pap, S. papillosum; S. pal, S. palustre; S. aur, S. auriculatum; S. mag, S. magellanicum; S. cap, S. capillifolium.*

S. cus	*S. pul*	*S. sub*	*S. pap* (1)	*S. pap* (2)	*S. pap* (3)	*S. pal*	*S. aur*	*S. mag*	*S. cap*
–	–	–	–	0.91	–	–	–	–	1.13
–	–	–	–	0.01	–	–	–	1.13	1.12
–	–	0.98	1.03	0.96	–	–	–	1.13	1.25
–	0.88	0.97	1.01	0.95	1.00	1.04	1.14	1.14	1.22
–	0.87	1.00	0.99	0.95	0.93	0.83	1.14	1.11	1.19
0.73	0.88	0.96	0.89	0.91	0.89	0.68	1.01	1.07	1.15
-w-	-w-	-w-	-w-	-w-	-w-	-w-	-w-	-w-	-w-
0.83	0.76	–	–	0.78	0.87	–	0.84	–	–
0.73	–	–	–	–	–	–	–	–	–

Many of the phenomena of cation exchange in dead plants can be accounted for by a simple model based on two compartments. One, probably the plant cell walls, contains indiffusible anions (the carboxyl groups) and the other compartment is the water outside the cell walls. The equilibrium conditions in such a system can be calculated (Donnan, 1911) and show that in the chemical environment that is usual for *Sphagnum*:

(a) the walls will contain a much higher concentration of cations than will the solution;

(b) that the higher the cation valence the greater the selective concentration in the walls; and

(c) both effects are more marked the more dilute the solution outside the walls.

The general equilibrium is described by:

$$(x_{\mathrm{i}}^{+v})^{1/v}/(x_{\mathrm{o}}^{+v})^{1/v} = K$$

where x^{+v} is the concentration of cation of valence v, i and o refer to the inside and outside (wall and solution) compartments, and K is a constant for the particular set of conditions. (The same relationship is the basis of Schofield's ratio law applied to soils). This equation is satisfied for all cations simultaneously and, given the high concentration of exchange sites, implies that the concentration of cations in solution is strongly buffered. There are complications however. The exchange capacity may be considered as measured by the total number of carboxyl groups per unit volume or mass but the special affinity of H^+ for the COO^- (describable by a dissociation coefficient) ensures that as pH falls below about 5 a significant and increasing number of the carboxyl groups is tied up as COOH. This means that the effective exchange capacity ('exchange ability') falls as pH falls. The other cations may also have individual specificities not included in the simple Donnan analysis. In particular, the larger ones such as Ni, Pb etc. show a special affinity which may be described as chelation.

None of these processes is unique to *Sphagnum* – they are found in most bryophytes (Brown, Chapter 11 of this volume). Nor is *Sphagnum* particularly extraordinary in its concentration of exchange sites; other mosses have concentrations that are half or more those of *Sphagnum* (Clymo, 1963) and exceed the concentration in *S. cuspidatum* growing in wet places.

Possession of high cation exchange capacity does not of itself confer the ability to maintain the surrounding flowing water acid: if a freshly killed *Sphagnum* plant in a tube is slowly flushed with a large volume of solution the pH of the effluent solution falls dramatically during the first few minutes, but then rises steadily until eventually the pH of the effluent is the same as that of the inflowing solution (Clymo, 1967). In fact, as Brehm (1971) points out, a whole *Sphagnum* hummock might behave as if it were a cation exchange column. A similar sequence of changes in pH is found if live plants are flushed at a velocity of about 100 cm day^{-1} with a dilute solution of salts at concentration similar to those in rainwater. It is only when the flushing velocity falls to say, 0.3 cm day^{-1} (corresponding to rainfall of about 100 cm year^{-1}) that the pH of the effluent remains consistently below that of the inflow. This could be because the plants are excreting whole organic acids, but the amount of such excreted acids seems to account for less than 10% of the observed acidity (Clymo, 1967). Another possibility is that the *Sphagnum* plants can in some way regenerate the exchange sites – that is to replace other cations by H^+. This possibility has not been tested experimentally and could not contribute much in the long term because other cations would accumulate. In any case, Brehm (1970) shows that, if the sites are regenerated artificially with dilute HCl, the plants grow more slowly, probably as a result of the removal of other cations. In normal conditions, the concentration of cations inside the cytoplasm seems to remain fairly constant (Brehm, 1968) even if the concentration in the cells and outside solution changes greatly. A peroxidase extracted from *S. magellanicum* (Tutschek, 1979), has maximum activity at pH 5, so it may be that the cytoplasm is isolated by the plasmalemma from the more acid conditions outside. It is clear, however, that newly produced *Sphagnum* tissue contains large amounts of exchangeable H^+, and it seems reasonable to suppose that the carboxyl groups in the cell are formed as COOH. The ability to *maintain* an acid environment whilst rain (a dilute solution of salts) is flushing the *Sphagnum* carpet must then depend on continued growth and production of new exchange sites. Green and apparently rapidly growing *S. papillosum* plants do maintain a lower pH around them than do less bright green plants (Fig. 8.10). Values for the annual production and net water supply (precipitation – evaporation) can be combined with the Donnan system

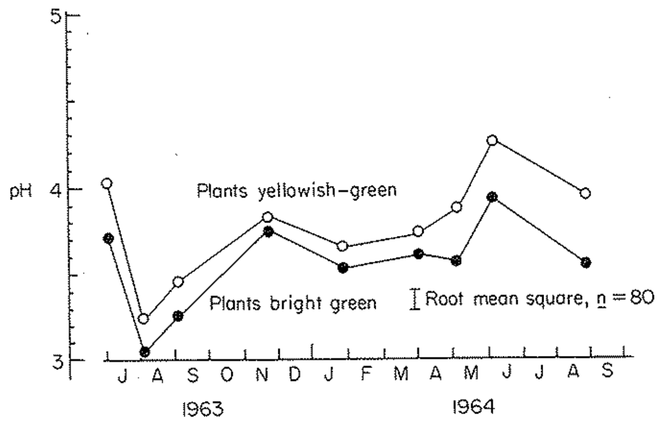

Fig. 8.10 Seasonal course of pH of water squeezed from *S. papillosum* plants growing at Thursley Common, southern England. On each occasion, five measurements were made on water from plants which were bright green and five on water from plants which were live but less bright green. The samples were paired, the individuals in each pair being no more than 2 m apart. The difference between bright green and less bright green plants is highly significant, as is the seasonal change. Clymo (unpublished).

exchange model to predict the equilibrium pH which would be produced (Fig. 8.11). From such calculations, it is apparent that, with productivity of 1 kg m^{-2} $year^{-1}$ (10 t ha^{-1} $year^{-1}$) and net water supply of 50 cm containing about 0.1 mmol dm^{-3} of dissolved salts, then an average pH of about 4 could be maintained by the plants. Such an average conceals the effects of three factors which could cause much greater acidity at particular times in particular places. Firstly, the net supply of water is not uniformly distributed during the year and the times of least supply (lowest rainfall, highest evaporation) coincide with the times of most rapid plant growth, *D*. Both should lead to greater acidity in summer. Second, the hummock species have a greater exchange capacity and can cause correspondingly more acid conditions. Third, the amount of water around hummock plants

is much smaller than it is around pool plants, so the water volume, *V*, with which the plants can equilibrate is much smaller. During periods without rain it may happen that there is very little water movement around the plants, and the addition of new plant material effectively increases *D* in the *D*/*V* expression, whilst *V* remains constant or even decreases. One might then expect that the hummocks in summer would become considerably more acid than pH 4. All these effects may be seen in the field measurements shown in Fig. 8.12: the high acidity during periods of rapid growth and low water supply in summer, most marked on hummocks, and the autumn 'washout' after which the pH in all habitats is close to that of rain.

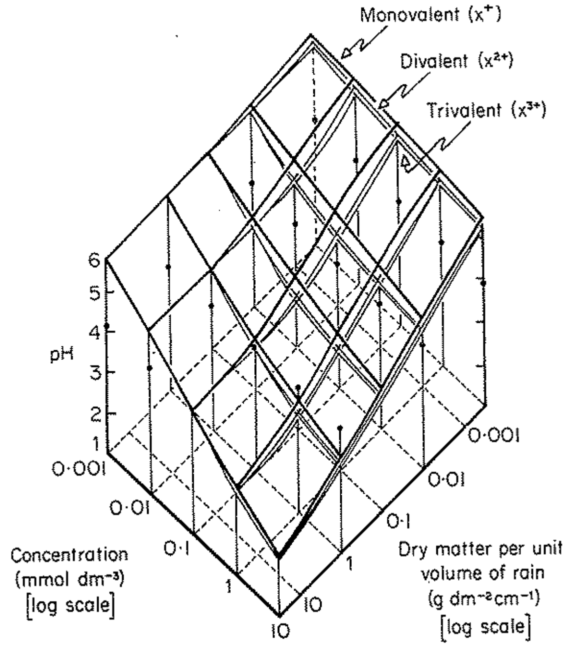

Fig. 8.11 Calculated equilibrium pH of the solution around a cation exchange phase (the *Sphagnum* cell walls) in relation to the initial concentration of cations of different valence (cation concentration in the rain). The cell walls are assumed to have 20% uronic acid of dissociation constant 10^{-4} and chemical concentration 1.0 mol l^{-1}. These values are typical of *Sphagnum* (Clymo, 1963). The third axis gives the quotient of new dry mass produced by the plant (growth, *D*) and rainfall (*V*). The units are g dm^{-2} $year^{-1}$ (= t ha^{-1} $year^{-1}$) and cm $year^{-1}$. For growth of 5 t ha^{-1} and rainfall 50 cm $year^{-1}$ then $D/V = 0.1$ g dm^{-2} cm^{-1}. Filled circles define a plane of pH 4. Redrawn from Clymo (1967).

It is perhaps surprising to find the rain to be so acid, though the general phenomenon of acid rain is now well known. The acidity is associated with sulphur oxides produced by burning coal and oil. This additional load of acid is probably relatively recent and one might expect it to have favoured the growth of *Sphagnum*, but this does not seem to be so. *Sphagnum* has almost disappeared from large areas of the Southern Pennines where it was abundant (as evidenced by its dominance in recent peat) even a hundred years ago (Tallis, 1964). The sulphur containing anions, particularly bisulphite, HSO_3^-, damage *Sphagnum* even in low concentration. For *S. recurvum*, HSO^-_3 concentration of 0.1 mmol dm^{-3} reduces both ^{14}C fixation and O_2 evolution rates by about 30–40% at pH about 4.5, and by even more if the pH is lower (Ferguson and Lee, 1979), though very low HSO_3^- concentration may stimulate ^{14}C fixation. Both HSO_3^- and SO_2, at concentrations commonly found in the Pennines, reduce the growth of *Sphagnum*, though the extent of impairment differs between species: the general order of sensitivity is *S. tenellum* > *S. imbricatum* = *S. papillosum* > *S. capillifolium* ≥ *S. magellanicum* > *S. recurvum*. The immersed species *S. cuspidatum* seems to be very sensitive too (Ferguson *et al.*, 1978). Most convincing of all though is the fact that the growth of *Sphagnum* in field conditions is substantially reduced by occasional treatments with HSO_3^- solutions, simulating the natural episodic nature of acid rain 'events' (Fig. 8.13).

The high cation exchange capacity of *Sphagnum* led to its selection as a material suitable for trapping, and hence sampling, aerial heavy metal pollutants. It proved highly successful, but probably mainly because of its ability to trap airborne particulate matter. It has been used for trapping water-borne particles and solutes (for example those containing uranium) too. Live plants of various species of *Sphagnum* have also been used to estimate deposition rates over large geographic areas (for examples, see Ruhling and Tyler 1971; Pakarinen and Mäkinen, 1976). The vertical distribution of the commoner cations, of heavy metals, and of radioactive isotopes such as ^{137}Cs have also been studied (for example Pakarinen and

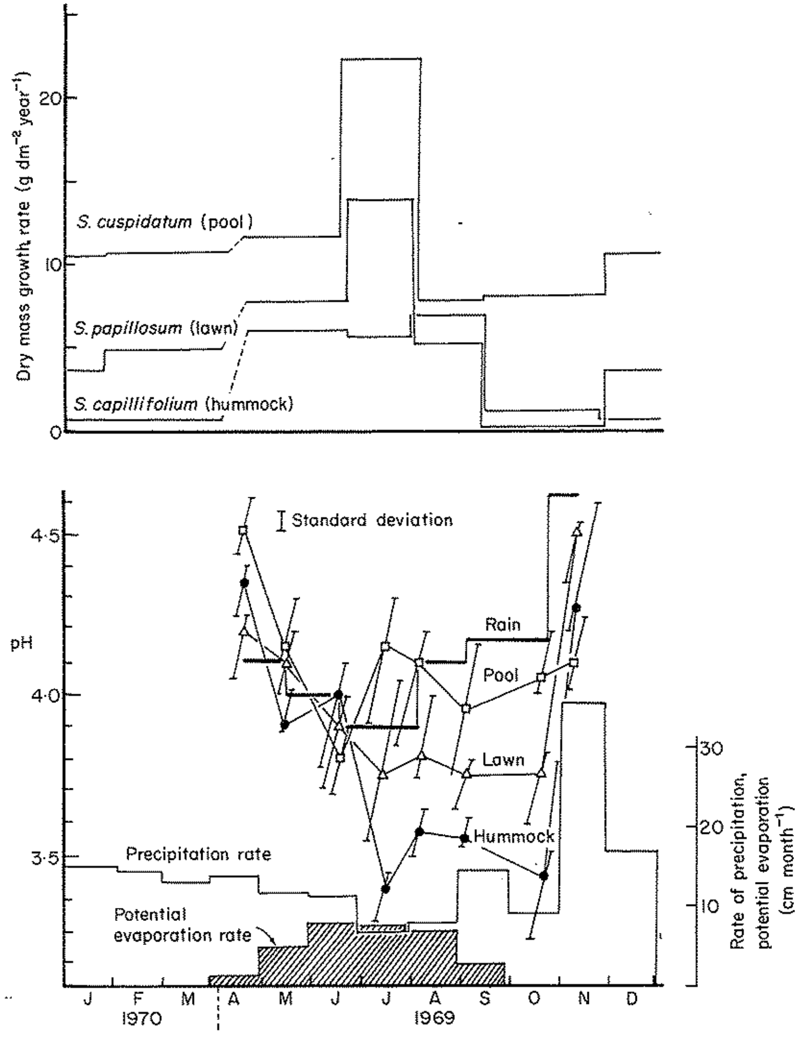

Fig. 8.12 Growth of *Sphagnum*, precipitation, potential evaporation, and pH of rain and water in three habitats at Moor House, northern England. Pools contained *S. cuspidatum*, lawns were of *S. papillosum* and hummocks of *S. capillifolium*, with less than 5% cover of other species. The same five sites in each habitat were sampled on each occasion. Values shown are the median; diagonal bars show range (in many cases the extremes are the same at sites on most occasions). The standard deviation of the difference between 15 samples on successive days is shown by a vertical bar. The first three months of 1970 are shown before the last nine of 1969. Clymo (unpublished).

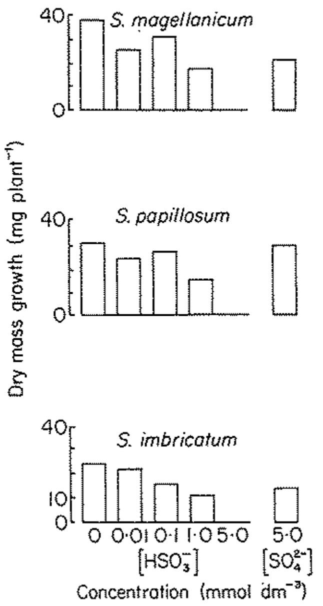

Fig. 8.13 Growth of three species of *Sphagnum* between February 1977 and July 1978 on unpolluted blanket bog in Snowdonia treated with various concentrations of bisulphite or with sulphate. The rainfall is 200 cm year^{-1} and solutions were sprayed on the experimental plots at about weekly intervals from February 1977 to March 1978 at a rate corresponding to about 50 cm year^{-1}. The mean concentration of HSO_3^- in rain in Manchester during the winter of 1975–76 was 0.02 mmol l^{-1}, with a range from undetectable to 0.15 mmol l^{-1}. Redrawn from Ferguson and Lee (1980).

Tolonen, 1977a, 1977b; Clymo, 1978, 1981; Damman, 1978; Pakarinen, 1978b). Most of these studies are more concerned with peat than with the live plants however.

8.4 INTER-RELATIONS OF *SPHAGNUM* AND WATER

It is convenient to consider how *Sphagnum* as an inert physical system affects the states of water surrounding and permeating it, first at equilibrium and then when the water is moving. The responses of the plants can then be considered.

8.4.1 Equilibrium states

The concepts of water potential (ψ) and water content (volume per volume, ϕ, or volume per unit dry mass, ϕ_m) give a convenient framework and allow recognition of the relationship with structural features of the plant (Fig. 8.14). The potential, ψ, may be given in the form of a pressure. The units of measurement are conveniently given as Pa (Pascal). The equivalence with older units is 100 kPa = 10^5 Pa = 10^5 N m^{-2} = 1 bar ≃ 1 atmosphere. Dilks and Proctor (1979) give a schematic diagram more complex than Fig. 8.14, including cytoplasmic water and osmotic and plasmolysis effects, but for a moss plant (rather than a carpet of plants) and using a linear scale for water content. The proportion of the *Sphagnum* carpet occupied by the chlorophyllose cells is so small however that osmotic and plasmolysis phenomena are not visible in Fig. 8.14. Potentials spanning seven orders of magnitude are involved. At the lower end, the water content increases slowly as potential rises from −1000 MPa to about −2 MPa. In this range, it is water absorbed on surfaces and filling the spaces within the cell walls and differences in relative humidity of the air which are involved. At relative humidity of about 0.99, just distinguishably different from saturated, the water content has reached about 0.8 and is rising rapidly (Fig. 8.15). The water content is greater than that of cellulose, perhaps because of the high concentration of carboxyl groups and associated cations. The water content is almost the same if the plants gain water to reach equilibrium as it is if they lose it: there is little hysteresis. The dry matter of the cell wall occupies about 1–2% of the total space in a *Sphagnum* carpet (Fig. 8.3). The wall and the water which it contains and encloses in chlorophyllose cells occupies about 10% of the total space (Figs 8.14 and 8.17).

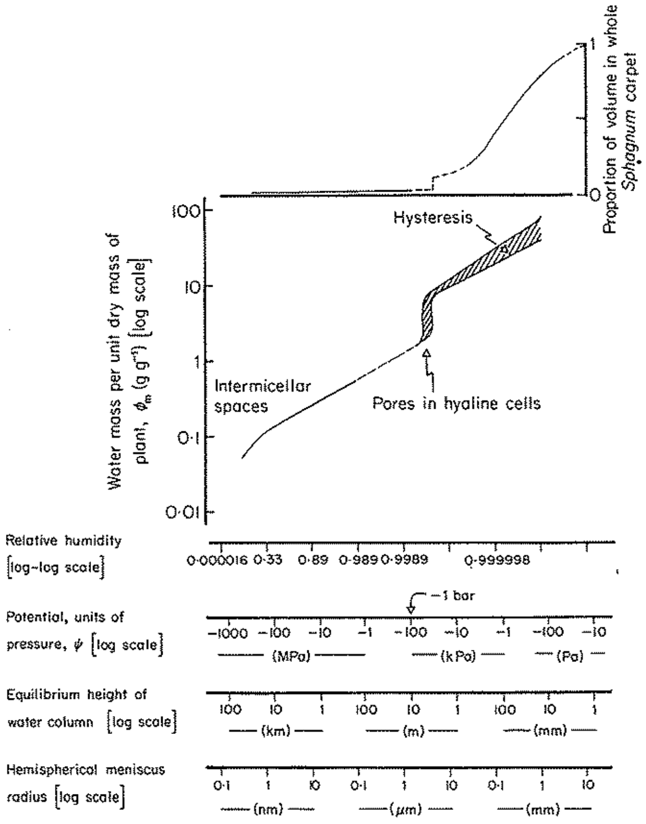

Fig. 8.14 The relationship between water potential (ψ) and water mass per unit dry mass of *Sphagnum* (ϕ_m), and with the proportion of space in a *Sphagnum* carpet occupied by water (ϕ, upper graph). The equivalence between water potential and relative humidity, the radius of a hemispherical meniscus, and the height to which water could rise in a circular capillary of the same radius and with contact angle 0° are also shown. Full lines are measured (see Figs 8.3, 8.15, 8.17, 8.18, 8.19); dashed lines are inferred. Hatched regions show hysteresis.

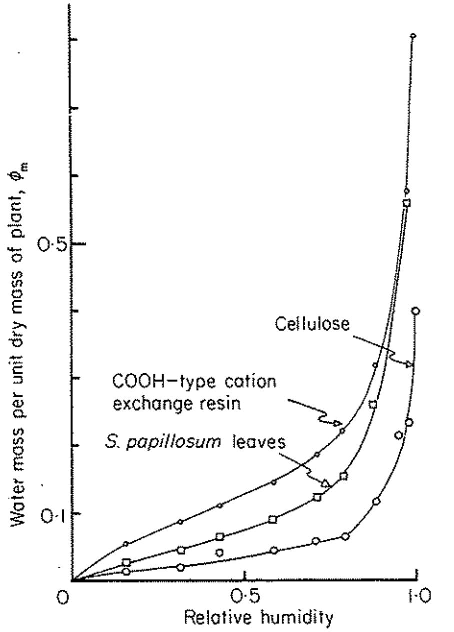

Fig. 8.15 Isopiestic water sorption by dry *S. papillosum*, by a cation exchange resin with carboxyl functional groups, and by cellulose. The samples were in closed tubes with humidity controlled by sulphuric acid solutions of different concentration (Hodgman *et al.*, 1961). Very similar results were obtained if the *S. papillosum* started wet: hysteresis was usually less than 2% of the value at any humidity. Clymo (unpublished).

The next important point is reached at $\psi \simeq -20$ kPa, corresponding to a circular wettable capillary radius of about 5 μm. The upward step in water content corresponds to the filling of hyaline cells. Water can move by diffusion through the wet cell wall but it does so much more rapidly by mass flow through the pores which occur in almost all hyaline cells. These pores are circular or nearly elliptical holes. Scanning electron micrographs (Mozingo *et al.*, 1969; Troughton and Sampson, 1973; Dickinson and Maggs, 1974) show that in the species examined the pores have a border, and that a hyaline cell may have several such areas which are covered by a thin wall, but it also has others which are perforated. It is not known whether the pores form in different ways initially, or form in the same way initially but differ later on in that some pores have the wall resorbed to different degrees, or are broken mechanically. The pores have a diameter characteristic for a particular species (Table 8.2). The diameter is less than that of the hyaline cell, and the constriction causes hysteresis (Fig. 8.16). Because there are many hyaline cells and pores of similar dimension the ψ *vs* ϕ graph shows a step transition from water content of about 1 to about 8. The potential, about −30 kPa, corresponds to a circular capillary able to support a water column of about 3 m, so the hyaline cells will never be emptied by any likely fall in the water table. As the water potential is raised further, however, the remaining 90% of space in the *Sphagnum* carpet gradually becomes filled. Here it is, at first, the capillary spaces between

Table 8.2 Size and number of pores in hyaline cells, and number of branches, in some species of *Sphagnum*. From Hill (1978).

	Abaxial pores		Adaxial pores		Branches	
	Diameter (μm)	No. per cell	Diameter (μm)	No. per cell	Pendant	Spreading
S. imbricatum	1–18	3–8	usually none		1–2	2
S. papillosum	3–22	3–10	absent		1–2	2
S. magellanicum	1–19	3–6	absent or few		1–3	2
S. palustre	8–25	3–16	absent or few		1–4	2
S. capillifolium	8–25	4–7	absent or few		1–2	2
S. fuscum	2–30	3–7	absent or few		1–2	2
S. subnitens	6–30	4–10	absent		1–2	2
S. compactum	5–12	0–4	absent		1–5	1–2
S. auriculatum	3–8	0–30	3–12	0–25	0–4	2–3
S. subsecundum	2–5	20–40	absent or few		2–4	2–3
S. cuspidatum	2–6	0–1	4–8	4–10	3–5	3-5
S. tenellum	4–12	0–1	4–18	0–2	1	2
S. pulchrum	3–8	0–1	4–8	3–9	2	2
S. recurvum	4–9	0–1	5–9	3–7	3	2

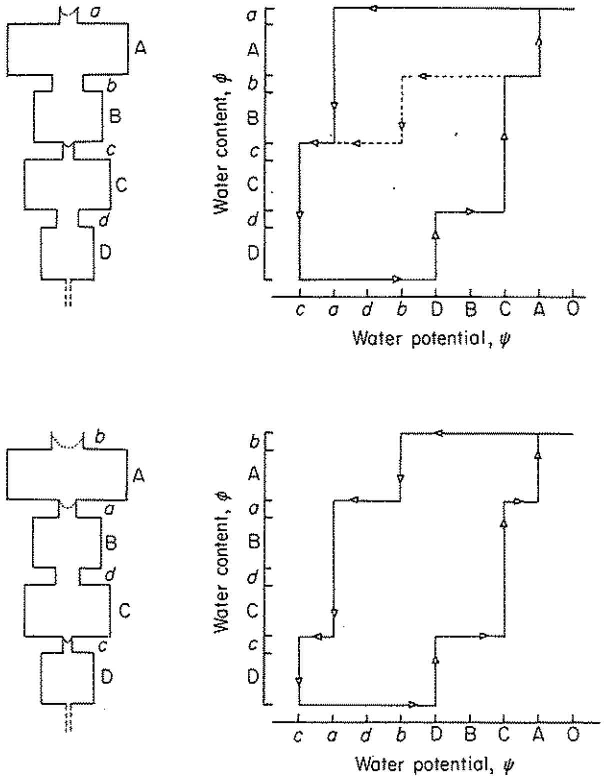

Fig. 8.16 Hysteresis in the ψ *vs* ϕ relation resulting from the presence of a multichambered system with constrictions (the 'cavern' or 'ink-bottle' effect). The water content axis identifies which part of the system is water-filled. The water potential axis identifies the rank order in which the meniscus in capillaries of the radius of the caverns and constrictions would just be maintainable. In the upper example suppose the system is water-filled at $\psi = 0$, and that the water column is put under tension (ψ being slowly reduced) and that the cavern D is in contact with capillary spaces smaller than any of those above. The system remains full until *a* can no longer maintain a meniscus, at which point the system empties to the next smaller constriction, *c*. This in turn will eventually break allowing C and D to empty. If the water potential is now increased it has to reach a point high enough for the cavern D to be bridged before filling begins. Next, C is bridged and both C and B fill (because B is of smaller radius than C). Finally A fills. These are the primary drying and wetting curves. If, at the point where B and *b* have just refilled, the potential is lowered, then the dashed line is followed. This is a secondary curve. The lower example shows the effect of rearranging the constrictions, but retaining the same order of caverns. The drying curve is changed but the wetting one is not.

For very small capillaries, and water potential changed by changing the relative humidity, the model should be one which is open at both ends.

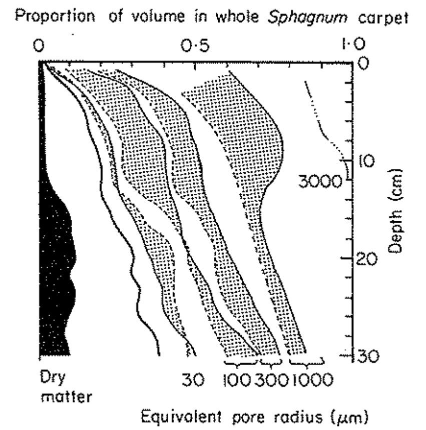

Fig. 8.17 Profiles of cumulative proportion of pore volume (circular capillary equivalents) of various sizes, calculated from profiles of water content (measured by absorbance of soft gamma radiation) with the water table at different depths below *S. capillifolium*. The black area at the left is dry matter; to the left of the bold line are pores which remain full under tensions equivalent to 120 cm of water ($\psi = -120$ kPa). The solid lines to the right of the bold line are those obtained with a falling water table; dashed lines are for water table rising from 120 cm deep. Shaded areas show hysteresis. Redrawn from Hayward and Clymo (1982).

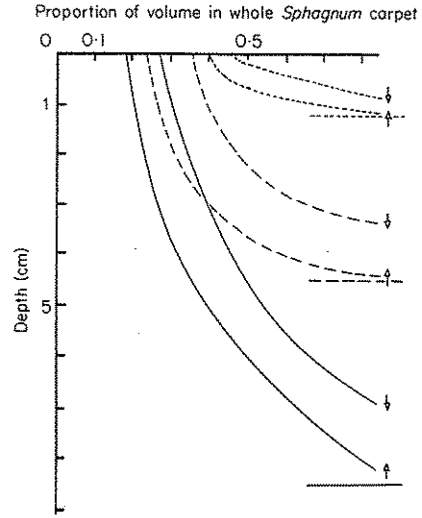

Fig. 8.18 Water content profiles for *S. papillosum* with the water table at three different depths. For each depth there are two curves: one when the water table rose to the specified level, the other when it fell to that level. The difference is a measure of the amount of hysteresis. Redrawn from Hayward and Clymo (1982).

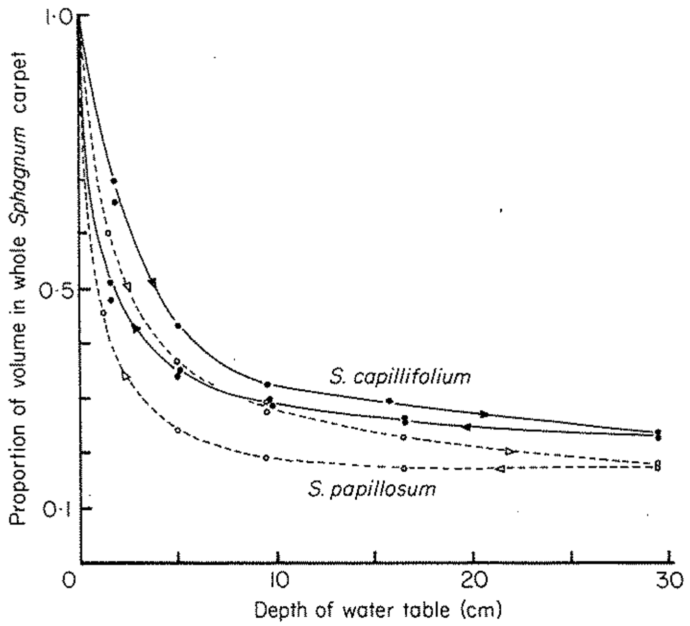

Fig. 8.19 Effect of raising and lowering the water table between the surface and 30 cm deep on the proportion of water in the capitulum (top 1 cm) of *S. papillosum* and *S. capillifolium*. Redrawn from Hayward and Clymo (1982).

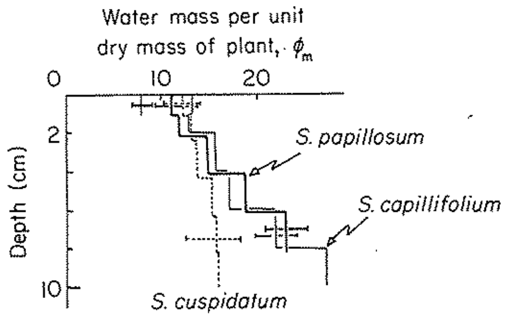

Fig. 8.20 Water content profiles of three species of *Sphagnum*. Plants were removed, with forceps, from carpets of plants in the field and cut into 2 cm-sections whilst held vertically. All plants were collected within two hours on a dry day. Bars show 95% confidence intervals. The left-most isolated 0–2 cm result is for capitula of *S. papillosum* growing as isolated plants in a carpet of *S. capillifolium*. Redrawn from Clymo (1973).

imbricate leaves, and between pendent branches and stem, that are involved. Again, there are constrictions which cause the hysteresis effects shown in Fig. 8.17. This is the range within which the water content depends very much upon the water table, upon whether the water table is rising or falling (Fig. 8.18), and upon the detailed distribution and proportion of spaces of different sizes. This last differs considerably between species (Fig. 8.19): *S. capillifolium* has a higher water content (ϕ_m) in its capitula than does *S. papillosum*, whatever the water potential (ψ). The same phenomenon may be seen in field measurements (Fig. 8.20) but these are far less accurate than the laboratory ones because the plants must be removed and this must necessarily disturb the capillary films. Similar values may be seen in Fig. 8.3.

8.4.2 Dynamic states

The details of water movement about the *Sphagnum* plant are still unclear but are of great importance. The height to which water might rise in a wettable circular capillary at *equilibrium* is of less importance as water potential or capillary size decrease, partly because below 100 kPa (equivalent to a meniscus of about 1 μm radius) the height (10 m) is vastly greater than is necessary, and mainly because the rate of movement in such small spaces is so slow. For a straight-sided tube and a constant potential drop the volume rate of flow in a *single* tube is proportional to the fourth power of the radius. But it is possible to fit more small capillaries than large ones into a given cross-sectional area, and the *total* volume rate of flow over the whole cross-section is then proportional to the square of the radius.

The rate of movement of water up the *Sphagnum* plant is rapid, and large fluxes may occur. This was shown by Overbeck and Happach (1956), and may be seen in more detail in Fig. 8.21. The greater rate of loss from *S. capillifolium*, and the increase in this difference as the water table was lowered, may be partly explained by the capillary structure already revealed by the equilibrium measurements. It seems unlikely that higher water content *per se* is the explanation. Rather, it is likely to be a smaller total resistance to transport in capillary spaces outside the cell walls. If one inspects a *Sphagnum* carpet during a drought it is common to find individuals or groups of *S. papillosum* plants which have dried out and become papery and white while adjacent (touching) plants of *S. capillifolium* are still wet. Cavers (1911) noted that 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'. If most of the water moves in the pendent branches then the linear velocity of water on a fine day with rapid evaporation may be well above 1 mm min^{-1}, a rate which, if Stokes' Law applied, could keep pollen grains and spores of 10 μm diameter in suspension (Clymo, 1973). Experiments have confirmed this (Mackay, unpublished).

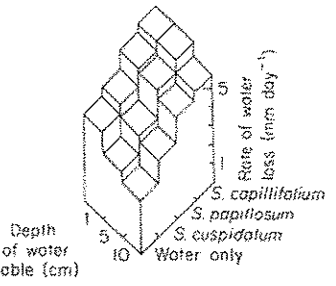

Fig. 8.21 Rate of loss of water from three species of *Sphagnum* in 0.6 l beakers with water table at one of three levels. The capitula were level with the top of the beaker. Guard rows of unmeasured *Sphagnum*-filled beakers surrounded the experimental ones, and the experimental ones were re-randomized each day. Measurements were made for nine consecutive days. Redrawn from Clymo (1973).

That such mass transport is possible is easily shown. A few wet leaves of *S. papillosum* may be put on a microscope slide, without a coverglass, and observed as they dry. When the surface water has evaporated there is a short pause, for a minute or so, until, with explosive suddenness, a hyaline cell becomes part filled with air (Fig. 8.22). Within a few seconds many hyaline cells are 'popping' in this way and water, with entrained particles, is moved violently from one place to another. The series of events seems to be as follows. As water evaporates from the wet hyaline cell walls the menisci in the pores, which were flat, become increasingly concave though the major and minor radii of curvature are still greater than those of the pore. Beneath this curved meniscus there is a reduction in pressure appropriate to the head of water which a meniscus with these curvatures is capable of supporting. The net of chlorophyllose cells is relatively strong and not easily deformed. The hoops of thickening on the hyaline cells are not so strong, and the unthickened wall between is even weaker, so the abaxial and adaxial walls are sucked in. Under the microscope the walls can be seen to go slowly out of focus. That this reduction in pressure is real can be seen if a small air bubble is trapped in a hyaline cell. The bubble grows as the pressure falls – indeed the growth of the bubble can be used to measure the change in pressure. A pore, in *S. papillosum*, of 8 μm radius can support a pressure reduction of 19 kPa – about 0.2 bar. Eventually, so much water has evaporated that the meniscus reaches a radius of curvature smaller than that of one of the pores. The meniscus then breaks, the cell wall springs out again, and the remaining water, which is sufficient to fill perhaps half the cell may appear at one end of the cell. In *S. papillosum* the hyaline cell is lined with papillae which have capillary spaces less than 1 μm

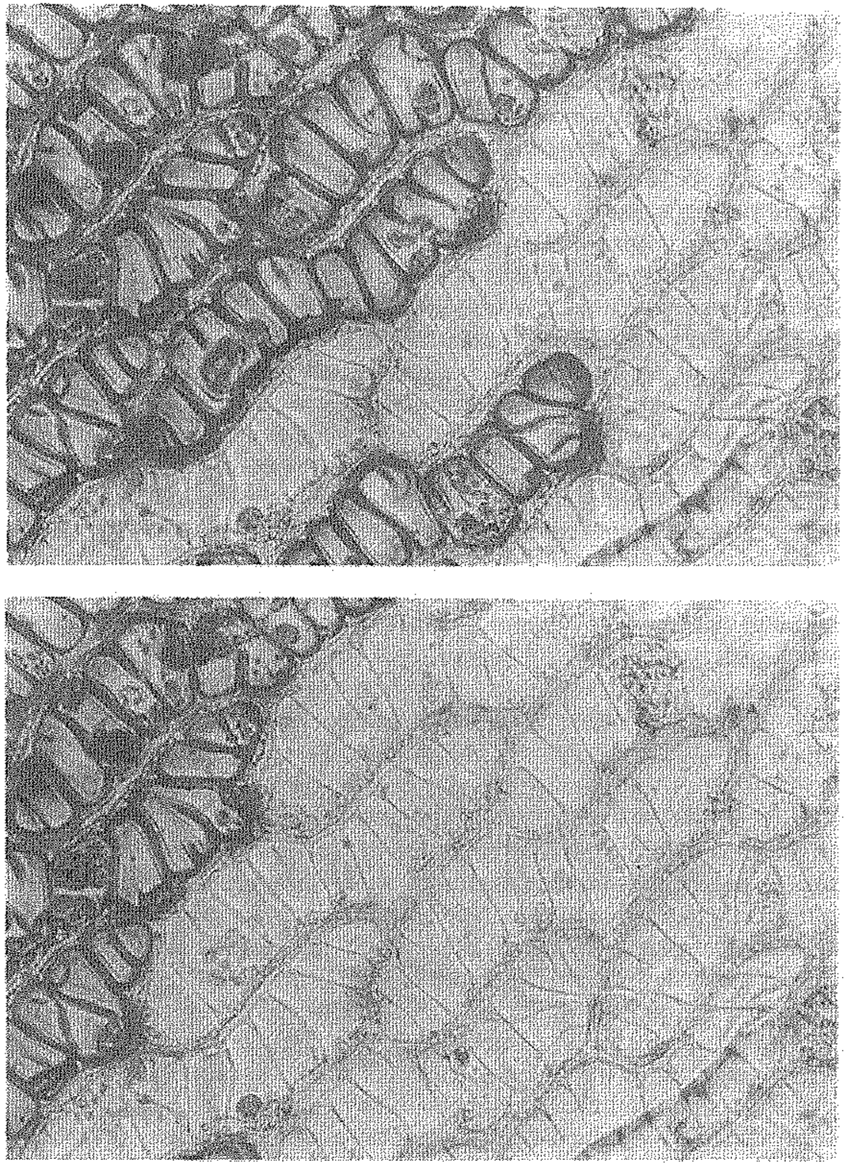

Fig. 8.22 Part of a leaf of *S. papillosum* drying out. The ~~lower~~ upper photograph was taken 5 s after the ~~upper~~ lower one. In this time three more hyaline cells have 'popped' and (apparently) become air filled. See text for further explanation. The width of the hyaline cells is about 25 μm. Photographs by R. S. Clymo.

across between them. When the meniscus breaks, the water therefore forms a thin layer lining the cell and with the centre filled by a large air bubble. The lining layers of water are not easily visible, so the cell appears to be magically completely empty of water. A little later the hyaline cell appears to flicker, as the mensci retreat between the papillae. The whole leaf may empty in this way in less than five minutes, and then appears white and papery.

Such simple observations reveal in a dramatic way the importance of surface tension as it changes the physical pressure and moves water bodily in the microscopic world.

It is not only the size and proportion of spaces of different sizes which affect the movement of water. The exact position of the spaces in relation to one another is crucial. In a system showing marked hysteresis of equilibrium states there must be interlinked 'caverns' (Fig. 8.16). The dynamic behaviour of this system will be determined largely by the bottlenecks, because the volume rate of flow through these is so much restricted. The primary 'drying' curve (the case where the water table starts at the surface and is slowly lowered) is determined largely by the size, number and position of bottlenecks, whilst the primary 'wetting' curve is determined mainly by the maximum width, number, and position of caverns. The difference between the two curves then gives some indication of the shape and arrangement of the spaces. It seems that the widest parts are no more than twice the size of the bottlenecks at any water potential, probably because, in this three-dimensional system, many of the spaces are open round much of their perimeter. In any case this gives only a crude indication because the *order* of caverns matters too: the same bottlenecks and maximum widths would, if re-ordered, give a different hysteresis result but might not affect the volume rate of flow. It is also possible to imagine reservoirs connected through a single opening to the main line of flow. These would contribute to hysteresis in the ψ *vs* ϕ curve, but would scarcely affect the volume rate of flow.

The general pattern is shown if an undisturbed *Sphagnum* carpet is arranged in a glass jar with the water table 10 cm below the capitula and the whole apparatus placed in a stream of dry air so that evaporation occurs. An anionic dye solution (for example, eosin) is injected on one plant just above the water table and its progress followed. This experiment is similar to, but much more complex than, the systems used in gas, gas–liquid, or liquid chromatography. The dye remains mostly around the stem and pendent branches to which it was applied but it moves upward. The concentration profile becomes attenuated. The profile is clearly not just that of laminar mass flow with diffusion broadening: there is mixing with reservoirs along the route too. There is a small amount of lateral spread to other plants, and much more occurs if the pendent branches are removed from one node of the treated plant. In this case the water is moving sideways along the spreading branches to adjacent plants. It is important to recognize that it is not only the potential difference but also the resistance to flow which determines the volume rate of flow: an isolated plant with pendent branches removed may lose water by evaporation and develop a lower water potential, but the water can move directly upward only in the very small intermicellar spaces and at a very slow rate. These effects may be seen in the results (Fig. 8.23) of an experiment in which different parts of the plant were removed 8–10 cm below the apex and the water content of higher parts measured. One set of plants was placed in still, damp air, and another was placed in moving drier air so that evaporation was rapid. In still air, the water content of capitula was only slightly reduced by removing either or both the spreading and pendent branches, though it was much reduced if the stem too was replaced by a water filled 1 mm diameter glass tube – exactly why is not obvious. When evaporation was rapid however the water content of capitula was markedly reduced if both pendent and spreading branches were removed but less so if only one or the other was removed. On the segment immediately above the one from which branches were removed, however, the water content was much reduced if either sort of branch had been removed below. This strongly suggests that, when pendent branches had been removed, water then moved sideways to adjacent plants and returned again higher up: the further from the site of removal the more touching branches there were through which lateral movement would occur.

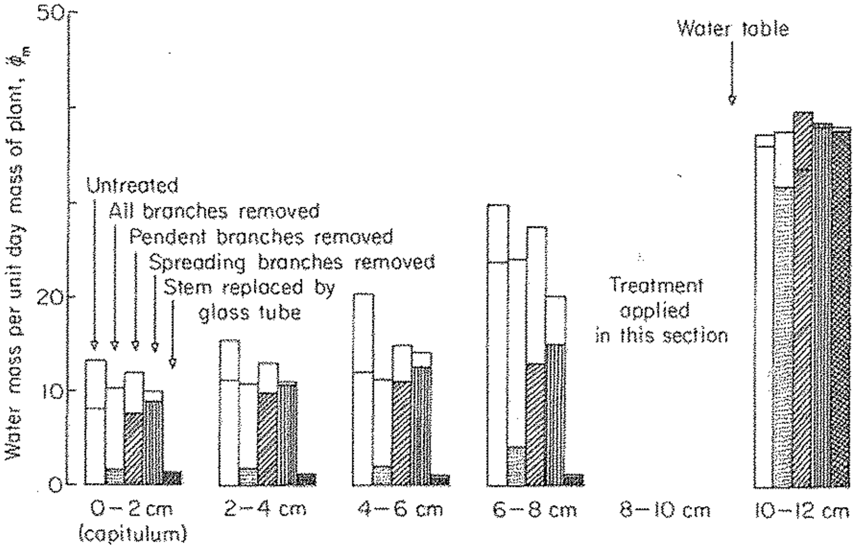

Fig. 8.23 Water content of successive 2 cm-sections of *S. papillosum* treated in various ways. The treated plant was surrounded at natural density by untreated ones. All were in 1 l beakers. The upper bars are for plants kept in still, moist air; the lower ones are for plants in moving unsaturated air. The water table was at 10 cm depth, and treatments were applied to the section between 8 and 10 cm. The treatments were: all branches removed; pendent branches removed; spreading branches removed; all branches removed and stem replaced by a water-filled glass capillary of 1 mm diameter into which the cut stems were pushed. Clymo (unpublished).

Change in water content has other effects on *Sphagnum* too. If the water table starts at the surface and is then lowered the water potential at a fixed point decreases and the water content decreases. The reduction in pressure below the menisci is sufficient to suck the pendent branches in around the stem. At a later stage, imbricate leaves may be similarly sucked down onto one another. The distribution of spaces of different size is not constant therefore: as the water table is lowered the proportion of smaller spaces increases. From the point of view of water transport, a small but water-filled space is infinitely better than a larger empty one.

Another rather unexpected effect is that the whole carpet shrinks as the water table is lowered. For example, a cylindrical carpet of *S. papillosum* (30 cm diameter, 17 cm deep) was put on top of a membrane filter covering a water-filled space, so that water tensions of more than 17 cm could be applied (Hayward, 1980). As the water table was lowered from the surface (0 cm) to the equivalent of 30 cm deep so the 17 cm carpet shrunk by 2.5 cm to 14.5 cm. This effect was reversible and probably results from the replacement of water by air, so that the weight of water-filled *Sphagnum* is no longer supported by the water (just as one's weight increases on getting out of a bath). Capillary forces may contribute too. The movement is distinct from the bodily upward and downward floating movement of some peat systems with rainfall and evaporation (Green and Pearson, 1968).

In a *Sphagnum* carpet, the height of the water table at a particular time is determined by many processes: precipitation, evaporation, hydraulic conductivity in both vertical and horizontal directions. The flow of water through a mat of recently dead *Sphagnum* usually obeys Darcy's law (Fig. 8.24) though this is not true of more highly humified peat (Ingram *et al.*, 1974; Rycroft *et al.*, 1975). The consequent local variations in water level below hummocks, in lawns and in pools are complex (Goode, 1970; Boatman and Tomlinson, 1973; Hulme, 1976; Ingram, 1981; Bragg, unpublished). The vertical range of the water table level may be about 20 cm in an average year, but the water table may rise 5–10 cm within a few hours in some cases (see, for example, Tallis, 1973). The vertical range of water table amplitude below some hummocks is more than it is in pools, and the water table in hummocks may, at some times, be above that in adjacent pools and at other times below. Such temporal and spatial variations have obvious implications for the ecology of *Sphagnum* but cannot be pursued here.

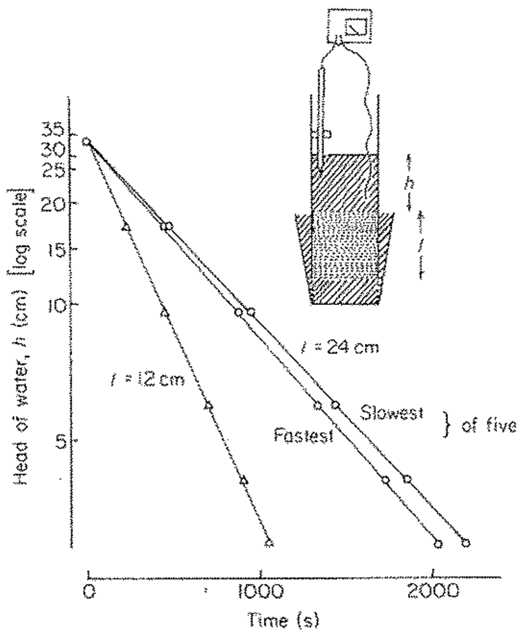

Fig. 8.24 Vertical hydraulic conductivity, K, of *S. fuscum* at Stordalen, Abisko, in Artic Sweden. A core, 20 cm diameter and 12 or 24 cm deep (from 3 cm below the capitula) was a tight fit in a plastic cylinder. The velocity with which water flowed through was recorded. The straight line on a plot of log (h) *vs* t shows that Darcy's law is obeyed. It can be shown that $\ln(h/h_0) = -K/lt$, and that $K = 0.693/t_{½}$ where $t_{½}$ is the time needed for the head of water to fall to half what it was. This gives $K = 0.035$ cm s^{-1}. Clymo (unpublished).

8.4.3 Effects of water supply on *Sphagnum*

It is convenient to recognize two ranges in the continuum of states; 'normal' conditions and 'exceptional' (or 'catastrophic') conditions. To be successful a plant must survive both. The commonest catastrophe for *Sphagnum* is desiccation. The effects of this under fairly natural conditions were studied in the desiccation experiments shown in Fig. 8.25, upper half. The results are shown as survival of 5 cm-long plants of different species drained of water and allowed to dry for different periods. Two interacting effects can be seen: the larger plants, such as *S. imbricatum* and *S. papillosum* survived relatively well, presumably because they held larger amounts of water. In *S. imbricatum* these water stores were not exhausted by the end of the experiment after 16 days but once the stores had gone from *S. papillosum* the plants died rapidly. Plants of the smaller species dried out early during the experiment. Of these, *S. fimbriatum* showed poor survival, but some plants of *S. capillifolium* survived even after 16 days, and plants with dead capitula produced many new lateral shoots from lower down the stem. The results of another experiment examining the inherent ability to resist low water potential are shown in Fig. 8.25 (lower half). This shows the survival of capitula of seven species which had reached equilibrium after 21 days with atmospheres of relative humidity corresponding to menisci of radius less than 1 μm (less than the hyaline pore sizes). A larger proportion of capitula remained green than were able to resume growth but the two measures gave parallel results. The ability to survive these treatments seems to be uncorrelated with capitulum size, pore size or ecological habitat: *S. auriculatum* survived desiccation best but normally grows immersed whilst *S. capillifolium*, which grows on hummocks, survived rather poorly. The most sensitive species was *S. papillosum*. But the conditions in this second experiment were very artificial: no air movement, continuous dim light and a temperature of 25°C. Desiccation resistance *per se* seems to have rather little part in determining which species can survive in which habitat. The rate of transport of water up from the water table is probably of greater importance.

Particularly puzzling is the ability of species such as *S. compactum* and, especially, the very delicate *S. tenellum* to survive and grow on wet heath. Both species are minor though widespread components of wet *Sphagnum* lawns, usually growing as isolated individuals amongst other species. On wet heath, however, they form tussocks or single-species carpets which may become dried out and even burned over during droughts.

The responses of *Sphagnum* to rare but extreme drought conditions (say once in 20 to 100 years) may be of importance but are poorly documented. Catastrophes of this kind are not usually predictable and long-term recording of detailed changes, though it would almost certainly be valuable, appears at any one time to be a time-consuming and risky venture.

The responses of *Sphagnum* to water supply in 'normal' conditions are equally important and experiments to measure the growth of *Sphagnum* in such conditions are less risky than long-term recording. Results of such work show that light flux is important too, and that water supply and light flux have interactive effects on *Sphagnum* growth. The experiments will therefore be considered in the next section.

It is worth commenting here, however, on the peculiar case of *S. imbricatum*. Records and studies of peat deposits show that this species was once widespread and, at least locally, abundant in the southern Pennines (Tallis, 1964). It seems to have declined in abundance from perhaps the fourteenth to early nineteenth century and is now absent from the southern Pennines altogether. Various possible causes have been suggested amongst which burning, grazing, draining and poisoning (by aerial pollutants) are the most often given. The species grows today in two sorts of habitats: in a compressed growth form on hummocks and (for example in western Ireland) as a lax growth form in wet *Sphagnum* carpets. This lax growth form is the one which is abundant in Pennine peat. The difference is not genetically determined but is a response to water supply conditions (Green, 1968). The rate of elongation of shoots is particularly sensitive to change in water potential, but there is no evidence that the species is particularly drought sensitive (Fig. 8.25); its occurrence on hummocks makes this unlikely anyway (though *S. capillifolium* appears to be desiccation-intolerant, yet grows on hummocks). Further, it is recorded that *S. imbricatum* has disappeared from undissected (and still very wet) peat bogs in the middle Pennines, just as it has from the southern Pennines (Tallis, 1964). The work of Ferguson and Lee (1979), 1980) already described, shows that *S. imbricatum* is usually sensitive to low concentration of HSO_3^-, and the reduction of its growth rate from this cause seems to be the most likely explanation for the disappearance of *S. imbricatum* from the industry-girt southern Pennines.

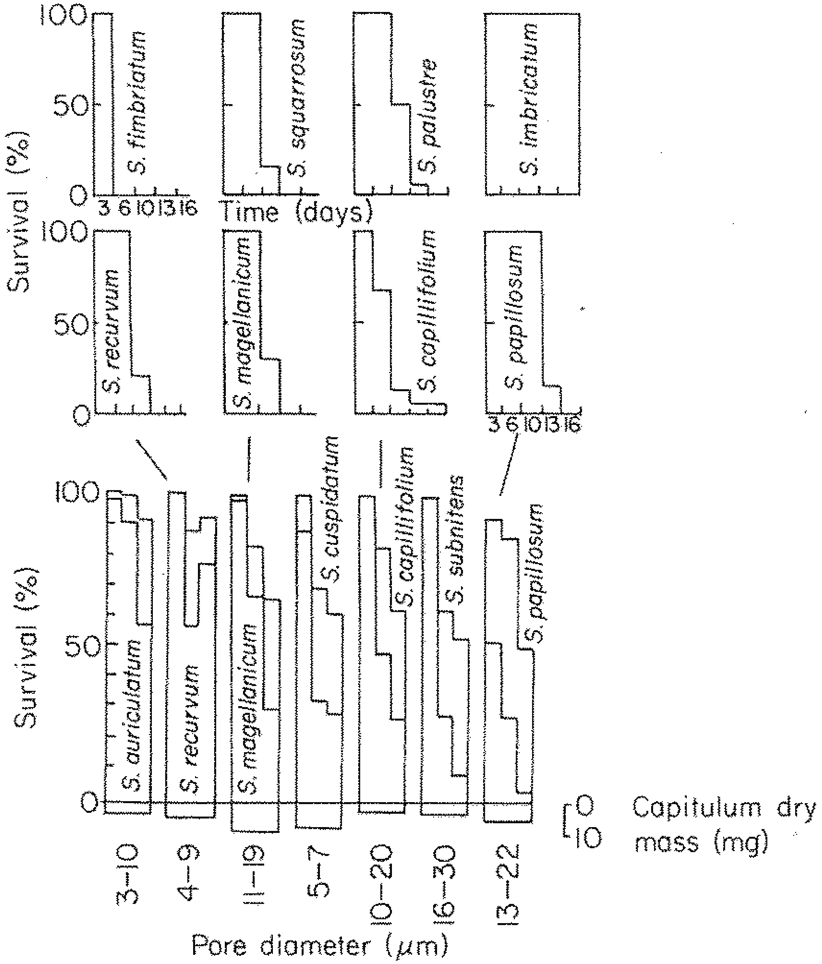

Fig. 8.25 Survival of *Sphagnum* spp. in desiccation experiments. Upper half: plants in beakers drained of water and allowed to dry for up to 16 days. Some plants were re-watered after 3, 6, 10, 13 or 16 days and the proportion resuming growth at the apex was recorded. Lower half: capitula put in closed containers, with humidity kept constant by sulphuric acid solutions (Hodgman *et al.*, 1961), and kept in dim light for 21 days. After this the capitula were kept on damp filter paper in the light for a futher 21 days. Humidity (left to right): 0.998, 0.991, 0.981. Upper histograms are proportion of capitula with branches remaining green; lower are proportion showing new growth. Below the axis are histograms of capitulum size, and the size of pores in leaves. Lines join species common to the two experiments. Redrawn from Green (1968) and Clymo (1973), and from Hill (1978).

8.5 THE GROWTH OF *SPHAGNUM*

8.5.1 The growth of individuals and populations

In some species there is a marked annual variation in the length of branches and in their density on the stem (Malmer, 1962b). In *S. papillosum,* the branches formed during winter are relatively short and the internodes are also short. In early summer, there is a sharp change to longer branches and longer internodes followed by a gradual reduction in shoot- and internode-length in late summer and winter. Such a cyclic pattern of growth may be seen in other species too, but it is more often absent than present and it is not obvious in Fig. 8.1 for example. Both branch and internode length can be markedly affected by water supply in experimental conditions (Fig. 8.26) but, in the field, the variation during a year is not necessarily, or even probably, related primarily to water supply. In vascular plants, the length of internodes is linked with factors such as plant hormones, temperature, and the balance between red and far-red irradiation.

The same factors are often involved in the development of red pigments, so it is of interest to note that *S. magellanicum*, for example, is often apple green in early summer (and remains so all the year round in shade) but produces a wine-red pigment later in the year. Production of red pigment can be induced by low temperature (Rudolph, 1978). The same is true of *S. capillifolium.* In this species the pigment forms not only in the leaves but also in the stem. The stem can be seen to have annual bands consisting of a green section, formed in early summer, through a transition zone to a deep red section formed in late summer. The boundary between dark red and apple green is often very abrupt, just as the winter–summer transition in branch pattern is sharp. The red pigment is related to the anthocyanins but is unusual in being firmly attached to the cell wall (Goodman and Paton, 1954; Rudolph, 1964, 1968; Paton and Goodman, 1955; Bendz *et al.*, 1966). Different species produce a variety of other pigments: *S. fuscum* and some forms of *S. recurvum* are well known for their brown colouration. *Sphagnum subnitens* has an irridescent blue sheen when dry, but not when wet. This has been shown to result from thin-film interference (Morris, 1977) – an unusual phenomenon in plants. In all cases the pigment-produced colours are at their best in late summer, when, as Braithwaite (1880) observes: 'Few persons can have traversed our moorlands without having had their attention attracted to the great masses of *Sphagnum* which adorn their surface – now in dense cushions of lively red – now covering some shallow pool with a vast sheet of light green, inviting it may be by its bright colour, but woe betide the inexperienced collector who sets foot thereon, for the spongy mass may be many feet in depth, and he may run the chance of never reaching *terra firma* again.'

Growth hormones are also probably involved in the peculiar growth of *S. recurvum* (Overbeck and Happach, 1956). This species has many growth forms. One is commonly found where the water is flowing past the plants in spring mires, in the channels in eroded peat, on flushed hillsides and so on. The plants in such habitats have stems which are mostly horizontal, and may be traced back for 30 to 60 cm or more to the point where they have

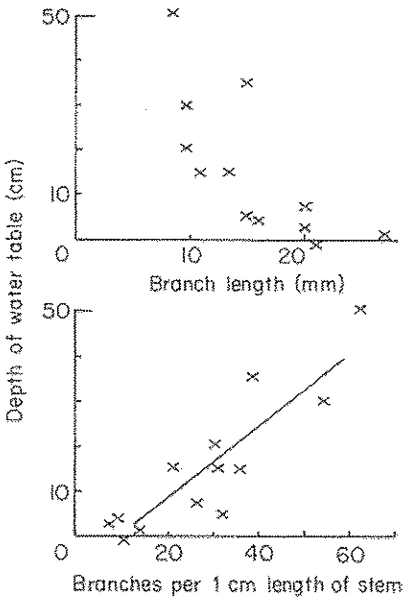

Fig. 8.26 Effect of water table depth on the morphology of *S. imbricatum*. The plants were grown in beakers with controlled water table. Redrawn from Green (1968).

decayed. The stems lie in a thick mat on top of one another but the capitula, which are often a bright and inviting green, are densely packed in the usual upright position with the stem immediately below them standing vertically. About a centimetre below the capitulum the stem turns through 90° to run horizontally. As the capitulum grows on, extruding more stem and branch behind it, the position of the bend in the stem moves too. This series of growth movements appears to be controlled by starch statoliths (Bismarck, 1959) which form in the tissue just behind the stem apex. A similar but less obvious pattern of growth is seen in *S. cuspidatum*. Both this species and *S. recurvum* have juicy brittle stems, which crack across very easily and seem to have high turgor. Most other species have tougher stems.

Again, by analogy with vascular plants, it seems likely that fruiting is controlled by hormones, day length, and perhaps by the balance of red and far-red light. *S. subnitens* is reported to be a short-day species (Benson-Evans, 1964), but capsules appear on different species at different times. For example, *S. tenellum* has abundant capsules in early May almost every year around the margins of southern English valley bogs, though *S. papillosum* a few metres away more often produces capsules in June or July.

The pattern of branch formation varies, and so does the frequency with which the capitulum divides (forks) to form two separate stems. The

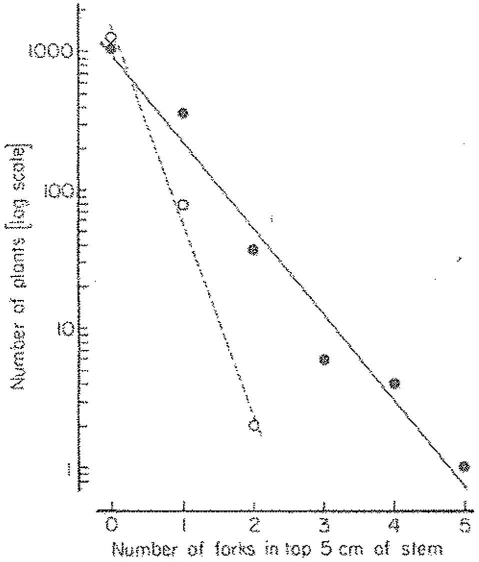

Fig. 8.27 Frequency of forking of the main stem in the top 5 cm of *S. papillosum* in relation to spatial density. Symbols: O, at Moor House, northern England; ●, at Thursley Common, southern England. Redrawn from Hayward (1980).

number of plants with 0, 1, 2 etc. forks for two populations of *S. papillosum* is shown in Fig. 8.27. The relationship is

$$\log (n/n_0) = -kf$$

where n is the number of plants, n_0 the number of unforked plants, and f the number of forks. The slope, k, is a measure of the probability that a plant will fork. Casual observation suggests that large capitula are the most likely to fork and that k is largest for populations that appear to be colonizing or invading a new area. The straight line implies that the probability that a plant will fork is independent of whether it has forked already or not.

The daughter apices produced by forking are each smaller than the parent. By the time the leaves on their branches have died the daughter plants are, for most functions, independent. A carpet of *Sphagnum* may thus contain several genets each represented by several ramets. It would be interesting to know how many of each there are in a *Sphagnum* carpet. Detailed recording over many years, or isoenzyme studies might provide the answer. A genet with recognizably distinct characters would give a partial answer. No such observations have been reported however.

Individuals of the same species growing together differ considerably in size, as do the different parts of the plants. Some of these differences may be related to local water supply and to spatial density of plants. Fig. 8.28 shows, for *S. papillosum*, the mass per plant per 1 cm-depth as an indication of size. The samples chosen were taken from sites over the full range of water table depth, and were collected on a single day during a dry period, so the water table depth is probably a useful indicator of the relative water supply to the different populations. The spatial density of plants shows a maximum (about 180 dm^{-2}) falling to about 130 dm^{-2} on the drier side and to about 80 dm^{-2} for an immersed population. In all but one population the average mass (per cm) of capitulum is greater than that of the product (stem plus branches) which it produces. This is simply a result of stem internode elongation. The exception (population D) had very densely packed branches, but population E, with a similar water table and spatial density, had much laxer growth. Most populations showed rather skewed distributions of individual plant size, generally with a tail of larger sizes, but the degree of skewness differed considerably. This phenomenon is now well known in vascular plant populations (for example, Bazzaz and Harper, 1976). There is clearly a lot more to be discovered about the factors which control size of *Sphagnum* plants, and the spatial arrangement of plants of different size has not been investigated at all.

The bulk density of capitula and of their product (stem plus branches) seems to be rather uniform over a range of densities and water tables, though the product of population D and both capitula and product of

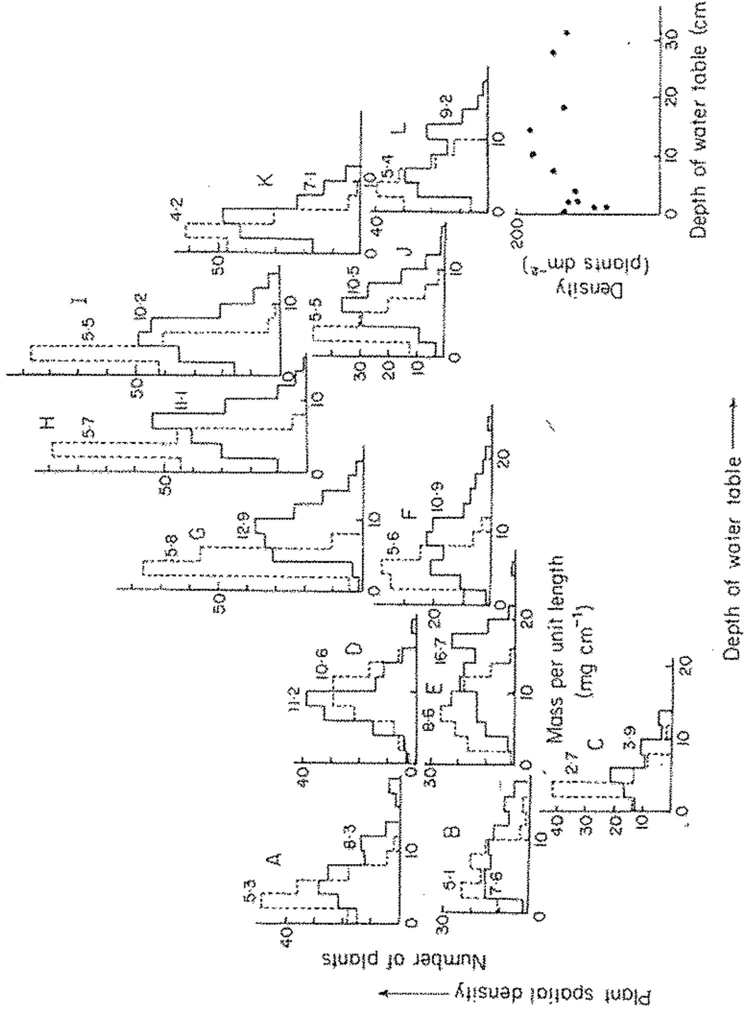

Fig. 8.28 Distribution of size of capitulum (0–1 cm, full lines) and of the top 5 cm of plant (broken lines) in twelve populations of *S. papillosum* at Moor House, northern England. Numerical values are bulk density (mg cm^{-3}). The histograms are arranged approximately in relation to spatial density and the depth of the water table on the day of collection (which was in a dry period). The detailed relationship is at the lower right. Hayward (unpublished).

population E seem to be exceptional. A wider range of results is shown in Fig. 8.29. The populations sampled were all from the centre of their range of normal occurrence. It appears that the bulk density of capitula of plants growing anywhere other than in immersed habitats is nearly constant whatever the species: high density compensates for small individual size. (The estimates for capitula in Fig. 8.29 are rather larger than the central ones in Fig. 8.28, probably because the definition of 1 cm of capitulum is an operational one and depends on how hard the capitulum is pressed against the end of the cutting board). There is much greater variation, for a single species, in the bulk density of product, however, which may be related to the species' response to environmental forces. The species differ too. Clearly, the structure of the individual plants can itself modify the environment to which the branches are exposed, and this effect is now considered.

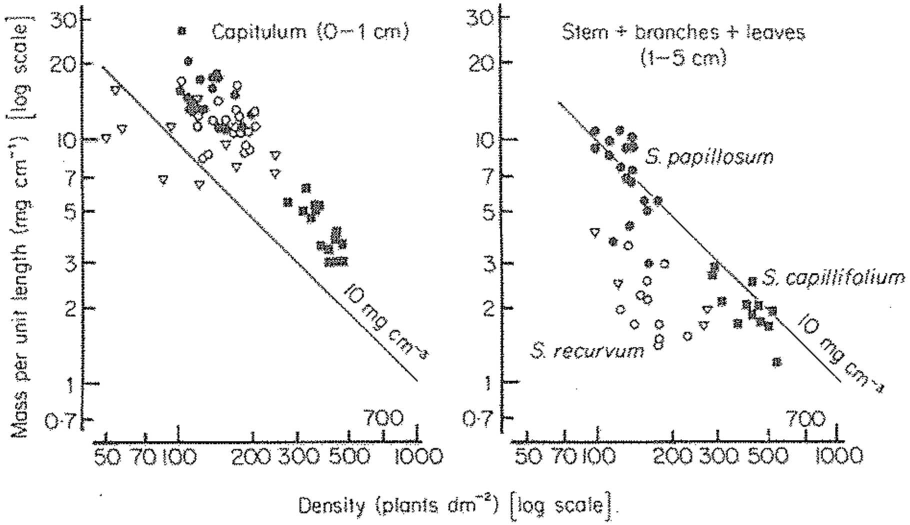

Fig. 8.29 Relationship between spatial density and individual size for capitula (0–1 cm) and stem plus branches (1–4 cm) of *Sphagnum* spp. from various sites in all of which the plants seemed to be growing well. Symbols: ■, *S. capillifolium*; ●, *S. papillosum*; △, *S. cuspidatum*; ○, *S. recurvum*. Redrawn from Clymo (1970).

8.5.2 Physical environment in a *Sphagnum* carpet

The way in which *Sphagnum* affects water supply and potential has already been considered. The plants themselves also affect the light and temperature microclimates.

The light climate in a *Sphagnum* carpet is shown in Fig. 8.30. The semi-logarithmic plot should give a straight line if Beer's law is obeyed. On the whole the results are quite close to a straight line, but they pass through 40–60% transmission at the surface, rather than the expected 100%. There are several possible explanations for this. Definition of the surface is rather arbitrary because the capitula are not flat either individually or *en masse*. An error of only 3 mm would account for most of the difference. Where light has passed through only a few mm of *Sphagnum* canopy then there may be 'light fleck' effects which are less common lower down. The depth would be better measured in units of cumulative mass below the surface because it is the matter which is absorbing and reflecting light. The effects of this are also shown in Fig. 8.30. Some of the surface anomaly is thus accounted for, but not all. The depth of the euphotic zone (within which all but 1% of the incident light is absorbed) is about 1–2 cm in unshaded stands of both *S. papillosum* and *S. capillifolium* and 4–5 cm in the lax growth of shaded stands. Much the same is true in both natural conditions and in

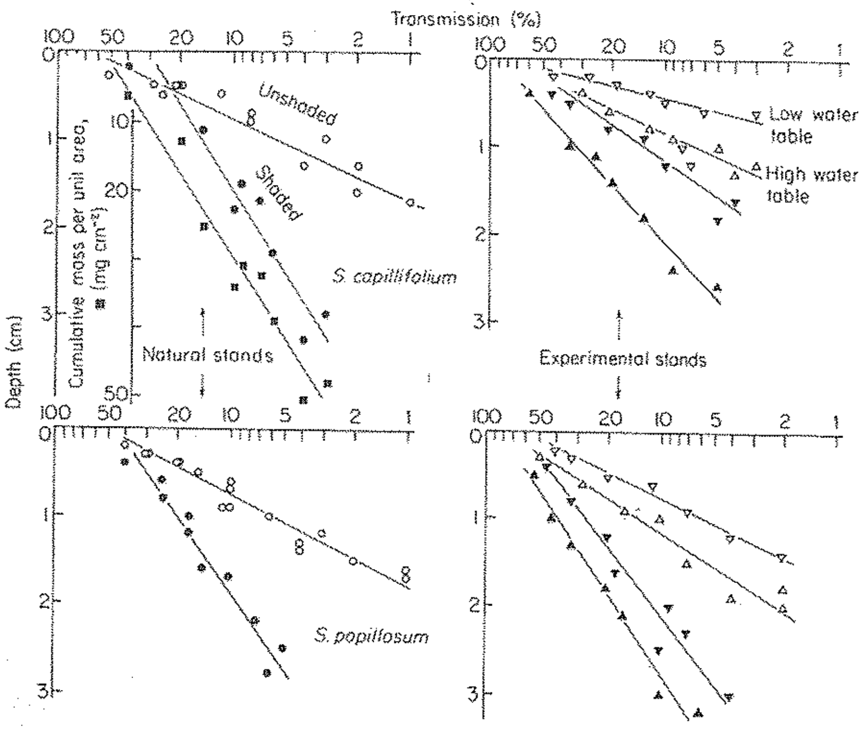

Fig. 8.30 The attenuation of light in carpets of *S. capillifolium* (upper) and *S. papillosum* (lower) both in natural stands (left), and in stands grown with controlled water table and shade in 50 cm-diameter experimental containers (right). Open symbols, unshaded; filled symbols, shaded. The results for the shaded natural stand of *S. capillifolium* are plotted again with depth measured by cumulative mass (squares, top left). Redrawn from Hayward (1980).

experiments. The latter show that the euphotic zone is deeper when the water table is high than when it is low. Again, the growth form of the plants is probably the main cause.

The temperature climate of *Sphagnum* carpets varies in a complex way. Some of these variations are shown in Fig. 8.31, which shows measurements made over five fairly fine days at the end of May and beginning of June. The second, fourth and fifth days had intermittent cloud, and about 6 mm of rain fell on the fifth day. The daily range in air temperature (at 152 cm height) was about 15°C. The temperature about 5 mm below the capitula of a *S. papillosum* carpet was consistently higher than the air temperature except for 2–3 hours just after sunrise; water has a large thermal capacity. By noon the *Sphagnum* temperature was 20–25°C which was about 5°C warmer than the air temperature on sunny days, but little different on the cloudy fourth day. The daily amplitude of *Sphagnum* temperature was about 20°C. Deeper down the temperature fluctuated less. At 5 cm below the surface the temperature oscillations were damped to about 6°C amplitude, lagging 2–3 hours, and with a slower fall than rise; at 29 cm deep the daily fluctuation was less than 0.5°C, but the temperature did rise steadily by 2°C during five days. The reduced amplitude and lag are well known, and from them the thermal diffusivity of the surface layers can be estimated (very approximately). There are distinct differences in the thermal regime in different bog habitats. For example, *S. cuspidatum* in pools warms surprisingly rapidly and on sunny days is about 2°C warmer by noon than is *S. papillosum* and remains so until the early hours of the morning. The north face of a *S. capillifolium* hummock warmed more quickly on a sunny morning than did *S. papillosum* in the early morning and the south-west face of the hummock warmed more slowly. By mid-morning, however, the north face of the hummock was about 5°C cooler than was *S. papillosum*, whilst by noon the hottest place was the south-west face of the hummock. Rain on the fifth day – a heavy shower – reduced the temperature of all habitats by about 7°C.

The temperatures shown in Fig. 8.31 were measured with thermistors shaded from direct radiation if in the air, and not visible from above if just below the capitulum of the plants. The true surface temperature however is probably considerably higher. An infra-red thermometer is necessary for accurate measurements. Values in *S. capillifolium* consistently above 40°C during the greater part of the day have been recorded, during drought, at a site close to that where the measurements for Fig. 8.31 were made (Tattersfield, 1976). The plants were not permanently damaged.

The following points seem clear: *Sphagnum* must tolerate quite high temperatures during summer; it must cope with a fairly large daily fluctuation of temperature; hummock species are exposed to a greater range of temperature than are other species; and, rather surprisingly, lawn

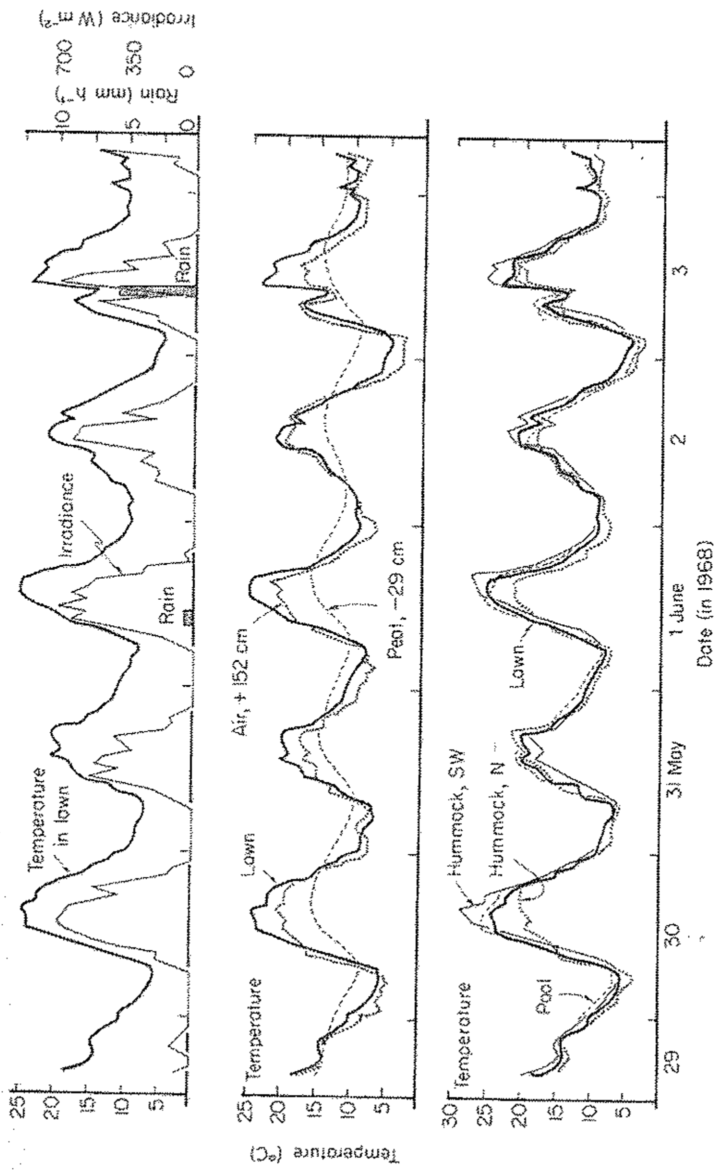

Fig. 8.31 Course, on blanket bog at Moor House, northern England, during 5 days in summer 1968, of irradiance, of rainfall, and of temperature just below the surface of a *S. papillosum* lawn (upper graph), of temperature 15 cm above the surface, just below the surface of a *S. papillosum* lawn, 5 cm below and 29 cm below (centre graph), and of temperature just below the surface of *S. cuspidatum* in a pool, of *S. papillosum* in a lawn, and of *S. capillifolium* on the north face of a hummock and on the southwest face of the same hummock (lower graph). (The *S. papillosum* lawn temperature is repeated to provide a reference trace). Records were made once an hour for 5 s: the irradiance record is therefore rather noisy. Above-ground thermistors were shaded. Those at the surface were horizontal and just sufficiently far below the capitula to be not visible – usually about 3 mm deep. Clymo (unpublished).

species such as *S. papillosum* appear to be exposed to the smallest range of temperature (in sunny weather at least).

There are important features of the regimes in other seasons too (Popp, 1962). In the spring and autumn the bog surface temperature may be high enough to permit active growth for a few hours each day when air or peat temperature, or both, are too low to allow growth of vascular plants.

8.5.3 Growth in relation to shade and water supply

The most detailed experiments are those of Hayward (1980). For *S. capillifolium*, *S. papillosum*, and *S. recurvum* grown in a factorial design with the water table at 0, 3, 6, 10 or 14 cm below the capitula, and with 0, 0.54, 0.80, 0.91, and 0.96 shading (using 0–5 layers of black nylon gauze), there were marked effects associated with species, water table level and shade. For dry matter increase there were no significant interactions, so the effects are summarized in Table 8.3. Water level had little effect, shading reduced growth and there were specific differences associated with plant size. None of these effects is surprising, and they agree in general with the results of other less detailed experiments (Clymo, 1973). For growth in length, however, there were highly significant interactions, individual species behaving differently in response to shade, and to a lesser extent, in response to water level (Fig. 8.32). In unshaded conditions, water level had a large effect on elongation of *S. capillifolium* and *S. recurvum* but not of *S. papillosum*. All three species have an 'optimum' shade, and for *S. papillosum* (but not *S. capillifolium*) a fall in the water table reduces the elongation at the shade optimum. These results are again consistent with those of Clymo (1973). The results of experiments in arctic Sweden are also consistent. *Sphagnum riparium* was grown in differing degrees of shade in natural conditions (Sonesson *et al.*, 1980) and the elongation of the plants

Table 8.3 Main effects of shading and of water-table depth on the growth of three species of *Sphagnum*. The experimental design was factorial (5×5×3) and a log transform was used to remove the dependence of error on treatment effect. There were no significant interactions between treatments for growth in mass, but, for growth in length, there were very highly significant interations ($P < 0.001$) between species and shade, and between species and water-table level. These are shown in Fig. 8.32. Water-table depth had little effect on growth in mass. From Hayward (1980).

	Growth in mass		Growth in length (cm)
	per plant (mg)	per unit of stem (mg(mg cm^{-1})$^{-1}$)*	
Species	$P < 0.001$	$P < 0.001$	$P < 0.001$
S. capillifolium	3.0	6.2	2.7
S. papillosum	8.5	7.3	2.6
S. recurvum	6.2	13.1	4.9
Shade (proportion of full light absorbed)	$P < 0.001$	$P < 0.001$	$P < 0.001$
0.0	9.2	14.4	2.2
0.54	7.4	12.0	4.0
0.80	5.8	8.1	4.4
0.91	4.0	6.5	3.9
0.96	2.9	4.7	2.5
Water table depth (cm)	$P < 0.05$	$P < 0.05$	$P < 0.001$
0	4.8	7.6	4.2
3	5.4	8.7	4.4
6	5.4	8.4	3.3
10	5.9	9.1	2.7
14	5.6	8.4	2.3

---

*This measure attempts to make allowance for the difference in size between species by using the mass of a unit length of stem for comparison.

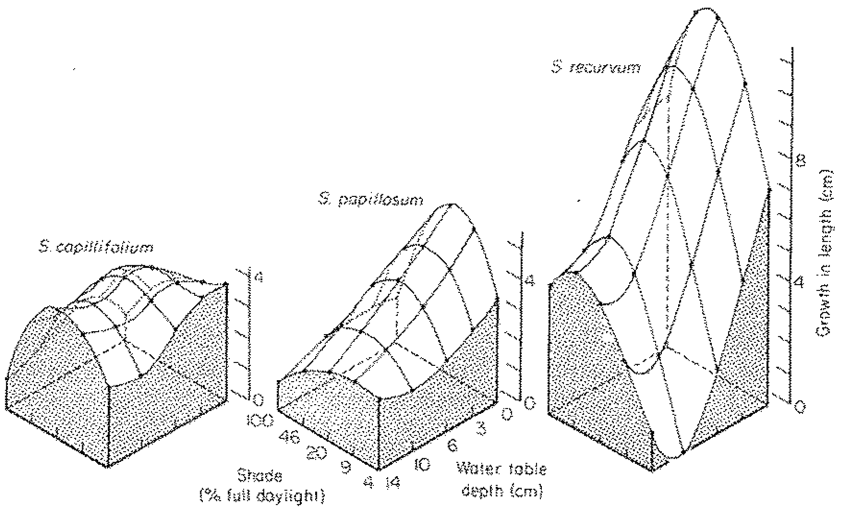

Fig. 8.32 Growth in length of three species of *Sphagnum* in experiments with constant water table and shade. The shapes shown are the least squares fit of the cubic:

$$L = a + bW + cA + dW^2 + eA^2 + fWA + gW^3 + hA^3 + iW^2A + jWA^2$$

where L = growth in length, W = depth to the water table, A = absorbance of the nylon net used for shading, and a to j are parameters. The underlying shapes are not so easy to see in the original results, in which 'noise' is added to the undulating surface but analysis of variance shows highly significant effects of all three main treatments and first order interactions. Redrawn from Hayward (1980).

measured, though the growth in mass was, unavoidably, not measured. The control of growth in length of *Sphagnum* is obviously not simple, and different species differ in their behaviour. The association of red pigments with unshaded, unetiolated, plants has been mentioned.

A prediction can be made on the basis of the experimental results (Clymo, 1973; Hayward, 1980): the roughness or irregularity of a carpet of *Sphagnum* will be smaller the lower the water table is. Figure 8.33 shows that this is indeed observed, as it is too in experiments with controlled water table (Hayward, 1980).

The effects of water table depth in natural conditions are shown in Fig. 8.34. Batches of similar plants of four species were transplanted to pools, lawns or hummocks. Of particular interest is the observation that *S. capillifolium* which normally grows on hummocks, grew best in pools, but it out-grew *other* species on hummocks. All four species grew better than other species in that habitat in which they are usually found. This emphasizes that relative performance and interspecific competition are probably important in field conditions – a point which is often assumed but less often demonstrated – and that the results of laboratory experiments which have not been confirmed by field experiments must be treated with caution.

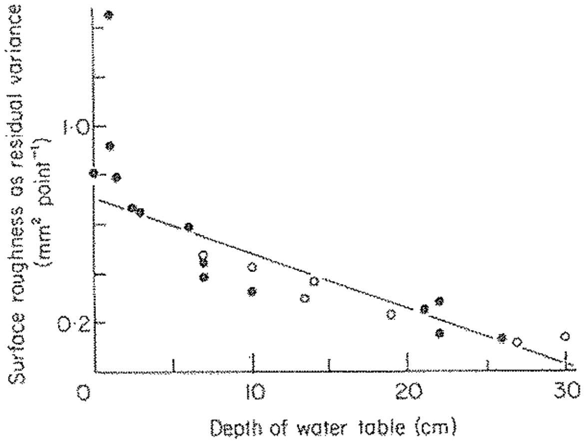

Fig. 8.33 Roughness of the surface of *S. papillosum* lawns in relation to water table depth measured after several days without rain. Open symbols, at the Silver Flowe, southern Scotland; filled symbols, at Moor House, northern England. Roughness is the residual variance in height of a grid of 4×8 light pointers (10 cm lengths of culms of *Deschampsia caespitosa*), 0.8 cm apart, after allowing for larger scale curvature of the surface by fitting,

$$H = a + bX + cY + dX^2 + eY^2 + fXY$$

where H is the height of the pointer, X and Y the grid co-ordinates, and a to f are parameters. The point at (1, 1.45) was excluded from the linear regression shown. Redrawn from Hayward (1980).

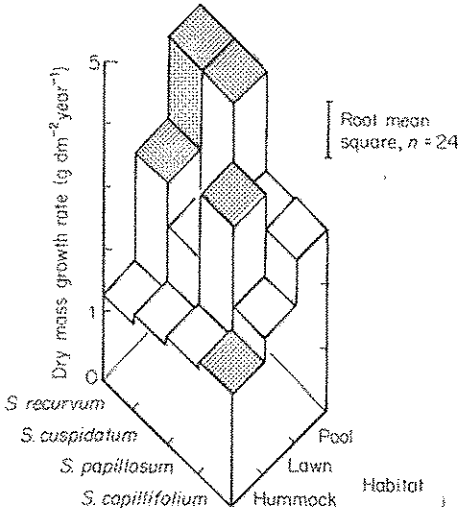

Fig. 8.34 Growth of four species of *Sphagnum* in three habitats at Moor House, northern England. The plants, cut to 5 cm long, were transplanted in groups and allowed to grow for 12 months. Stippling shows natural habitat. Redrawn from Clymo and Reddaway (1971).

It seems that specific structural differences are sufficient, acting through control of the water supply, to affect the growth of the individual plants, and that the habitat preferences of different species may be determined mainly by competitive growth during 'normal' conditions, sharpened by selective survival of some plants during drought. Nothing in the detailed ecology of the species encourages the view that there is likely to be a hummock and hollow cyclic succession (Tansley, 1939; Watt, 1947), but nor can widespread synchronous changes (Walker and Walker, 1961) involving the extension or contraction of carpets of a particular species be explained either. Climatic change still seems the most likely cause of such changes.

8.5.4 Productivity

Accurate measurement of productivity is not easy. The methods causing least disturbance to the intact *Sphagnum* make use of the carpet plant's innate pattern of branch density (Malmer, 1962b) or utilize some sort of external marker such as vertical wires. More disturbance is caused by removing plants, cutting them to known length, and replacing them (Clymo, 1970) or by marking them with thread (Overbeck and Happach, 1956) though these methods do allow transplant experiments to be made. It may be necessary to use a method which allows for that part of the capitulum carried up passively by internode elongation; for the different size of individual plants; and, in the measurements of growth in length, for the average bulk density of the stem-plus-branch product produced by the capitulum factory (Clymo, 1970). The method using vertical wires has been refined by Sonesson (personal communication) to the point where the standard deviation of replicate measurements of length in the field is less than 0.3 mm.

Estimates of productivity of fairly continuous carpets of *Sphagnum* seem generally to be in the range 100–600 g m^{-2} year^{-1}. On British blanket bog, productivity (g m^{-2} year^{-1}) of 150 (hummocks), 500 (lawns) and 800 (pools) has been recorded (Clymo, 1970; Clymo and Reddaway, 1974; Smith and Forrest, 1978). The high value for pools is largely because *S. cuspidatum* seems to continue to grow throughout most of the year, whilst growth in the other habitats stops in winter. Similar values (100–600 g m^{-2} year^{-1}) are reported for the drier hummocks and wet depressions of Stordalen mire near Abisko in arctic Sweden (Sonesson, 1973) and in Finland (Pakarinen, 1978a). The arctic values are the more remarkable because the summer there is short, and the average temperature over the whole year is little above 0°C. The rate of growth in wet habitats during the few weeks of continuous light in midsummer is remarkably high: the linear growth rate of *S. riparium* is about 1 cm week^{-1} (Sonesson *et al.*, 1980), corresponding to an instantaneous rate of about 2500 g m^{-2} year^{-1}. Of course, this high rate is sustained for a brief period only, and presumably, there is no growth at all during the long arctic winter.

8.5.5 Rate of photosynthesis and respiration

It is likely that the rate of photosynthesis and respiration by a given branch of a particular species of *Sphagnum* will depend on the light flux, temperature, water content and history of the branch at least. The earliest measurements for *Sphagnum* are those of Stålfelt (1938). He showed that *S. girgensohnii* was light-saturated at about 20% of full summer midday light flux, and that in these conditions assimilation was maximal at 18°C. Nowadays these measurements would be considered to be technically crude, and Stålfelt gives no indication of the plant's water content or history. More recently, Grace (1970) examined rates of photosynthesis and respiration in *S. capillifolium* in relation to light flux, temperature and water content in laboratory experiments in which he measured the change in CO_2 concentration of a gas stream passing over the plants. He found that the rates varied greatly from one experiment to the next. If plants were allowed to dry out slowly then the rate of photosynthesis was greatest at a water content of about 10 g g^{-1}. At water content above that value it declined slowly, presumably as a result of longer diffusion paths for CO_2, as found for other bryophytes (Tallis, 1959; Willis, 1964). In drier conditions, the rate declined abruptly as the hyaline cells emptied (Fig. 8.35). It is of interest that this threshold value of water content is just that most often found in natural conditions (see Fig. 8.20). It is not clear how far the rapid decline as the water content dropped below 10 g g^{-1} was a result of reduced water content *per se* or of a lowered water potential. Grace (1970) showed that neither the temperature of storage, for up to one month, nor the time of year at which measurements were made, had much effect on the relationship of rate of photosynthesis with light flux or temperature. One set of results is shown in Fig. 8.36. The water content in these experiments was greater than 10 g g^{-1}. There is some indication of light saturation at the highest light flux used (about half that of full summer midday values), but it is much less clear than in Stålfelt's experiments with *S. girgensohnii*. The photosynthesis rate, at moderate to high light fluxes, increases with temperature up to 27°C at least. This may be important in the field, because the temperature on *Sphagnum* hummocks is often above this, as already described. The compensation point increases as temperature does: dark respiration rate increases approximately exponentially with temperature (Grace, 1970) and it seems likely that the temperature optimum for photosynthesis is lower than that for respiration, as it is in so many plants, though there is no published direct experimental evidence of this in *Sphagnum*.

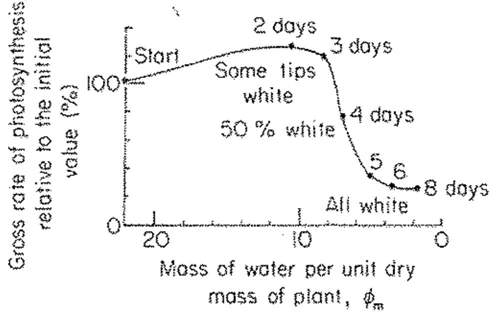

Fig. 8.35 Rate of gross photosynthesis (relative units) of *S. capillifolium* in relation to water content. The plants were allowed to dry during the experiment, so water content is confounded with history, as it is in the field. Redrawn from Grace (1970).

Complementing these laboratory experiments are two sets of field measurements. Johansson and Linder (1980), working in arctic Sweden, used the rate of incorporation of ^{14}C to measure the net rate of photosynthesis of *S. fuscum* (a hummock species) and *S. balticum* (a species of wetter habitats, similar to *S. recurvum*). Their experimental plants were in unnatural conditions to the extent that the plants were removed from the carpet and enclosed at near-natural spatial density in an experimental chamber. They relied on changing climatic conditions to create natural experiments. In practice, only a limited range of *combinations* of light flux and temperature were observed and the effects of these are confounded. Nor did they record the water content, though Grace's results suggest that this may be of less importance in natural conditions than might have been expected. The response to light flux is shown in Fig. 8.37, which includes measurements made with temperature between 10 and 20°C. The rate of photosynthesis is much the same as that of *S. capillifolium* at the same light flux, and with the same variability. The rate for *S. balticum* is perhaps rather higher than that for *S. fuscum*. Both

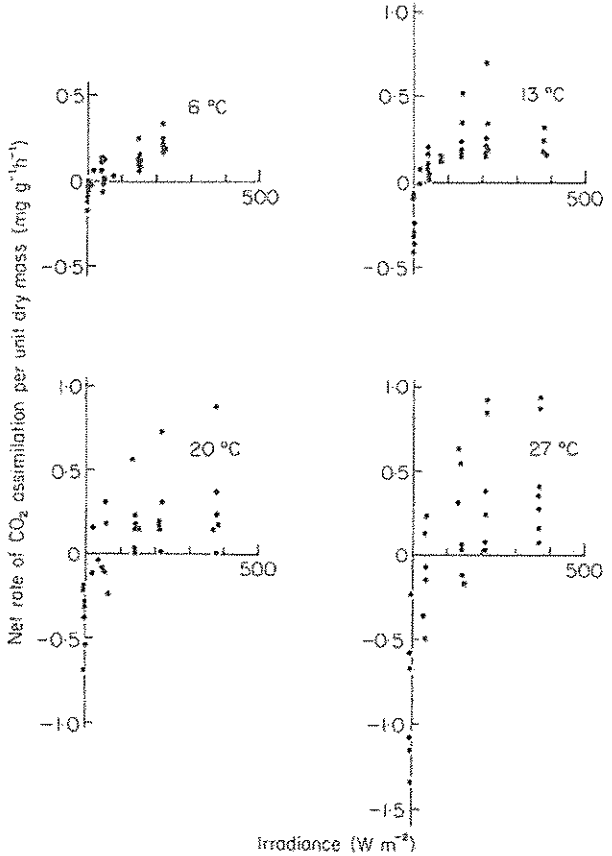

Fig. 8.36 Rate of net photosynthesis of *S. capillifolium* in relation to irradiant flux and temperature. The plants were in a container through which a stream of air passed. The rate of photosynthesis was calculated using the change in CO_2 concentration of the gas stream. The light source was artificial. Redrawn from Grace (1970).

show signs of becoming light-saturated at the highest irradiance, but the hyperbola of best fit for *S. balticum* gives a saturation asymptote for photosynthetic rate (as CO_2 per unit time per unit dry mass of plant) of 1.2 mg g^{-1}, h^{-1}, and half-saturation at a light flux of 300 W m^{-2}. The daily

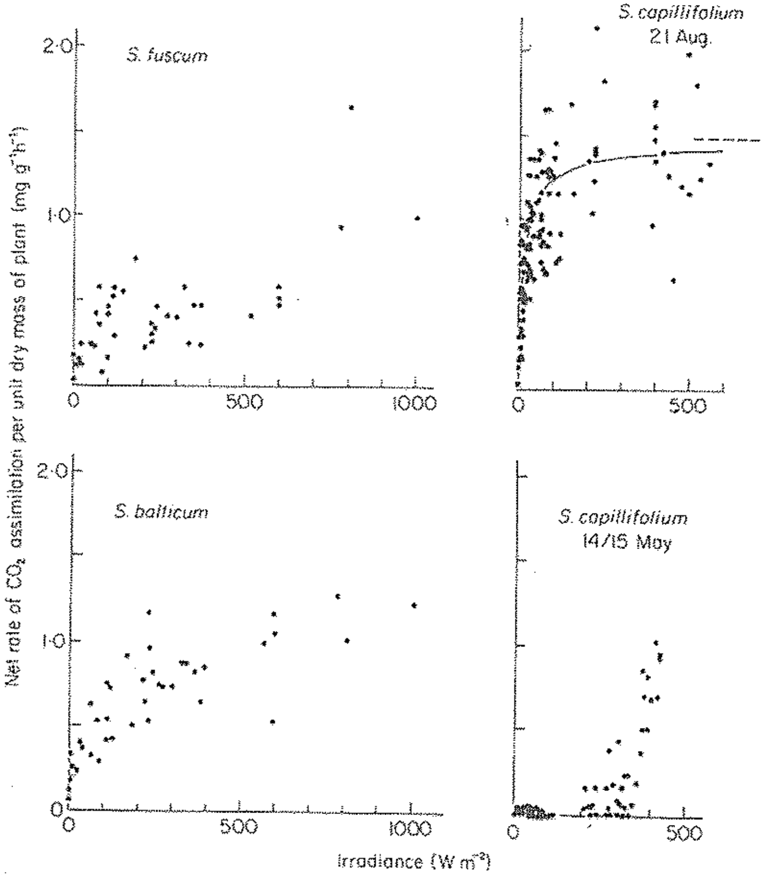

Fig. 8.37 Rate of assimilation of $^{14}CO_2$ by *S. fuscum* and *S. balticum* throughout the growing season at Stordalen, Abisko, arctic Sweden and of *S. capillifolium* at Moor House, northern England on two single days. The hyperbola of best fit is shown for one day; broken line is asymptote. Capitula of the plants (top 1 cm for *S. capillifolium*) were put in experimental chambers in the field and measurements made at the prevailing temperature and water content (10–20°C in the Swedish plants, values shown in Fig. 8.39 for the British plants). The original values for *S. capillifolium* are per unit area of carpet, and light flux was measured as quantum flux. To allow comparisons to be made it has been assumed that the capitula have a bulk density of 20 mg cm^{-3} (Fig. 8.29) and that on average 1 W = 4.15 μmol s^{-1}. The results for 14–15 May 1980 are exceptional, being taken when the plants were unusually dry (Fig. 8.39). Redrawn from Johansson and Linder (1980) and from S. Daggitt (unpublished).

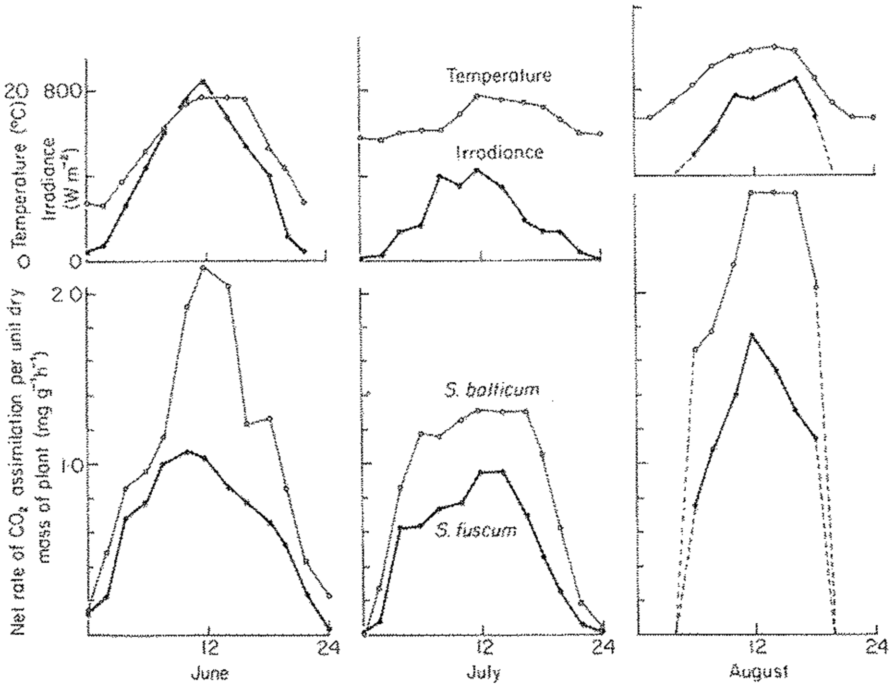

Fig. 8.38 Course of irradiance, temperature, and the rate of CO_2 assimilation by *S. fuscum* and *S. balticum* on three days during the growing season at Stordalen, Abisko, arctic Sweden. Redrawn from Johansson and Linder (1980).

course of photosynthetic rate is shown in Fig. 8.38. Differences between species are not easy to interpret, because the sampling method was necessarily destructive, and because the proportion of photosynthetic machinery is not necessarily closely related to dry mass: one species may, for a given cell volume, have thicker walls and this would make it appear to be less efficient. This may be one cause of variability between plants too. There is need for an investigation of the best basis for comparisons. The higher rates in August, when temperature was relatively low, than in June or July may be because the rate of respiration is proportionately lower than is the rate of gross photosynthesis.

The other set of field measurements were made by Daggitt (unpublished) working on *S. capillifolium* at Moor House, northern England. He too removed capitula (the top 1 cm) of plants, packed them at natural density in an experimental chamber, and measured the incorporation of ^{14}C using a method which gives a result somewhere between gross and net photosynthesis. Some of his results are shown in Fig. 8.37. Those for 21 August, typical of most days, again show considerable scatter but a tendency to saturate. The hyperbola (maximum likelihood fit)

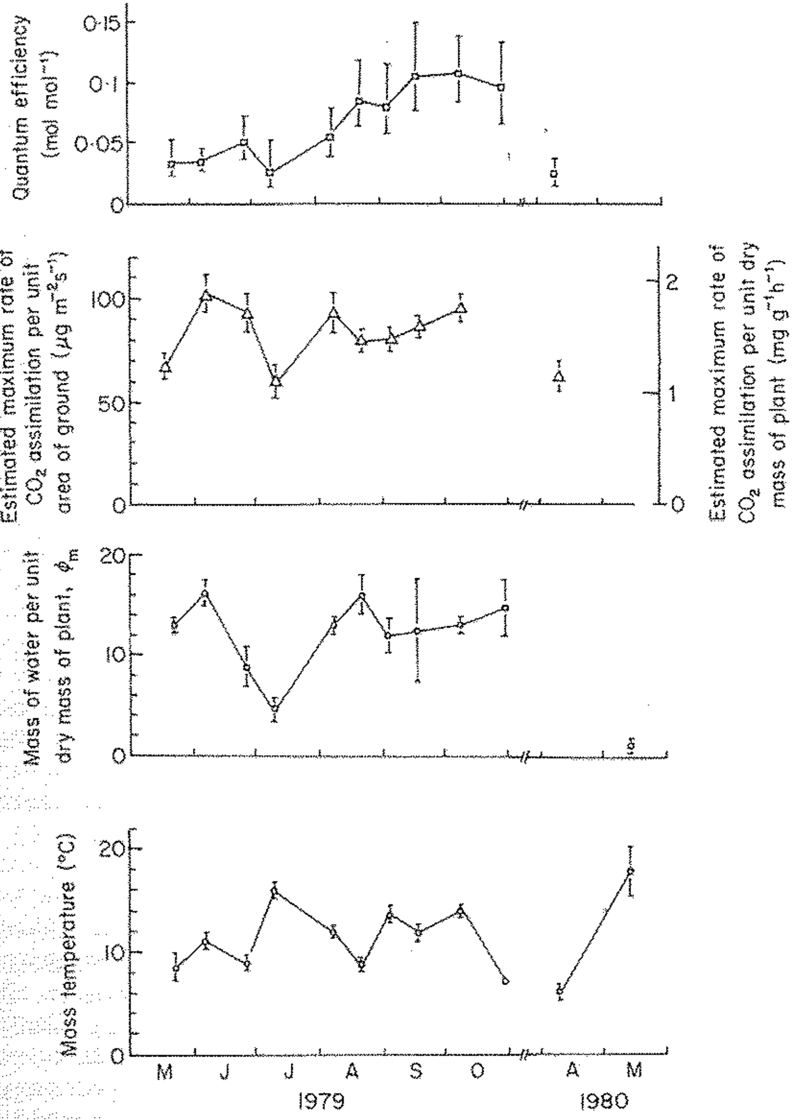

Fig. 8.39 Seasonal course for *S. capillifolium* at Moor House, northern England, of quantum efficiency (the slope of the maximum likelihood hyperbola, Fig. 8.37, at zero light flux), of maximum rate of photosynthesis (the asymptote of the maximum likelihood hyperbola, Fig. 8.37), of capitulum water content, and of mean temperature in the *Sphagnum* capitula during the day of measurements. (For much of the time the temperature was above the mean). From S. Daggitt (unpublished).

has an asymptote, of about 1.4 mg g^{-1} h^{-1}, similar to that of the arctic measurements. Daggitt found that this estimated maximum rate was fairly constant throughout the growing season, except for lower values in May and July (Fig. 8.39). The low early summer value may be attributed to damage caused to capitula during the winter. The lower midsummer value is correlated with extremely dry conditions when the water content fell well below the 10 g g^{-1} level. An extreme case of this kind was found in May 1980. The water content was about 2 g g^{-1} and the response to light flux was so atypical (Fig. 8.37) that no hyperbola could be fitted. Quantum light fluxes were measured so it is possible to estimate the quantum efficiency as the slope of the hyperbola at zero light flux. The units are moles of carbon assimilated per mole (6.02×10^{23} quanta) of light. The efficiency starts at about 0.03 in May and rises to about 0.1 by September.

The experiments of Grace, of Johansson and Linder, and of Daggitt agree in showing that nominally replicate samples differ considerably, and that the light saturated rate of photosynthesis is about 1–2 mg g^{-1} h^{-1}. Daggitt's results show that this rate is much lower in very dry conditions, and that the quantum efficiency increases steadily during the growing season. But there is still much to be learned about the physiology of photosynthesis in *Sphagnum*.

8.6 ASSOCIATED PLANTS AND ANIMALS

Sphagnum carpets and the climate in which they flourish combine to create a habitat characterized by a physically open interdigitating network of gas and liquid filled spaces over a waterlogged peat, and which is chemically unusually acid and poor in inorganic solutes. Relatively few other species seem to be able to flourish in these conditions.

8.6.1 Plant associates

Amongst the vascular plants the commonest associates are probably the cotton grasses (*Eriophorum* spp.) and other 'sedges' in the broad sense (*Carex* spp., *Rhynchospora* spp., *Trichophorum cespitosum*), and members of the Ericaceae (such as *Calluna vulgaris*, *Erica* spp., *Kalmia* spp., *Vaccinum* spp., *Andromeda* spp.). Conspicuous shrubs are *Empetrum* spp. and *Ledum* spp., and there are also a range of insectivorous plants including the closely related pairs *Drosera* spp. and *Sarracenia* spp., and *Pinguicula* spp. and *Utricularia* spp. It is remarkable that the insect-trapping mechanisms in these closely related pairs are so different: sticky leaf and pitcher, sticky leaf and bladder respectively. The nutritional advantages of the insectivorous habit to a plant growing amongst *Sphagnum* are obvious and have been demonstrated by

experiment. The name of the beautiful yellow bog asphodel, *Narthecium ossifragum*, conceals an instructive confusion of correlation and regression concerned with the low supply of calcium. Plants with broad soft leaves are rare on bogs, the notable (and delicious) exception being *Rubus chamaemorus*. Some of these species (*Calluna vulgaris* for example) grow some way above the water table (Fig. 8.4) and have few or no roots in the waterlogged peat. Others, such as *Eriophorum* spp. and *Rubus chamaemorus* have at least some roots with large aerenchyma which provides an effective conduit for the downward movement of O_2 to the root tip (Armstrong, 1964). The roots may grow down 180 cm or more (Stavset, 1973). Most of the species are rhizomatous perennials; annuals are rare on bogs. *Calluna vulgaris* is particularly interesting. On dry, sandy soils in southern and eastern England it has a determinate pattern of growth and life-span of about 30 years (Watt, 1947); in the Cairngorm mountains it grows in arcs, driven before the prevailing wind, and appears to be potentially immortal. It seems to be potentially immortal too in association with *Sphagnum capillifolium* on blanket bog: the *Sphagnum* plants grow up around the stem and create conditions which stimulate the development of roots (Smith and Forrest, 1978). The *Calluna* plant behaves rather like the *Sphagnum* itself, growing at the shoot tips and dying where completely buried, but persisting as an individual and moving steadily upwards, as *Ammophila arenaria* does in sandy habitats. The equilibrium between *S. capillifolium* and *Calluna* seems as though it might easily be disturbed, but this has not been demonstrated. A similar rejuvenation with potential immortality has been shown for *Calluna* growing on Swedish sand dunes with much accumulation of organic matter (Wallén, 1980). This last example provides an interesting comparison with the behaviour of *Calluna* on southern and eastern English sandy soils.

The physical and chemical conditions created by *Sphagnum* seem to favour the growth of a number of other bryophytes, particularly small leafy liverworts. These may sometimes be abundant forming a fibrous network just below the *Sphagnum* capitula and binding the whole mass of plants together. Some of these leafy liverworts (such as *Mylia*, spp., *Lepidozia setacea* and *Odontoschisma sphagni* are not only common amongst *Sphagnum* but also rare elsewhere. Others (such as *Gymnocolea inflata*, *Cephalozia biscuspidata* and *C. connivens*) are found in almost any acid habitat. Similar patterns are seen in the associated mosses. The grouping of *Sphagnum recurvum* and *Polytrichum commune* (often with the grass *Molinia caerulea*) is characteristic of rather flushed habitats, but *P. commune* is widespread in other habitats too. So are *Aulacomnium palustre*, *Racomitrium lanuginosum*, and, in oceanic Britain, *Campylopus atrovirens*. A few mosses are almost entirely restricted to *Sphagnum* bogs however: *Dicranum undulatum* (= *D. bergeri*) is an example.

Amongst the algae there is a large number of species associated with *Sphagnum*. Almost any gathering of plants when examined with a microscope, is seen to contain abundant algae, many of them motile and passing in and out of the hyaline cells of the leaf. The most extensive studies of algal abundance and diversity amongst *Sphagnum* are those of Flensburg (1965, 1967), Flensburg and Malmer (1970), and Hooper (in press). Desmids and diatoms predominate, but several species of heterocystous blue-green algae also occur. In the arctic mire studied by Basilier *et al.* (1978), these algae were especially associated with the immersed species *Sphagnum riparium* growing in flushed depressions. The commonest algae were of the genera *Calothrix*, *Chlorogloea*, *Fischerella*, *Hapalosiphon*, *Nostoc*, *Scytonema*, *Tolypothrix*, and free-living *Anabaena*. This association of *S. riparium* and algae was found to reduce acetylene to ethylene at appreciable rates – an indication of potential nitrogen-fixing ability. Reasonable assumptions about the relationship between N_2 fixation and acetylene reduction gave a rate for nitrogen fixation of up to 6 g m^{-2} $year^{-1}$, which is a significant contribution to the nitrogen budget of these oligotrophic areas. The rate was independent of pH in the range 4.5 to 7, but reduced to 10% at pH 3. The rate was positively correlated with light flux and with temperature, and was greatest at mid-day and in mid-summer. The greatest rate occurred a few cm below the *Sphagnum* capitulum.

Associations of this kind may be fairly common in flushed habitats, but seem to be absent, or at least less active, in the majority of *Sphagnum* carpets with less lateral movement of water.

8.6.2 Animal associates

A remarkable feature of *Sphagnum* is that almost nothing eats it. In spring, frogs may spawn in bog pools amongst *S. cuspidatum*. They often die there and their bodies may perhaps be significant as concentrators of plant nutrients in the pools. Owls often perch, and defaecate, on *Sphagnum* hummocks. Again, they leave a local concentration of nutrients. Many invertebrates burrow in *Sphagnum*, particularly tipulids and enchytraeid worms, and one tipulid *Phalacrocera replicata*, ingests *Sphagnum*. Adult midges (chironomids) can be so numerous as to make work impossible; the larvae live amongst *Sphagnum*. Some invertebrates are restricted almost entirely to *Sphagnum*: the ant *Formica transkaucasica*, for instance, often nests in *Sphagnum* hummocks. The hunting spiders *Pirata piraticus* and *Lycosa pullata* both live in the top few cm of 'forests' of *Sphagnum recurvum*, but *P. piraticus* spends most of the time a few cm below the surface (out of sight to casual inspection) whilst *L. pullata* runs on the surface of the *Sphagnum* capitula (Nørgaard, 1951). *Pirata piraticus* will bring cocoons to the surface, but the two species do not usually meet or compete. When given the choice *L. pullata* prefers a temperature in the range 28–36°C, whilst *P. piraticus* generally prefers the range 18–24°C (and prefers higher humidity too). These preferences, combined with the *Sphagnum* microclimate already described, are sufficient to account for the separation of the species. Clear associations between oribatid mites and different degrees of wetness have been shown by Tarras-Wahlberg (1952). Here again, it seems that *Sphagnum* simply provides suitable physical and chemical conditions. Rotifers are common amongst *Sphagnum*. Again, the degree of restriction varies: *Keratella serrulata* is free-swimming and common in other habitats too, but *Habrotrocha angusticollis* builds a 'house' in a hyaline cell of a *Sphagnum* leaf and is not common elsewhere.

Perhaps the best known invertebrates associated with *Sphagnum* are the various species of testate rhizopod (Paulson, 1952; Heal, 1962; Corbet with Harding, 1973; Meisterfeld, 1977; and many others). These beautiful protozoa cover themselves with a house (test) made of plates. The houses, whose structure is characteristic of the species, persist after the occupant dies and become incorporated in peat. Different species prefer habitats of different wetness, so the discovery of tests in peat may allow the conditions

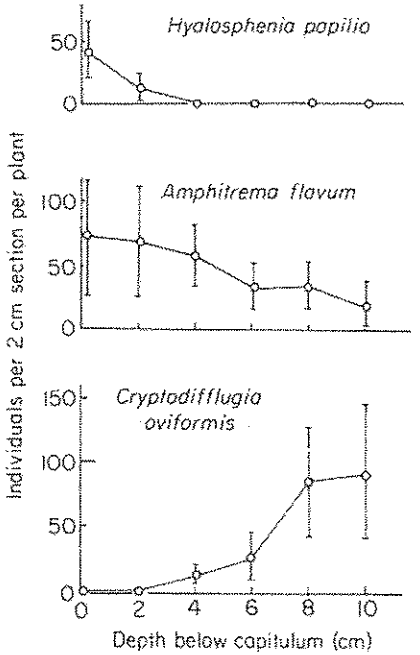

Fig. 8.40 Abundance of three species of testate amoeboa (rhizopods) at different depths below the capitulum of *S. recurvum*. The vertical bars are 90% confidence limits. Redrawn from Heal (1962).

at the time the peat formed to be deduced (e.g. Aaby and Tauber, 1975). For example, species such as *Difflugia bacillifera* are associated with the wettest conditions, *Amphitrema* spp. and *Nebela* spp. with drier conditions, and *Trigonopyxis arcula* and *Bullinularia indica* with the driest conditions on hummocks. Within these broad divisions there are clear differences associated with vertical position on the *Sphagnum* too (Fig. 8.40). Information on other invertebrates is given in Chapter 9.

8.7 CONCLUSION

The bulk of *Sphagnum* is greater than that of any other bryophyte genus (or perhaps of any plant genus) and the plants have the ability to produce and maintain an unusually acid environment given a suitable water supply. They grow upwards, decay slowly beneath, and accumulate as waterlogged peat. This combination of acidity, upward blanket-like growth, and waterlogging determines what other species, both plant and animal, can grow with them. The individual species of *Sphagnum* differ in their structure and water relations in ways consistent with their ecology.

All in all, *Sphagnum* is a beautiful and remarkable genus of plants.

ACKNOWLEDGMENTS

We thank Mrs P. Ratnesar for technical help over many years, S. Daggitt and the members of the Mires Research Group named in the caption to Fig. 8.4 for permission to use as yet unpublished results, Dr K.E. Clymo for comments on the manuscript and Dr B. Bolton, Dr J.C. Coulson, and Professor J.E. Green for information about animal associates of *Sphagnum*.

REFERENCES

Aaby, B. and Tauber, H. (1975), *Boreas,* **4,** 1–18.
Anschutz, I. and Gessner, F. (1954), *Flora, Jena,* **141,** 178–236.
Armstrong, W. (1964), *Nature,* **204,** 801–2.
Basilier, K., Granhall, U. and Stenstrom, T-A. (1978), *Oikos,* **31,** 236–46.
Bazzaz, F.A. and Harper, J.L. (1976), *J. appl. Ecol.,* **13,** 211–16.
Bendz, G.O., Mårtensson, O. and Nilsson, E. (1966), *Arkiv für Kemi,* **25,** 215–21.
Benson-Evans, K. (1964), *Bryologist,* **67,** 431–5.
Bismarck, R. von (1959), *Flora, Jena,* **148,** 23–83.
Boatman, D.J. and Lark, P.M. (1971), *New Phytol.,* **70,** 1053–9.
Boatman, D.J. and Tomlinson, R.W. (1973), *J. Ecol.,* **61,** 653–66.
Braithwaite, R. (1880), *The Sphagnaceae or Peat Mosses of Europe and North America,* Bogue, London.
Brehm, K. (1968), *Planta, Berlin,* **79,** 324–45.

Brehm, K. (1970), *Beitr. Biol. Pflanzen,* **47,** 91–116.
Brehm, K. (1971), *Beitr. Biol. Pflanzen,* **47,** 287–312.
Cavers, F. (1911), *New Phytol.,* **10,** 1–21.
Clymo, R.S. (1963), *Ann. Bot. N. S.,* **27,** 309–24.
Clymo, R.S. (1965), *J. Ecol.,* **53,** 747–58.
Clymo, R.S. (1967), Control of cation concentrations, and in particular of pH, in *Sphagnum*-dominated communities. In: *Chemical Environment in the Aquatic Habitat* (Golterman, H.L. and Clymo, R.S., eds), pp. 273–84. North Holland, Amsterdam.
Clymo, R.S. (1970), *J. Ecol.,* **58,** 13–49.
Clymo, R.S. (1973), *J. Ecol.,* **61,** 849–69.
Clymo, R.S. (1978), A model of peat bog growth. In: *Production Ecology of British Moors and Montane Grasslands* (Heals, O.W. and Perkins, D.F., eds), pp. 187–223. Springer, Berlin.
Clymo, R.S. (1982), Peat. In: *Ecosystems of the World,* (Gore, A.J.P., ed.), Vol. 4, Mires: Swamp, Fen, Bog and Moor, pp. 159–224. Elsevier, Amsterdam.
Clymo, R.S. and Reddaway, E.J.F. (1971), *Hidrobiologia,* **12,** 181–92. Reproduced without arbitrary cuts as: *Moor House Occasional Papers,* No. **3.**
Clymo, R.S. and Reddaway, E.J.F. (1974), *J. Ecol.,* **62,** 191–6.
Corbet, S.A. (1973), *Field Studies,* **3,** 801–38.
Coulson, J.C. and Butterfield, J. (1978), *J. Ecol.,* **66,** 631–50.
Damman, A.W.H. (1978), *Oikos,* **30,** 480–95.
Dickinson, C.H. and Maggs, G.H. (1974), *New Phytol.,* **73,** 1249–57.
Dilks, T.J.K. and Proctor, M.C.F. (1979), *New Phytol.,* **82,** 97–114.
Donnan, F.G. (1911), *Zeit. Elektrochem.,* **17,** 572–81.
Ferguson, P., Lee, J.A. and Bell, J.N.B. (1978), *Environ. Pollut.,* **16,** 151–62.
Ferguson, P. and Lee, J.A. (1979), *New Phytol.,* **82,** 703–12.
Ferguson, P. and Lee, J.A. (1980), *Environ. Pollut.,* Ser. A, **21,** 59–71.
Flensburg, T. (1965), *Acta phytogeog. suec.,* **50,** 159–60.
Flensburg, T. (1967), *Acta phytogeog. suec.,* **51,** 1–132.
Flensburg, T. and Malmer, N. (1970), *Bot. Notiser,* **123,** 269–99.
Goode, D.A. (1970), *Ecological Studies on the Silver Flowe Nature Reserve.* PhD thesis, Univ. Hull.
Goodman, P.J. and Paton, J.A. (1954), *Trans. Br. bryol. Soc.,* **2,** 470.
Gorham, E. (1956), *J. Ecol.,* **44,** 375–82.
Grace, J. (1970), *The Growth-Physiology of Moorland Plants in relation to their Aerial Environment.* Ph.D. thesis, Univ. Sheffield.
Green, B.H. (1968), *J. Ecol.,* **56,** 47–58.
Green, B.H. and Pearson, M.C. (1968), *J. Ecol.,* **56,** 245–67.
Hayward, P.M. (1980), *Effects of Environment on the Growth of Sphagnum.* Ph.D. thesis, Univ. London.
215, 299–325.
Hayward, P.M. and Clymo, R.S. (1982), *Proc. Roy. Soc. B.* (in press).
Heal, O.W. (1962), *Oikos,* **13,** 35–47.
Heal, O.W., Latter, P.M. and Howson, G. (1978), A study of the rates of decomposition of organic matter, In: *Production Ecology of British Moors and Montane Grasslands,* (Heal, O.W. and Perkins, G.F., eds), pp. 136–59. Springer, Berlin.

Hill, M.O. (1978), Sphagnopsida. In: *The Moss Flora of Britain and Ireland* (Smith, A.J.E., ed.). Cambridge University Press, London.

Hodgman, C.D., Weast, R.C. and Selby, S.M. (1961), *Handbook of Chemistry and Physics,* 43rd edn., Chemical Rubber Co., Cleveland, Ohio.

Hooper, C.A. (in press), *Oikos.*

Hulme, P.D. (1976), *Developmental and ecological studies on Craigeazle Bog, the Silver Flowe National Nature Reserve, Kirkcudbrightshire.* Ph.D. thesis, Univ. Hull.

Ingram, H.A.P. (1978), *J. Soil Sci.,* **29,** 224–7.

Ingram, H.A.P. (1982), Water relations of mires. In: *Ecosystems of the World* (Gore, A.J.P., ed.), Vol. 4, Mires: Swamp, Bog, Fen and Moore. Elsevier, Amsterdam.

Ingram, H.A.P., Rycroft, D.W. and Williams, D.J.A. (1974), *J. Hydrol.,* **22,** 213–18.

Johansson, L-G. and Linder, S. (1980), Photosynthesis of *Sphagnum* in different microhabitats on a subarctic mire. In: *Ecology of a Subarctic Mire,* (Sonnesson, M., ed.), pp. 181–90. Swedish Natural Science Research Council, Stockholm.

Johnson, A. (1960), *Trans. Br. bryol. Soc.,* **3,** 725–8.

Kivinen, E., Heikurainen, L. and Pakarinen, P. (1979), *Classification of Peat and Peatlands,* International Peat Society. Obtainable from I.P.S., V.V.T. Fuel Research Lab., Biologinkiya 3, SF 02150, Espo 15, Finland.

Lange, B. (1973), *Lindbergia,* **2,** 81–93.

Malmer, N. (1962a), *Op. Bot.,* **7:1,** 1–322.

Malmer, N. (1962b), *Op. Bot.,* **7:2,** 1–67.

McVean, D.N. (1959), *Ecol.,* **47,** 615–18.

Meisterfeld, R. (1977), *Arch. Hydrobiol.,* **79,** 319–356.

Moore, P.D. and Bellamy, D.J. (1974), *Peatlands,* Elek Science, London.

Morris, R.B. (1977), *J. Bryol.,* **9,** 387–92.

Mozingo, H.N., Klein, P., Zeevi, Y. and Lewis, E.R. (1969), *Bryologist,* **72,** 484–8.

Newbould, P.J. (1960), *J. Ecol.,* **48,** 361–83.

Nørgaard, E. (1951), *Oikos,* **3,** 1–21.

Nyholm, E. (1969), *Illustrated Moss Flora of Fennoscandia.* II. *Musci.* Fasc. 6., pp. 647–799. Natural Science Research Council, Stockholm.

Olsen, C. (1923), *C. R. Trav. Lab. Carlsberg,* **15 (1),** 1–166.

Overbeck, F. and Happach, H. (1956), *Flora, Jena,* **144,** 335–402.

Pakarinen, P. (1978a), *Ann. Bot. Fenn.,* **15,** 15–26.

Pakarinen, P. (1978b), *Ann. Bot. Fenn.,* **15,** 287–92.

Pakarinen, P. and Mäkinen, A. (1976), *Suo,* **27,** 77–83.

Pakarinen, P. and Tolonen, K. (1977a), *Oikos,* **28,** 69–73.

Pakarinen, P. and Tolonen, K. (1977b), *Suo,* **28,** 95–102.

Paton, J.A. and Goodman, P.J. (1955), *Trans. Br. bryol. Soc.,* **2,** 561–7.

Paul, H. (1908), *Mitt, K. Bayer. Mookulturanstalt,* **2,** 63–117.

Paulson, B. (1952), *Oikos,* **4,** 151–65.

Popp, E. (1962), *Int. Rev. ges. Hydrobiol. Hydrograph.,* **47,** 431–64.

Ratcliffe, D.A. and Walker, D. (1958), *J. Ecol.,* **46,** 407–45.

Rudolph, H. (1964), *Flora, Jena,* **155,** 250–93.

Rudolph, H. (1968), *Planta,* **79,** 35–43.

Rudolph, H. (1978), *Bryophytorum Bibliotheca,* **13,** 279–309.

Ruhling, A. and Tyler, G. (1971), *J. Appl. Ecol.,* **8,** 497–507.

Rycroft, D.W., Williams, D.J.A. and Ingram, H.A.P. (1975), *J. Ecol.,* **63,** 535–56, 557–68.

Skene, M. (1915), *Ann. Bot.,* **29,** 65–87.

Smith, R.A.H. and Forrest, G.I. (1978), Field estimates of primary production. In: *Production Ecology of British Moors and Montane Grasslands* (Heal, O.W. and Perkins, G.F., eds), pp. 17–37. Springer, Berlin.

Sonesson, M. (1973), Studies in production and turnover of bryophytes at Stordalen, 1972. In: *International Biological Programme – Swedish Tundre Biome Project Progress Report 1972* (Sonesson, M., ed.), pp. 66–75. Swedish Natural Science Research Council, Stockholm.

Sonesson, M., Persson, S., Basilier, K. and Stenström, T.A. (1980), Growth of *Sphagnum riparium* Ångstr. in relation to some environmental factors in the Stordalen mire. In: *Ecology of a Subarctic Mire* (Sonesson, M., ed.), pp. 191–207. Swedish Natural Science Research Council, Stockholm.

Spearing, A.M. (1972), *Bryologist,* **75,** 154–8.

Stavset, K. (1973), *Medd. Norsk. Myrselskap,* **4,** 153–156.

Stålfelt, M.G. (1938), *Planta,* **27,** 30–60.

Tallis, J.H. (1959), *J. Ecol.,* **47,** 325–50.

Tallis, J.H. (1964), *J. Ecol.,* **52,** 345–53.

Tallis, J.H. (1973), *J. Ecol.,* **61,** 1–22.

Tansley, A.G. (1939), *The British Islands and their Vegetation.* Cambridge University Press, Cambridge.

Tarras-Wahlberg, N. (1952), *Oikos,* **4,** 166–171.

Tattersfield, D.M. (1976), A physiological study of *Sphagnum rubellum* in relation to microclimate. In: *Moor House 17th Annual Progress Report* (Rawes, M. ed.), p. 23.

Theander, O. (1954), *Acta Chem. Scand.,* **8,** 989–1000.

Tibbets, T.E. (1968), Peat resources of the world. In: *Proceedings of the Third International Peat Congress, Quebec 1968* (Lafleur, C. and Butler, J. eds), pp. 8–22. No publisher. Sponsored by Department of Energy, Mines and Resources, Ottawa, Canada & National Research Council of Canada.

Troughton, J.H. and Sampson, F.B. (1973), *Plants. A Scanning Electron Microscope Survey,* Wiley, Sydney.

Tutschek, R. (1979), *Phytochemistry,* **18,** 1437–9.

Walker, D.A. and Walker, P.M. (1961), *J. Ecol.,* **49,** 169–85.

Wallén, B. (1980), *Oikos,* **35,** 20—30.

Watt, A.S. (1947), *J. Ecol.,* **35,** 1–22.

Williams, K.T. with Thompson, T.G. (1936), *Int. Rev. Hydrobiology,* **33,** 271–5.

Willis, A.J. (1964), *Trans. Br. bryol. Soc.,* **4,** 668–83.

Woodwell, G.M., Whittaker, R.H., Reiners, W.A., Likens, G.E., Delwiche, C.C. and Botkin, D.B. (1978), *Science,* **199,** 141–6.