PHOTOSYNTHESIS, RESPIRATION AND WATER CONTENT IN BRYOPHYTES

BY T. J. K. DILKS* AND M. C. F. PROCTOR

Department of Biological Sciences, University of Exeter, EX4 4PS, U.K.

(Accepted 20 June 1978)

SUMMARY

Response curves of photosynthesis to water content of bryophytes of dry habitats (e.g. Tortula intermedia, Camptothecium lutescens) show an optimum, with photosynthesis declining again at high water contents. Respiration may be stimulated by water stress, but is unaffected by high water contents. The steep portions of the photosynthesis and respiration curves lie within a similar range at low water contents. Some species of constantly moist habitats (e.g. Pellia epiphylla, Hookeria lucens) show photosynthesis increasing progressively to water contents of 500 to 1000 % of dry weight, and affected at much lower water deficits than respiration as the plant dries out. The response of photosynthesis and respiration to water potential is broadly similar in the two groups. In the species investigated there was generally measurable photosynthesis at —60 to —100 bar, but little or none at —150 to —200 bar. Respiration continues to somewhat lower water potentials of which the limits were not determined.

Field measurements of the water content of shoots of five species over a period of 12 months showed much greater variation in Tortula muralis than in the woodland species. Maximum water contents in the field generally lay close to the optima of the photosynthesis response curves. The lower water contents recorded in these and in published data are considered in relation to sorption isotherms for bryophytes and other plant materials.

The water associated with bryophyte shoots can be divided into (1) water within the cell walls (apoplast water), (2) water within the cytoplasm (symplast water), and (3) external capillary water. Changes in water content below about —200 bar take place chiefly within (1), between c. —200 and c. —2 bar within (2), and at higher water potentials chiefly within (3). Water movement within the shoots is physiologically important; the distribution and movement of water are mediated by the geometry of the capillary spaces of the cell walls and the plant surface. In species with papillose leaves, rates of capillary conduction in the interstices between the papillae are more than sufficient to balance evaporation. Conduction within the cell walls is likely to be important in species with non-papillose leaves, but other pathways may also be involved, and water movement in these species requires further investigation.

INTRODUCTION

Bryophytes are typically poikilohydric plants. This has tended to focus attention on their tolerance of desiccation (see Dilks and Proctor, 1974, 1976a for references), which they share with the seeds of flowering plants (Roberts and Abdalla, 1968; Roberts, 1975) and various other organisms (Keilin, 1959; Brock, 1969; Crowe, 1971). However, the performance of the plant depends on its water relations and behaviour when it is moist. Although a substantial literature exists on these matters, it seemed to us that there were still considerable lacunae and uncertainties. The work reported in this paper was undertaken in an attempt to pull together the available data into a more consistent and coherent picture.

We have set out to examine the relationship of photosynthesis and respiration to

* Present address, Woodbridge School, Woodbridge, Suffolk.
water content and water potential in a representative range of bryophytes, and to consider these in relation to conditions observed in the field and in the light of some more theoretical aspects of water relations.

**Materials and Methods**

The bryophyte material used in the experiments was collected in the country around Exeter, and was maintained at the laboratory under a mist unit in the glasshouse. Collecting sites are indicated in the captions.

The photosynthesis curves of Figures 1 and 2 are based on $^{14}$CO$_2$ uptake using the aluminium and perspex assimilation chambers described by Proctor (1977). Samples of bryophyte shoots were allowed to dry to various water contents. They were placed in the assimilation chambers which were then immersed in a constant-temperature bath at 25 °C and allowed to equilibrate for 5 min before injection of 5 µCi Na$_2$ $^{14}$CO$_2$ into 0.5 cm$^3$ 10% lactic acid in a small plastic cup within the chamber, and exposure for 5 min to an irradiance of c. 250 µmol quanta m$^{-2}$ s$^{-1}$ (400 to 700 nm) from a tungsten reflector photoflood lamp. The samples were removed from the chambers, weighed, and then put into scintillation vials, remoistened and digested with 0.5 cm$^3$ Packard ‘Soluene-350’ before counting in a toluene-based scintillation fluid.

The corresponding respiration curves were obtained on a Gilson respirometer, using a similar method to Bewley and Thorpe (1974). Samples at arbitrary water contents were weighed and placed in reaction flasks with KOH in the centre wells. After 30 min equilibration, respiration was measured at 25 °C for 1 h. The bryophyte samples were then re-weighed, and finally oven-dried and weighed again. The respiration measurements are plotted at the water content corresponding to the mean of the two fresh weights. The difference between these was typically about 5 mg, with total water contents between 15 mg and 100 mg or more; at low water contents the difference was generally small, and an increase in water content was observed in some of the driest samples.

Our earlier osmotic stress experiments [Fig. 3(a) to (c)] were carried out using a Warburg apparatus, the later ones on a Gilson respirometer. The bryophyte material was placed in 5 cm$^3$ of solution in the reaction flask; osmotic potential was calculated from the data of Wolf, Brown and Prentiss (1973). In the Warburg experiments net assimilation was measured with a carbonate–bicarbonate CO$_2$ buffer integral with the bathing solution; for the Gilson experiments we used a diethanolamine CO$_2$ buffer in the centre wells. Illumination by tungsten lamps under the water baths gave respectively about 150 and 250 µmol quanta m$^{-2}$ s$^{-1}$ (400 to 700 nm). The flasks for measuring respiration had 20% KOH in the centre wells and were wrapped in foil to exclude light. On removal from the reaction flasks the material was thoroughly washed in water to remove the solute before oven-drying.

For the $^{14}$CO$_2$ uptake experiment described later, bryophyte shoots were equilibrated in the dark for 48 h at a constant 20 °C over deionized water and the salts listed in Table 1 in equilibrium with their saturated solutions. The moistened salt was placed in the shallow lid of a 5 cm Petri dish, in the centre of a 9 cm petri dish; the bryophyte material, moist but blotted free of excess water, was arranged in the annular space at the periphery. The lid of the larger Petri dish was sealed at the edge with petroleum jelly. A small hole in the centre of the lid, covered with ‘Sellotape’, allowed 0.5 cm$^3$
15% lactic acid followed by 5 μCi Na₂¹⁴CO₃ to be injected into each dish. The petri dishes were exposed for 10 min to an irradiance of about 200 μmol quanta m⁻² s⁻¹ (400 to 700 nm) from a Thorn ‘Kolorarc’ fluorescent metal halide lamp. The material was oven-dried and weighed before digestion and scintillation counting as above.

For the field water content measurements samples of shoots were collected with forceps into glass vials with snap-on plastic caps. The vials were weighed on return to the laboratory, while still closed, and again after oven-drying at 110 °C. The desorption isotherms of Figure 5 were obtained by incubating samples of (initially moist) shoots at 20 °C in wide-mouthed specimen tubes together with a range of salts in equilibrium with their saturated solutions (Table 1) until constant weight was reached.

Table 1. Salts used to maintain constant humidity. Data from Weast (1973)¹ and (for NaCl) Wylie (1961), with calculated approximate values of water potential

<table>
<thead>
<tr>
<th>Salt</th>
<th>R.H. (%) at 20 °C</th>
<th>ψ (bar)</th>
</tr>
</thead>
<tbody>
<tr>
<td>LiCl·H₂O</td>
<td>15</td>
<td>-2570</td>
</tr>
<tr>
<td>CaCl₂·6H₂O</td>
<td>32-3</td>
<td>-1530</td>
</tr>
<tr>
<td>K₂CO₃·2H₂O</td>
<td>44</td>
<td>-1110</td>
</tr>
<tr>
<td>Ca(NO₃)₂·4H₂O</td>
<td>54</td>
<td>-834</td>
</tr>
<tr>
<td>NaCl</td>
<td>75-5</td>
<td>-380</td>
</tr>
<tr>
<td>(NH₄)₂SO₄</td>
<td>81</td>
<td>-285</td>
</tr>
<tr>
<td>KHSO₄</td>
<td>86</td>
<td>-204</td>
</tr>
<tr>
<td>ZnSO₄·7H₂O</td>
<td>90</td>
<td>-143</td>
</tr>
<tr>
<td>Na₂SO₄·10H₂O</td>
<td>93</td>
<td>-98</td>
</tr>
<tr>
<td>Na₃HPO₄·12H₂O</td>
<td>95</td>
<td>-70</td>
</tr>
<tr>
<td>CuSO₄·5H₂O</td>
<td>98</td>
<td>-27</td>
</tr>
</tbody>
</table>

The water contents given in Table 2 were obtained by centrifuging samples of moist green bryophyte shoots at 3600 rev min⁻¹ (approx. 1200 g) for 10 min in screw-top ‘universal bottles’; approximately the bottom 3 cm of the bottles was occupied by a plug of dry paper towelling. The gravitational potential difference between the plant material and the bottom of the tube under these conditions is about 4 bar. The bryophyte material was immediately transferred to glass weighing bottles for weighing and oven-drying.

**Response curves of photosynthesis and respiration to water content and water potential**

Curves relating photosynthesis and respiration to water content have been published for a number of bryophytes, including *Rhytididiadelphus triquetrus* (Plantefol, 1927), *Hylocomium splendens* (Stålffelt, 1937), *Camptothecium sericeum* (Romose, 1940), *Cnöopealum conicum* (Ensgraber, 1954; Slavik, 1965) and *Rhacomitrium lanuginosum* (Tallis, 1959). Stålffelt pointed out that the photosynthesis curve for *Hylocomium splendens* exhibited an optimum, with the rate declining again at high water contents, in contrast to the behaviour of respiration. This is probably a consequence of the much slower diffusion of gases through water than through air; excess water would be expected to restrict gas exchange at the low concentration gradients available for CO₂ uptake but should have negligible effect on respiration. Romose and Tallis found that *Camptothecium sericeum* and *Rhacomitrium lanuginosum* behaved similarly; the
The same phenomenon in lichens is excellently illustrated in the data of Ried (1960a), Bertsch (1966), Harris (1971) and Kershaw (1972). By contrast, Slavik found that the maximum rate of photosynthesis in *Conocephalum conicum* was reached only at a water content above 700% of dry weight, and that the rate declined with even small water deficits.

![Figure 1](image-url)

Fig. 1. Relative photosynthesis and respiration of bryophytes at different water contents; photosynthesis from $^{14}$CO$_2$ uptake, respiration by manometry. Cubic (or where noted quadratic) regressions have been fitted, excluding outlying groups of points for respiration at very high water contents. Each set of data has been scaled by taking the calculated maximum of the regression as unity. Linear regressions have been calculated for water contents above the maxima of the curves where this seemed useful in interpreting the results. (a) *Pellia epiphylla*, oakwood in Dart valley near Holne, Dartmoor; (b) *Hookeria lucens*, shady stream gully, Stoke Woods, Exeter; (c) *Plagiothecium undulatum*, (d) *Plagiochila spinulosa* (quadratic regressions), (e) *Bazzania trilobata*, all from rocky north-facing oakwood in Dart valley, near Holne, Dartmoor.

The results set out in Figure 1 and 2 broadly confirm these conclusions. The thalloid liverwort *Pellia epiphylla* [Fig. 1(a)] shows photosynthesis increasing progressively up to water contents approaching 1000% of dry weight, with only a slight hint of a decrease at the highest water contents. Respiration, on the other hand, shows little
Physiological ecology of bryophytes

change over a wide range of water contents. The highest rates occur at water contents around 200%, below which respiration falls steeply to very low values. The behaviour of the other species in Figure 1 is qualitatively comparable with *P. epiphylla*. *Hookeria lucens* yields very similar curves at a somewhat lower water content, while the others differ mainly in the narrower range of water contents over which the changes take place.

![Graphs and data](Fig. 2. Relative photosyntheses and respiration of bryophytes at different water contents; for further explanation see Fig. 1. (a) *Dicranum majus*, (b) *Thuidium tamariscinum* (quadratic regressions), both Stoke Woods, Exeter; (c) *Tortula intermedia*, exposed limestone rocks, Chudleigh, Devon; (d) *Anomodon viticulosus*, shady limestone rock faces in wood, Chudleigh, Devon (quadratic regression for respiration, linear regression calculated for all points above highest individual value); (e) *Pleurochaete squarrosa*, thin turf around limestone outcrops, Chudleigh, Devon; (f) *Camptothecium lutescens*, calcareous fixed-dune turf, Braunton Burrows, Devon.)

Most of the mosses of Figure 2 show essentially the pattern that Stålfelt found in *Hylocomium splendens*. Photosynthesis rises to a well-defined maximum, beyond which it declines again, often to 50% or less of the maximum value. Respiration follows much the same course as in *Pellia epiphylla* – rising rapidly with increasing water content
to a maximum, and then remaining essentially constant at a slightly lower value as water content is further increased over a wide range. The portions of the curves over which photosynthesis and respiration are steeply related to water content are not conspicuously separated. Close examination of the curves shows that the situation may be quantitatively rather than qualitatively different from that in *Pellia epiphylla* or *Hookeria lucens*, and the species investigated evidently represent a continuous spectrum of behaviour between the two extremes.

The curves of Figures 1 and 2 leave unanswered a number of questions. They give no indication of the relation of gas exchange to water potential; there is no certainty that all parts of the material are at a uniform water potential for each measurement. All of the respiration curves show apparently negative values at low water contents. These appear most likely to be due to a progressive, purely physical, displacement of adsorbed gases from the cell walls as water is taken up from the humid atmosphere over the KOH in the reaction flasks. Filter paper shows the same behaviour; it is probably related to the ‘wetting burst’ shown by dry lichens and bryophytes on remoistening with liquid water (Hinshiri and Proctor, 1971; Smith and Molesworth, 1973; Farrar and Smith, 1976; see also Preston, 1974). This evolution (and potential adsorption) of gas means that gas exchange data obtained at low water contents in air must be treated with caution.

Most published response curves relate photosynthesis and respiration to water content as a percentage of dry weight or of the ‘saturated’ water content. Slavik (1965) also gave a curve of photosynthesis in *Conceophalum conicum* plotted against the cryoscopically determined osmotic potential of cell sap expressed from heat-killed material. He found an osmotic potential of 12.6 atm (−12.8 bar) at the point where photosynthesis fell to zero; the osmotic potential of the turgid cells was about −5 bar. The data of Peterson and Mayo (1975) for *Dicranum polysetum*, based on thermocouple psychrometer measurements of water potential as the moss dried out progressively in an infra-red gas analyser, are unfortunately too limited for critical interpretation.

The alternative of applying water stress osmotically (Figs 3 to 5) makes it easy to apply a uniform and constant stress of known value, though it is open to question how rigorously osmotic and vapour-phase stress can be compared (Adebayo and Harris, 1971; Brock, 1975). The choice of solute is important. It should be metabolically inactive, and should penetrate the cell membranes as slowly as possible. In addition, solutions of the required strength should have as low a viscosity as possible to minimize resistance to diffusion of CO₂ to the cells. For photosynthesis measurements at normal CO₂ concentrations this rules out the use of solutions of polyethylene glycol (PEG) of high mol. wt, which otherwise have suitable properties (Michel and Kaufmann, 1973; Dhindsa and Bewley, 1976). For the experiments of Figure 5 we used glycerol, which gave comparable results to PEG 6000 and other solutes for respiration, and appeared to behave satisfactorily in other respects. In particular, cells of *Hookeria lucens* and *Pellia epiphylla* remained plasmolysed after 3 h, which suggests that it penetrated membranes fairly slowly.

The most striking feature of the results is the similarity of the response of the different species; their behaviour is very much more alike in terms of water potential than in terms of water content. In general, net assimilation declines progressively over a wide range of water potential and in *Camptothecium lutescens* was still positive at −107 bar. Respiration is generally (but not always) stimulated by even mild water
Physiological ecology of bryophytes

Fig. 3. Relation of net photosynthesis and respiration to osmotic stress. Net assimilation in water is taken as unity; all other values are relative to this. • — , NaCl; ○ — — ○ , sucrose in (a), mannitol in (b). The NaCl and sucrose experiments were done with a carbonate–bicarbonate buffer integral with the bathing solution, the mannitol experiment with a diethanolamine buffer in the centre well. (a) Hookeria lucens, Stoke Woods, Exeter; (b) Anomodon viticulosus, Chudleigh, Devon. Points are means of six and four replicates respectively.

Fig. 4. Relation of respiration to osmotic stress. (a)–(c) PEG-6000, (d) glycerol. (a) Rhytidadelphus loreus, (b) Bazzania trilobata, both from rocky north-facing oakwood in Dart valley near Holne, Dartmoor; (c) Tortula intermedia, Chudleigh, Devon; (d) Pellia epiphylla, on ground in wet birch-sallow scrub, New Bridge, Dartmoor. Plotted points in (a) are single measurements; all others are means of two measurements. Rates are expressed in terms of oven-dry weight.
stress, but then commonly falls only slowly up to water potentials approaching −200 bar. There is some indication that stimulation of respiration persists over a wider range of water potentials in the moist-adapted species.

We investigated photosynthetic $^{14}$CO$_2$ uptake by shoots of six species—Hookeria lucens, Plagiothecium undulatum, Camptothecium lutescens, Plagiochila spinulosa, Anomodon viticulosus and Tortula ruraliformis—which had been equilibrated for 48 h in the dark in air at water potentials of 0, −27, −70, −98, −143, −204, −285 and −380 bar at 20 °C. The results were rather irregular [as Brock (1975) found in similar experiments with lichens], but there was a very clear division (a factor of 12 or more) between the samples at −98 bar and above, which gave high count rates for all six species, and those at −143 bar and below.

In IRGA experiments, Lange (1969) found that, of 14 species of bryophytes he studied, all but Mnium punctatum and three thalloid liverworts showed positive net assimilation following absorption of water from air at 98% r.h. (c. −30 bar); all the pleurocarpous mosses and Polytrichum piliferum did so also at 94% r.h. (c. −85 bar). All the species investigated showed measurable respiration at both humidities.

Taking all the data together, it is apparent that the relation of water potential to water content in such species as Tortula intermedia or Camptothecium lutescens is different in important respects from that seen in Pellia epiphylla or Hookeria lucens. In the former species, most of the range of water potential is passed through and full turgor reached at a water content below 250% of dry weight (Table 2); further water is held externally and makes little difference to water potential. In the latter species, the water held within the cells normally forms a major proportion of the total water associated with the plant. Water loss therefore quickly brings about a fall in tissue water potential and there is a wide range of water content over which photosynthesis is depressed but respiration continues unabated. The first of these two patterns is obviously the better suited to a poikilohydric plant. Ried (1960b) has demonstrated a similar contrast between terrestrial and aquatic species of lichens.
Physiological ecology of bryophytes

Our IRGA measurements on bryophytes gave no evidence of any substantial net loss of assimilate during drying out (Dilks and Proctor, 1976b). Whether or not this is true of Pellia epiphylla and Hookeria lucens, which were not included in the experiments, the pattern of response in these species must at least severely limit net carbon assimilation under conditions of varying water content.

Table 2. Water content of bryophytes at full turgor, but free of external water. Means of duplicate measurements

<table>
<thead>
<tr>
<th>Species</th>
<th>Locality</th>
<th>Water content (% dry wt)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dicranum majus</td>
<td>Quercus petraea coppice, Stoke Woods, Exeter</td>
<td>202</td>
</tr>
<tr>
<td>Tortula intermedia</td>
<td>Limestone outcrop, Chudleigh</td>
<td>233</td>
</tr>
<tr>
<td>Pleurochaete squarrosa</td>
<td>Thin turf close to limestone outcrop, Chudleigh</td>
<td>165</td>
</tr>
<tr>
<td>Rhacomitrium lanuginosum</td>
<td>Granite wall near Hexworthy, Dartmoor</td>
<td>142</td>
</tr>
<tr>
<td>Neckera complanata</td>
<td>Shady limestone wall, Chudleigh</td>
<td>162</td>
</tr>
<tr>
<td>Leptodon smithii</td>
<td>Trunk of Acer campestre, Chudleigh</td>
<td>187</td>
</tr>
<tr>
<td>Hookeria lucens</td>
<td>Shady stream gully, Stoke Woods, Exeter</td>
<td>516</td>
</tr>
<tr>
<td>Anomodon viticulosus</td>
<td>Limestone wall, Chudleigh</td>
<td>141</td>
</tr>
<tr>
<td>Thuidium tamariscinum</td>
<td>Shady bank of ride, Stoke Woods, Exeter</td>
<td>203</td>
</tr>
<tr>
<td>Camptothecium lutescens</td>
<td>Calcareous fixed-dune grassland, Brauntun Burrows</td>
<td>105*</td>
</tr>
<tr>
<td>C. sericeum</td>
<td>Rock garden, University Estate, Exeter</td>
<td>223</td>
</tr>
<tr>
<td>Brachythecium rutabulum</td>
<td>Limestone rock in wood, Chudleigh</td>
<td>249</td>
</tr>
<tr>
<td>Pseudoscleropodium purum</td>
<td>Grazed turf on limestone, Westleigh</td>
<td>207</td>
</tr>
<tr>
<td>Plagiothecium undulatum</td>
<td>Rocky north-facing oakwood in valley of R. Dart, Holne, Dartmoor</td>
<td>334</td>
</tr>
<tr>
<td>Rhytidiodelphus loreus</td>
<td>Rocky north-facing oakwood, Holne, Dartmoor</td>
<td>165</td>
</tr>
<tr>
<td>Bazzania trilobata</td>
<td>Rocky north-facing oakwood, Holne, Dartmoor</td>
<td>210</td>
</tr>
<tr>
<td>Plagiochila spinulosa</td>
<td>Rocky north-facing oakwood, Holne, Dartmoor</td>
<td>222</td>
</tr>
<tr>
<td>Porella platyphylla</td>
<td>Shady limestone wall, Chudleigh</td>
<td>230</td>
</tr>
<tr>
<td>Pellia epiphylla</td>
<td>Wet birch-sallow scrub, New Bridge, Dartmoor</td>
<td>1180</td>
</tr>
<tr>
<td>Conocephalum conicum</td>
<td>Glasshouse weed, University Estate, Exeter</td>
<td>871†</td>
</tr>
</tbody>
</table>

* This figure may be somewhat low owing to contamination of the material with blown sand.
† Water content of turgid, superficially dry thalli, not centrifuged.

The water content of bryophytes in the field, and some comments on bryophyte water relations

In a set of measurements of the water content of mats of Camptothecium sericeum in Copenhagen from February 1938 to January 1939, Romose (1940) recorded values ranging from around 10% to about 950% of dry weight. Klepper (1963) found water contents ranging from 23-8 to 258% in shoots of Dicranum scoparium during August and September in North Carolina. Morton (1977) found water contents ranging from 19 to 214% in Pseudoscleropodium purum and from 58 to 307% in Dicranum bonjeanii (and values within these limits for six other species) in chalk grassland at Aston Rowant National Nature Reserve in the Chiltern Hills (Buckinghamshire, England).
The results of measurements of our own on shoots of five species near Exeter are set out in Figure 6.

There is a striking contrast between the violent fluctuations of water content experienced by *Tortula muralis* on an exposed wall top and the relatively constant water regime of *Hookeria lucens* in a shaded woodland stream gully. The water content of *T. muralis* was commonly less than 10% during dry weather in summer; that of

![Figure 6](image-url)

**Fig. 6.** Water content (percentage of oven-dry weight) of five bryophyte species in the field on sampling occasions between May 1974 and April 1975. Note the logarithmic scale of the y-axis; the continuous line across the diagram is at 100% water content for each species. (a) *Tortula muralis* on wall of Hatherly Laboratories, Prince of Wales Road, Exeter; other species in Stoke Woods, Exeter. Of these, (c) *Dicranum majus* was on the floor of the wood and (b) *Isothecium myosuroides* on the bases of the trunks in *Quercus petraea* coppice, (d) *Thuidium tamariscinum* on the north-facing bank of a ride, and (e) *Hookeria lucens* in a shaded stream gully.
H. lucens never fell below 100%. The other mosses lay between the extremes of these two. It is noteworthy that the maximum water contents for each species lie at a fairly clearly defined level, approximating the maximum of the photosynthesis–water content curve in the species for which data are available.

A full understanding of the significance of data on field water content requires a knowledge of the relationship between water content and water potential for the species in question. For low water contents this is easily determined by equilibrating samples of shoots at known humidities and constant temperature. The adsorption and desorption isotherms of biological materials are similar in form, but combine to give a narrow hysteresis loop (Breese, 1955; Hubbard, Earle and Senti, 1957; Kelsey, 1957; Christensen and Kelsey, 1958). A number of desorption curves for bryophytes have been published (e.g. Planteol, 1927; Romose, 1940); Willis (1964) presented an adsorption curve for Tortula ruraliformis. As usually plotted, with relative humidity on the x-axis, these curves are sigmoid. If they are plotted with log ψ against the x-axis the lower part of the curve becomes approximately linear. We know of no theoretical justification for this straight-line relationship. The base line of the graph is set by
oven-drying, and the conventionally used temperatures do not appear to have any
privileged status in this context. However, it may be significant that the empirical curves
for various biological materials [brophytes; wood and wood cellulose (Kelsey, 1957;
Christensen and Kelsey, 1958); wheat (Hubbard et al., 1957); rice (Breese, 1955)] all
cut the x-axis at a value of $\psi$ approaching $10^{-4}$ bar, corresponding to the suction
generated by a capillary of near-molecular dimensions. This type of plot is familiar in
soil science through Schofield’s concept of pF (Schofield, 1935; Robinson, 1949,
pp. 279 ff.); the water content of soils also shows hysteresis and an approximately
linear relationship to pF at low water contents. Desorption curves for three mosses
from our own material are plotted in this way in Fig. 7, along with Willis’s curve for
*Tortula ruraliformis*, the data for Rhytidiadelphus triquetrus of Plantefol (1927, p. 73),
and hysteresis loops for wood shavings and for wheat.

The curves for the mosses show a well-marked break at about $-100$ to $-200$ bar
between the straight line portion at low water potentials, and the steeply rising
portion within the ‘physiological’ range. There is an indication of a similar break in
the curve for wheat. It seems a reasonable surmise that this is the point at which a free
liquid phase appears in the cytoplasm; it is in approximately this range that metabolic
activity begins.

The curves enable us to estimate $\psi$ from water content measured in the field.
Taking the four species we investigated as representative, a water content of 20% of
dry weight would correspond to water potentials ranging from about $-180$ to
$-400$ bar; these are reasonable figures for material in equilibrium with the humid air
in the shade of a wood or a grassland turf in summer. A water content of 10% corre-
sponds to a water potential of around $-1000$ bar ($40$ to $50\%$ r.h. at $20^\circ$C), corre-
sponding to dry, exposed (but not extreme) conditions in the open in summer. With
strong surface-heating in hot sun, water stress may be much greater than this; at the
by no means unusual temperature of $60^\circ$C (Lange, 1955; Dilks and Proctor, 1976a)
in equilibrium with an ambient water vapour pressure of $12$ mb (corresponding to
$50\%$ r.h. at $20^\circ$C), a moss would have a water potential of about $-2300$ bar.

The simple vapour equilibration method is not satisfactory for extending the curves
to high humidities, because precise temperature control is needed and equilibration
times become excessively long. Dhindsa and Bewley (1976) give estimates of the
relative fresh weight of *Tortula ruralis* under osmotic stress using PEG 6000. Their
results show a relationship of approximately the form that might be expected from
the Boyle-Van’t Hoff relationship (Nobel, 1974; Powell and Blanchard, 1976), with
fresh weight increasing progressively more rapidly from $-60$ to $-15$ bar, at which
point the curve begins to flatten off, fresh weight scarcely changing between $-10$ and
$0$ bar. Presumably the water potential at which the curve begins to flatten approximates
the osmotic potential of the turgid cells. Osmotic potentials around $-15$ to $-20$ bar
have been reported for a wide range of bryophytes (Patterson, 1946); we found
osmotic potentials in this range in *Tortula ruraliformis* and the majority of 15 other
species we examined. Water contents at full turgor for a number of species are sum-
marized in Table 2.

Once the cells are turgid, further water can be held only in capillary spaces outside
the cells. Some of these are of rather closely defined pore sizes, as for instance the
interstices between the papillae that cover the leaf surfaces of *Tortula intermedia* or
*Anomodon viticulosus*, and will fill over a correspondingly narrow range of water
potential. Others, such as the spaces within and between leaf bases, are more diffuse
and will fill progressively as the water potential approaches zero. Some features of the state and distribution of water in relation to bryophyte shoots are summarized schematically in Fig. 8.

![Diagram of water potential and water content](Image)

**Fig. 8.** Schematic relation of water content to water potential for a poikilohydric moss. From A to B most water is closely associated with surfaces and is relatively immobile (Bernal, 1965). At B a free liquid phase becomes important and from B to C increase of water content is mainly within the cells and is reflected by the changing osmotic potential of the cell solution. C is the point of incipient plasmolysis; from C to D the water content increases only slightly with the build-up of wall pressure and the first appearance of external capillary water associated with fine surface roughness and striation of the cell wall. From D to F the form of the curve will vary from species to species depending on the detailed architecture of the shoot, and the form of the curve in the diagram is to some extent conjectural. We have assumed a leaf-surface papilla system (interstices c. 1 μm radius), and spaces around leaf bases or in the concavities of the leaves (c. 20–200 μm radius). Region 1 of the diagram represents cell-wall (apoplast) water, region 2 symplast water, and region 3 external capillary water. The boundary between 1 and 2 corresponds to Kelsey’s sorption isotherms for wood, the region of rapid increase of water content within 2 approximates the Boyle–Van’t Hoff relationship. This form of diagram is imperfect in that it separates external water (3) from cell wall water (1) with which it is physically in contact and by which it is separated from symplast water (2).

It is instructive to consider the treatment of vascular plant water relations in relation to this diagram. Most physiologically important processes in vascular plants take place within the region of the diagram to the right of point B (largely to the right of point C), and below a horizontal line through point D. There is generally little external water even at high water potentials. Consequently, the water content corresponding to ‘full turgor’ is easily defined and measured, and forms a natural and convenient datum point for studies of tissue water content in the concept of ‘relative turgidity’ or ‘relative water content’ (RWC) (Weatherley, 1950; Slatyer, 1967, p. 150; Shepherd,
1976). In a poikilohydric bryophyte with external capillary water storage and conduction the excluded regions of the diagram are physiologically relevant and important. In principle, water relations of bryophytes can be considered in terms of RWC, just as theoretical analyses of relationships between cell water volumes and potentials (Slatyer, 1967, pp. 138 ff.; Nobel, 1974, pp. 77 ff.; Powell and Blanchard, 1976) are equally applicable to vascular plant and bryophyte cells. In practice, the water content at full turgor is much less easy to determine with acceptable accuracy in bryophytes, so the use of RWC loses much of its convenience. Uncritical use of 'saturated' water content (at which the effective RWC is likely to be well over 100%) as a datum in bryophytes is imprecise and potentially misleading.

**The control of water content and movement of water in bryophyte shoots**

Earlier in this paper we suggested that the response curve of photosynthesis to water content of *Tortula intermedia* is better adapted to a poikilohydric habit than that of *Pellia epiphylla*. It could still be said that if the plant merely moves up and down one of the curves of Figure 2 with changing availability of water in the habitat its adaptation is not very good. Mägdefrau (1937) suggested that the capillary space associated with moss shoots might function primarily for rainwater storage; Romose's observations on *Camptothecium sericeum* mats are consistent with this idea. Our own observations indicate that bryophyte shoots during wet periods tend to maintain a water content close to that resulting in maximum photosynthesis. The conditions of the isolated shoots in the experiments of Figure 1 and 2 are quite artificial; under natural conditions excess water could drain to the surroundings.

These apparently contradictory observations are in fact readily reconciled. In general, the capillary spaces of active, green, bryophyte shoots are highly organized and of regular dimensions. They hold only a well-defined amount of water and leave much of the surface of the shoot free for gas exchange. Excess water can drain freely to any diffuse capillary system (soil, litter or a cushion or mat of old shoots) with which they are in capillary contact. Romose's measurements reflect the state of the photosynthetic shoots – the functional element – plus the underlying mat of old shoots – the reservoir. In ours, the latter component of the system was excluded. So long as capillary contact is unbroken, the shoots will draw water from the reservoir of their immediate surroundings to maintain their own characteristic water content. The nib of a good fountain pen suggests an analogy in efficient capillary design.

Buch (1945, 1947) pointed out the antithesis between endohydric and ectohydric bryophytes, but made it clear that water conduction over short distances is still important in the biology of the latter. In general, any part of the plant with a net radiation income must of necessity lose water, even in a saturated atmosphere (Gates, 1968). This will usually be true of leaves receiving the light necessary for photosynthesis. The capillary adaptation of shoots and leaves of mosses therefore implies the solution of a dynamic problem. The resistances to water flow must be such that water movement can balance evaporation with a pattern of water potential gradients compatible with the metabolism of the plant.

The mosses with strongly papillose leaf surfaces offer no difficulty in this respect. Consider a section of a papillose leaf of a moss such as *Tortula intermedia* or *Anomodon viticulosus* [Plates 1 and 2, and compare the scanning electron micrographs of *T. ruralis*...
in Casas de Puig and Molinas (1974) and Robinson (1971)]. As a rough approximation let us regard the interstices between the papillae on the two surfaces as equivalent to one series of longitudinal capillaries of 1 μm radius spaced 10 μm apart. A capillary of this size would generate a tension of about 1.5 bar. If we assume a leaf 2 mm long, and consider the movement of water from the centre of the basal to the centre of the apical half, with a water potential difference of 0.5 bar, applying Poiseuille's formula gives a rate of flow of 6.125 mm s⁻¹. This is equivalent to a rate of supply to the upper half of the leaf of c. 200 μg cm⁻² s⁻¹, well above the flow needed to balance the most rapid rates of evaporation likely to be encountered in the field. Normal rates of water loss should leave an ample potential gradient to move water up from the base of the plant.

As Buch pointed out, the capillary systems of leaves are often isolated by regions in which the capillary spaces are much larger, so that conduction will be broken off at a water potential at which the papilla system can still readily distribute water throughout the leaf. This may well be adaptive; the effect will be that the individual leaf will either have an ample water supply or none, thus minimizing the time the leaf spends within the range of water potentials where respiration exceeds photosynthesis. Some features of the rather complex capillary conducting system of Thuidium tamariscinum can be seen in Plate 4.

Many mosses of dry habitats have non-papillose leaves (Plates 5 and 6, and examples in Robinson (1971)), and the water supply of these is not so easily understood in terms of their known structure. Calculation from the available data suggests that if the cell walls are similar in properties to those of vascular plants or of Nitella (Briggs, 1967; Tyrce, 1968; Preston, 1974; Lauchli, 1976), barely adequate flow-rates to maintain turgor could be produced within the cell walls with a water potential difference of 10 to 20 bar along the length of the leaf. It is notable that most mosses in this category have very thick cell walls; it could be that the high osmotic potentials reported for some mosses during dry periods (Ochi and Yonehara, 1954; Hosokawa and Kubota, 1957) are primarily an adaptation to permit water movement rather than to resist external water stress as such. Bryophyte cell walls may possibly contain larger voids and be more permeable than we have assumed, and (unpublished) scanning electron micrographs give some indication that this may be so, but much further investigation is needed. Other pathways of water movement may also be important. Even an inefficient external capillary pathway would greatly alleviate the situation. Evidence in other groups of plants indicates that cell membranes impose a much greater resistance to water flow than a normal thickness of cell wall. However, the very elongate cells of many hypnoid mosses could sufficiently increase the area of contact between adjacent cells, and reduce the number of cell membranes crossed between the base and apex of the leaves, for flow from cell to cell to contribute significantly to total longitudinal water movement.

Acknowledgement

Part of the work reported in this paper was carried out with the support of a grant from the Natural Environment Research Council, which we gratefully acknowledge.
REFERENCES


Physiological ecology of bryophytes


EXPLANATION OF PLATES

The black scale bar represents 10 \( \mu m \) in Plates 1 to 3, 5 and 6 and 100 \( \mu m \) in 4.

**PLATE 1**
Surface of upper part of leaf of *Tortula intermedia*. The cells are about 6 \( \mu m \) across; each projects into a single hollow, branched papilla, leaving a continuous, almost rectilinear, system of channels about 2 \( \mu m \) wide in between. Chudleigh, Devon. Freeze-dried.

**PLATE 2**
Leaf surface of *Anomodon viticulosus*. The large branched papillae correspond to single cells about 8 \( \mu m \) across and are separated by a continuous system of channels about 1.5 \( \mu m \) wide. Chudleigh, Devon. Freeze-dried.

**PLATE 3**
Surface of upper part of leaf of *Pleurochaete squarrosa*; lower surface. In structure, the papillae on the long tapering leaves of this species are an extreme form of those seen in *Tortula intermedia*. Chudleigh, Devon. Critical-point dried.

**PLATE 4**
Part of the shoot system of *Thuidium tamariscinum*. The abaxial surfaces of the leaves are covered with conical papillae defining a system of shallow channels of radius c. 5 \( \mu m \). The paraphyllia on the stem (middle left) form a 'wick' with capillary spaces in the region of 20 \( \mu m \) radius. The inner surface of the branch leaves is smooth (top right), and forms a potentially water-holding concavity of c. 100 \( \mu m \) radius. Stoke Woods, Exeter, Devon. Freeze-dried.

**PLATE 5**
Part of the plicate leaf of *Camptothecium sericeum*. The surface is smooth, but there are potential capillary channels a fraction of 1 \( \mu m \) in radius at the boundaries of the elongated cells; the longitudinal plicae in the lamina provide capillary channels an order of magnitude larger. East Prawle, Devon. Air-dried.

**PLATE 6**
Transversely cut leaf of *Leucodon sciuroides*. There is no continuous capillary conducting system on the leaf surface. The cell walls are about 3 \( \mu m \) thick, and the lumina occupy a relatively small fraction of the total cross-section. Holne, Dartmoor, Devon. Air-dried.
This document is a scanned copy of a printed document. No warranty is given about the accuracy of the copy. Users should refer to the original published version of the material.