

CHAPTER 7-3

WATER RELATIONS: PLANT STRATEGIES



Figure 1. *Leucobryum glaucum* demonstrating the tight cushions that maintain hydration. Photo by Michael Lüth.

Water Strategies

Mosses often appear to be completely dead, only to be revived by water. Angie Newton (pers. comm., Bryonet) reported that epiphytic mosses in the lowland tropical rainforests, where mosses may appear dead after severe desiccation, recover quickly with actively growing apical and axillary buds on completely dried out plants and even on plants scorched by fire (Figure 2)! Leaf and stem tissues from xerophytic mosses can regenerate after as many as 19 years of desiccation (Table 1); some spores remain viable after 70 years (Malta 1921).

Even though many bryophytes can tolerate high degrees of desiccation (Dilks & Proctor 1974; Nörr 1974; Dhindsa & Bewley 1976), **water content** and availability are important for potential accumulation of photosynthates (Alpert 1979). Patidar (1988) found that in *Asterella angusta* the moisture content is the most important determinant of thallus size. In *Plagiochasma appendiculatum*, optimum growth occurs at 60% moisture, whereas branching and growth are able to occur from 10-100% moisture (Vishvakarma & Kaul 1988)! *Reboulia hemisphaerica*, on the other hand, requires 70-80%

moisture for optimum growth, with growth and branching occurring from 40 to 90%. In other words, no matter how desiccation tolerant a plant might be, it requires water to grow. Representative water contents of bryophyte plants from a wide range of field habitats in the temperate zone, Great Britain, are given in Table 2.



Figure 2. *Polytrichum* showing fresh, green growth one week after a forest fire that scorched adjacent plants. Photo by Janice Glime.

Table 1. Records of revival after extended periods in a herbarium (Alpert 1982, *Volk 1984, †Glime pers. obs.).

<i>Anoetangium compactum</i>	19 years
<i>Dicranoweisia cirrata</i>	9 years
<i>Riccia canescens</i>	*7 years
<i>Grimmia elatior</i>	5 years
<i>Oxymitra</i>	*4 years
<i>Anomodon longifolius</i>	2 years
<i>Bryum argenteum</i>	2 years
<i>Orthotrichum rupestre</i>	2 years
<i>Grimmia muehlenbeckii</i>	18 months
<i>Andreaea rothii</i>	13 months
<i>Racomitrium lanuginosum</i>	11 months
<i>Syntrichia ruralis</i>	8 months
<i>Fontinalis flaccida</i>	†3 months

Table 2. Percent water content (compared to dry mass) of bryophytes at full turgor, not including free external water. Values represent means of two measurements. Table based on Dilks and Proctor (1979); those marked with * from Skre *et al.* (1983) include new growth and 1-year-old growth; those with † from Proctor (2000).

species	water content, % dry mass
Mosses	
<i>Sphagnum subsecundum</i> *	1225
<i>Pilotrichella ampullacea</i> †	>1200
<i>Hookeria lucens</i>	516
<i>Pleurozium schreberi</i> *	485-625
<i>Hylocomium splendens</i> *	485-545
<i>Brachythecium rutabulum</i>	249
<i>Syntrichia intermedia</i>	233
<i>Homalothecium sericeum</i>	223
<i>Pseudoscleropodium purum</i>	207
<i>Thuidium tamariscinum</i>	203
<i>Dicranum majus</i>	202
<i>Leptodon smithii</i>	187
<i>Rhytidiadelphus loreus</i>	165
<i>Pleurochaete squarrosa</i>	165
<i>Neckera complanata</i>	162
<i>Racomitrium lanuginosum</i>	142
<i>Anomodon viticulosus</i>	141
<i>Polytrichum commune</i> *	95-125
Liverworts	
<i>Pellia epiphylla</i>	1180
<i>Conocephalum conicum</i>	871
<i>Porella platyphylla</i>	230
<i>Plagiochila spinulosa</i>	222
<i>Bazzania trilobata</i>	210

Mosses grown in fully hydrated conditions afforded by saturated air enjoy optimal growth and development (Davy 1927). They exhibit more rapid development, more stem branching, more numerous rhizoids, smaller leaves, and smaller and fewer cells with larger chloroplasts than mosses existing at less than full saturation. Even at the scale of a single boulder, bryophytes distribute themselves according to their ability to achieve photosynthetic gain. When examining bryophytes that occupied various microsites on exposed granitic boulders, Alpert and Oechel (1987) found that those species that occurred in microsites with lower water availability were able to attain maximum net photosynthetic gain at a lower water content and to

recover better from prolonged desiccation than those taxa in less xeric microsites. Alpert (1985, 2000) supports the hypothesis that the reason even xerophytic mosses are limited in their ecological distribution is that they often are unable to maintain positive carbon balance during repeated cycles of wetting and drying. Alpert and Oechel (1985) demonstrated this with *Grimmia laevigata* (Figure 3), a desiccation-tolerant plant that was unable to maintain this balance under a natural, highly xeric regime of wetting and drying in certain microhabitats on exposed granitic boulders in California chaparral. Thus, there is "inherent trade-off between desiccation tolerance and growth rate."



Figure 3. *Grimmia laevigata*, a poikilohydric moss, in its dry state (**upper**) and wet state (**lower**). Photo by Michael Lüth.

Water content in a bryophyte ranges widely throughout the year. For example, Klepper (1963) measured 23.8-258% in *Dicranum scoparium*, Romose (1940) 10-950% in *Homalothecium sericeum*, Morton (1977) 19-214% in *Pseudoscleropodium purum* and 58-307% in *Dicranum bonjeanii*. Whereas many mosses benefit from high water content, too much water is not good for photosynthesis. Water on the surface blocks CO₂, and most likely high internal water content also interferes with physiological processes (Proctor 2000). Dilks and Proctor (1979) found optima as low as 200% water content and as high as 1500% among the same bryophytes shown in Table 2. Respiration seems to peak around 200% for most of these taxa.

Richardson (1981) divides mosses into three water strategies: **aquatic**, **mesophytic** (living in continually moist habitats), and **poikilohydric** (organism dries as its habitat dries and resumes normal metabolic activity after rehydration; Figure 3). Unlike most other plants, water content of predominantly poikilohydric bryophyte species is highly related to environmental conditions and weakly regulated by their internal and morphological structures.

This strategy permits them to colonize such xeric environments as boulders and tree trunks. In these environments, mosses enjoy release from competition by higher plants, but must still survive the low light intensity created by the trees above.

However, some bryophytes do appear to be able to survive in absence of precipitation. In caves in Poland, only 18.1% of the species occurred in very wet places or where there was dripping water, whereas in places that were continuously dry(!), 25% occurred (Jedrzejko & Ziober 1992). Certainly in those dry places atmospheric humidity must have provided the needed water for these very hygroscopic, ectohydric bryophytes. Shaun Russell (pers. comm.) found that in montane areas of Africa with virtually no rainfall, fog collected on bryophyte surfaces, providing sufficient water for them to survive. The drought-tolerant *Barbula aurea* seems to have compensated for its low water availability by having relatively low levels of light compensation and saturation responses for photosynthesis (Rundel & Lange 1980). Such low levels would permit the moss to carry out photosynthesis early in the morning when dew is available and before high evaporation stress occurs. These aerial sources of water are of little use to tracheophytes that must take water in by their roots, not their leaves.

As one would expect, degree of drought tolerance is generally greatest in plants from dry habitats (Clausen 1952, 1964; Johnson & Kokila 1970; Dilks & Proctor 1974). Seki and Yamaguchi (1985) suggest that on some islands with strong summer winds, Shannon diversity decreases as saturation deficits increase. Richardson (1981) claims that aquatic mosses and those that grow in humid forests are damaged quickly by drought. But even such high humidity plants as *Hookeria lucens* (Figure 4) are able to survive desiccation for days (Horst Tresp, Bryonet).



Figure 4. *Hookeria lucens*, a drought-intolerant moss. Photo by Michael Lüth.

Glime (1971) found that two aquatic mosses (*Fontinalis* spp.) were able to survive on the stream bank out of water for up to one year and still grow when rehydrated. However, those dried in the laboratory were apparently dead after only 55 hours. Steere (1976) found that *F. squamosa* from Alaska could not survive a week of air drying. One reason for apparent differences here is that it is difficult to determine when a moss is dead, and even though all leaves may be dead, the stem may still harbor life. *Fontinalis* is subject to annual emergence when stream level drops, and perhaps slow drying on the stream bank permitted it to become dormant and to preserve sufficient energy to repair its membranes upon rehydration. The rapid drying of a laboratory, with unnaturally low

humidity and no acclimation period, may have prevented the necessary physiological changes that could permit it to survive. It is well known that it takes longer for the cellular physiology to return to normal in a rapidly dried bryophyte than in a slowly dried one (Oliver & Bewley 1984).

A similar pattern of submersion and desiccation is endured by *Hydropogon fontinaloides* in the Amazon basin (Mägdefrau 1973). It hangs from trees during the dry season, but during the wet season it floats in water. The behavior of *Cratoneuron filicinum* (mistakenly published as *Hygrohypnum luridum*), typically a stream margin species, may explain the lab results. This moss was unable to synthesize protein when rehydrated after it was dried quickly over silica gel for one hour (Bewley 1974). However, it was able to tolerate drying down to 33% of its fresh mass when dried slowly, and slow drying for 5 hours to 66% of its fresh mass had no detrimental effects on protein synthesis.

Just what endows bryophytes with the ability to inhabit arid microsites that are totally inhospitable for tracheophytes? As you can see from the foregoing examples, we can divide these adaptations into anatomical/structural, growth/life form, and physiological adaptations.

Thallose Liverworts

The structure of most thallose liverworts is so different from that of mosses or leafy liverworts that their water relations warrant separate consideration. They are adapted for predominantly ventral uptake. Thallose liverworts like *Conocephalum conicum* and *Cyathodium cavernicum* use ventral appendages (**scales**; Figure 5) to provide capillary spaces that conduct water externally on the underside of the thallus. Marchantialian species use specialized capillary systems on the ventral surface of the thallus to conduct water in either direction. Cell walls of the scales contain **tannins** (McConaha 1939), perhaps acting as an antibiotic.

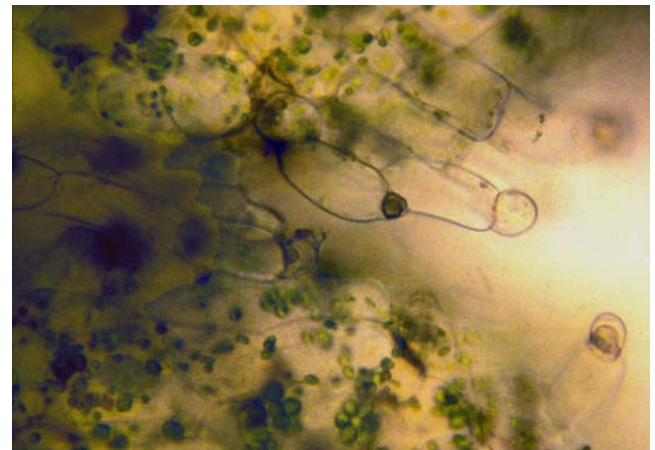


Figure 5. Scales of *Cyathodium cavernarum*. Photo by Noris Salazar Allen.

Exposed surfaces of scales and thallus are often reddish-purple due to the flavonoid pigment **phlobaphene**, formed by oxidation of tannic compounds (McConaha 1939), but the role of phlobaphene is not clear. It is possibly a defense against would-be toxins from tannic compounds that contact the ventral surface. (There is evidence that tannins are toxic to bryophytes, not within

their cell walls, but when they are able to act on cell constituents.) Since all these ventral surfaces are wettable, these cells are more susceptible to damage by such toxins. This high degree of wettability provides a greater possibility for water entry in thallose forms. For example, in *Marchantia*, water is conducted along the midrib as well as in interstitial spaces between the blade and scales, distributing water throughout the surface of the thallus. Water movement in *Marchantia* is relatively slow, at 0.4 mm per sec, improving slightly in *Lunularia* and *Reboulia*, to approximately 0.5 mm per sec, despite their less highly developed capillary systems. However, McConaha (1939) found that movement from base to apex in *Conocephalum conicum* generally takes only about 20-30 seconds, roughly 1 mm per sec. Despite its slowness, McConaha found this external movement to be much faster than would be possible by internal conduction.

Ventral structures seem to be important in this group. In Marchantialian liverworts, two types of rhizoids provide somewhat different functions. The smooth-walled rhizoids are alive (Duckett & Ligrone 2003) and emerge from beneath the ventral scales, providing contact with the substrate, whereas the tuberculate (pegged) rhizoids are dead (Duckett & Ligrone 2003) and form a capillary system parallel to the thallus beneath each scale (McConaha 1941). The pegs, extending into the cell, prevent the collapse of the cell when dehydrated, thus maintaining its capillary role (Duckett & Ligrone 2003). The pegged rhizoids are wrapped within the archegoniophore by the folded thallus and function in internal water conduction (Duckett & Ligrone 2003). The presence of the pegs also prevents the collapse of this stalk when the thalli dehydrate (Duckett & Ligrone 2003). These rhizoids have an outer layer of pectic material (like apples). Xerophytic liverworts such as *Riccia*, *Reboulia*, *Targionia*, *Asterella*, and *Lunularia* have both tuberculate and smooth rhizoids, scale leaves, and well-defined assimilatory and storage zones, whereas moisture-loving *Dumortiera*, *Cyathodium*, *Pallavicinia* (Daniels 1998), *Monoclea*, *Neohodgsonia*, and some aquatic *Riccia* species (Duckett & Ligrone 2003) lack these complex structures. Even in *Marchantia*, with its strong midrib, water moves externally along the midrib and in the spaces between the scales, providing a film of water throughout the thallus (McConaha 1941). In *Preissia*, it appears that the numerous rhizoids compensate for a less compact arrangement of the capillary system. Volk (1984) found that *Riccia*, a common inhabitant of ephemeral habitats such as flood plains, absorbs water by capillary action among the rhizoids and the lower surface of the thallus. The thallus rolls or folds when it is dry, thus exposing the rhizoids, scales, and/or cilia. These serve both to absorb water and to provide a reflective surface that protects the chlorophyllous cells of the thallus. In others, a crystalloid crust serves a similar function of reflectance.

Volk (1984) found that when *Riccia* has less than 150 mm of rainfall per year, it requires other means to survive, and it seems that dehydration/dormancy is the solution. Some thallose *Riccia* species are able to survive up to 7 years in this dehydrated state, enduring temperatures up to 80°C. The annual species compensate for this water loss by producing huge numbers of spores, taking advantage of their ornamentation for distribution by animals.

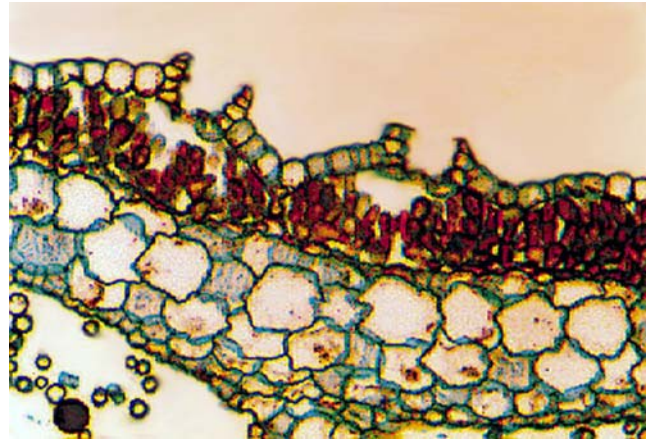


Figure 6. Cross section of *Marchantia* thallus, showing pore. Photo from Department of Botany Teaching Collection, Michigan State University.

But this wonderful ventral efficiency is counterbalanced by a dorsal surface that does little to conserve water. In fact, this dorsal surface water loss may facilitate the movement of water and nutrients through the plant, as it does in leafy tracheophytes. The pores on the dorsal surface function much as do the stomata of tracheophyte leaves in losing water (Figure 6, Figure 7). Maier-Maercker (1982) found that *Conocephalum conicum* loses water through transpiration from these dorsal thallus pores, accumulating radioactively labelled ions in the cells surrounding the air pores.

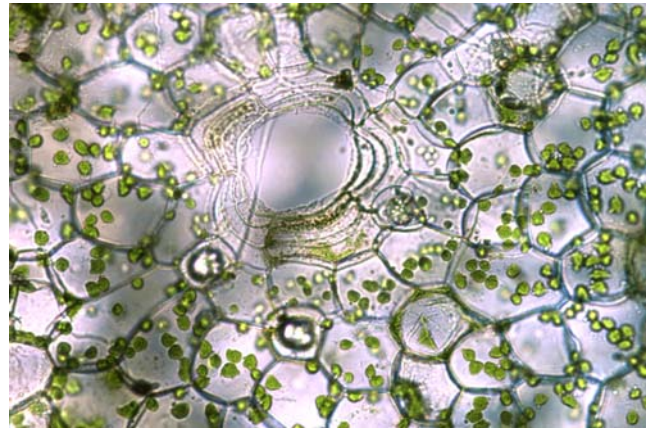


Figure 7. Pore opening in thallus of *Cyathodium cavernarum*. Photo by Noris Salazar Allen.

In some cases, thalloid liverworts seem to lose great quantities of water, 2-3 times that of leaves of the weeping birch tree *Betula pendula* (McConaha 1941). Under extreme conditions, they transpire equivalent to their total content of water in an hour. One reason for this rapid transpiration rate is the areolation of the thallus that creates a large surface area where water can be lost. The pores in these thalli, permitting contact between outside air and internal moisture, have only limited ability to close, thus being a major source of water loss. McConaha (1941) claims that the ventral specializations compensate for the losses from dorsal areolation and pores. Proctor (1980) found that these areolate thalli have internal resistances similar to those of mesophytic leaves of flowering plants (Proctor 1980). As in the flowering plants, the water loss is correlated with pore size and density.

Structural Adaptations of Mosses and Leafy Liverworts

In tracheophytes, we typically think first about structural adaptations for water retention, so we will start there. Safaris (1971) considered that *Polytrichum commune* had four ways of controlling water loss:

1. Community level – gregariousness
2. Plant level – leaf density & size, plant height
3. Organ level – leaf movement and inrolling
4. Molecular level – wax on leaf surface

These all relate to structure, but internal structure and cellular level physiology are additionally important.

After examining 439 taxa of pleurocarpous mosses, Hedenäs (2001) reported that most differences in character states between environments relate to two functions: 1) water conduction and retention; 2) dispersal. Those characters that seem important for water relations relate to **stem central strand, leaf orientation, leaf costa type, alar cells, paraphyllia, and pseudoparaphyllia**. But if acrocarpous mosses (upright mosses with terminal sporophytes) had been included, surely many more characters might be added, as it is mostly acrocarpous mosses that occupy the most xeric of habitats.

One feature of structural adaptations is that many are plastic. For example, **conducting strands** disappear in the liverworts *Moerckia flotoviana* and *Haplomitrium hookeri* under high humidity or liquid culture (Hébant 1977). **Hair points** (colorless, hairlike extensions at leaf tip) of *Schistidium apocarpum* likewise disappear in humid conditions (Figure 8).

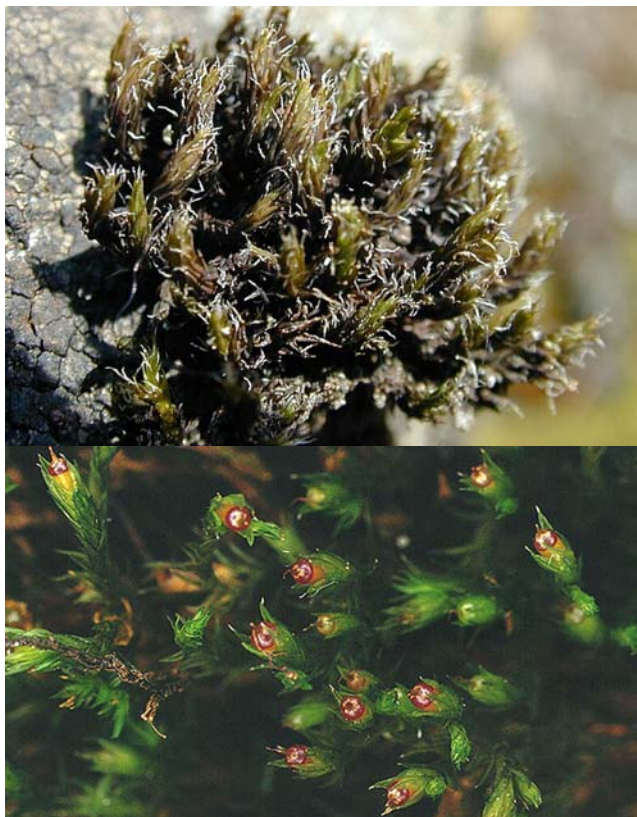


Figure 8. **Upper:** *Schistidium apocarpum* with hyaline hair points on an exposed rock. Photo by Michel Lüth. **Lower:** *S. apocarpum* without hyaline hair points in a more shaded or moist environment. Photo by Jan-Peter Frahm.

Rhizoids are less well developed or absent in wet conditions (Smith 1988), even in the same species. In *Andreaea blyttii*, increased moisture results in longer, wider leaves that are more curved with longer cells in the basal margin, wider costae (midrib of leaf), and longer stems, but with a decrease in number of leaves per stem (Heegaard 1997). Even in typically aquatic taxa such as *Drepanocladus (sensu lato)*, leaves become longer and falcation (leaf curvature) is lost in submersed leaves compared to those grown out of water, and the reduced light results in greater **internode** distances (distance between leaf insertions; Lodge 1959). A similar response is seen in *Fontinalis* (Figure 9). It is interesting that increases in salt concentration increase cell length in this genus. Plasticity itself is an important adaptation.



Figure 9. **Upper:** *Fontinalis novae-angliae* with normal submersed leaves. **Lower:** *F. novae-angliae* with leaves grown out of water, exhibiting an atypical falcate habit. Photos by Janice Glime.

Rhizoids and Tomentum

Mosses with dense rhizoids or **tomentum** (Figure 10) seem to be well equipped to retain and conduct water by capillary action. Smith (1988) found that *Bryum algens*, with a dense rhizoidal tomentum, held significantly more water than colonies with sparse rhizoids. But the tomentose form lost water more rapidly per unit dry mass than did the ones with sparse rhizoids. Could this be compensated if one considered only the mass without the tomentum? In *Schistidium antarcticum*, the xeric form has less densely packed shoots and thicker cell walls that maintain lower water content than the high-water-holding-capacity hydric turf form. Mosses in Smith's study took several times longer to drop to minimal water contents than did lichens in the same conditions.



Figure 10. *Rhizomnium magnifolium* showing dense brown rhizoidal tomentum on lower half of stem. Photo by Michael Lüth.

In acrocarpous mosses, rhizoids are produced all the way around the base of the stem, serving on the lower parts for anchorage, and in mosses like the Polytrichaceae, for limited conduction (Odu 1978). Rhizoids further up the stem provide capillary spaces that can both store water and facilitate movement. In pleurocarpous mosses, rhizoids appear only on the side of the stem toward the substrate (Odu 1978), except in the case of those in flowing water (Glime 1987). In *Fontinalis* (Figure 11), where rhizoids have a critical function in anchorage, and the moss may encounter its substrate in any direction from the stem, the rhizoids grow in a spiral until they encounter the substrate, then branch prolifically in a small space and cement themselves to the substrate, presumably offering no function of water movement (Glime 1987).

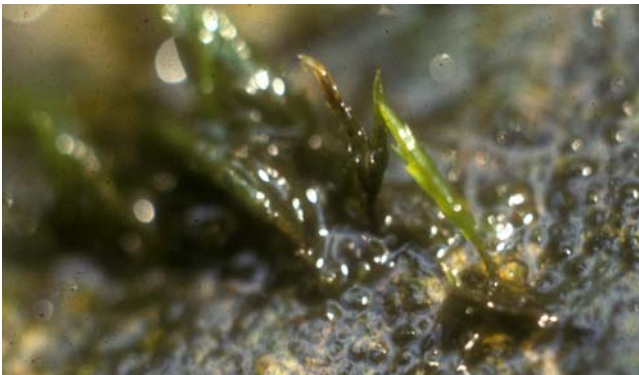


Figure 11. *Fontinalis novae-angliae* cemented to the rock by its rhizoids. Photo by Janice Glime.

Higuchi and Imura (1987) cultured three moss species to determine the effects of submersion on the rhizoid characters. The thickness, surface decorations, and positions where the rhizoids arise appear to be stable in altered moisture conditions, but in *Macromitrium gymnostomum* the mucilage that was present in terrestrial cultures was lost in water culture. Rhizoids generally are not produced on submersed mosses in standing water (Odu 1978), perhaps because ethylene, which inhibits their development, cannot escape. This conserves energy, because it would seem that they are needed neither for anchorage nor absorption and conduction.

Surprisingly, Trachtenberg and Zamski (1979) found a cuticle on the rhizoids of *Polytrichum juniperinum*, sharply contrasting with roots and root hairs of tracheophytes,

which serve as absorbing organs and have no waxy cuticle. This suggests that they may play little role in water uptake, but rather prevent water loss to the substratum. This raises questions about how widespread this cuticle is on rhizoids of other taxa and how it affects the capillary action they might otherwise afford. Perhaps they play only a role in conservation of water and not in its uptake.

Mucilage

Stem apices are protected by mucilage secreted by specialized hairs (Berthier *et al.* 1974). This mucilage seems to play a strong role in protecting the actively dividing tissue, permitting fragments to survive long periods before being able to grow again, and most likely playing a role in water retention, especially for the critical apical cells.

In liverworts and the moss *Takakia* there are **slime papillae** that may serve a water absorption/retention function as well (Figure 12). It is interesting that these slime papillae appear first in the green alga *Coleochaete*, the genus that seems most closely related to embryophytes, causing one to wonder if they may have been a prerequisite for land adaptation in early plants.



Figure 12. Stem of *Takakia lepidozoides* showing slime papillae. Photo from Botany 321 website, www.botany.ubc.ca/bryophyte/LAB8.htm, with permission.

The thallose liverwort *Conocephalum conicum* has mucilage ducts in its thallus. Clee (1943) suggests that these may aid in water retention.

Capillary Spaces

Although several adaptations to holding water seem to exist [porose leaf cells, ridges, folds, sheathing leaf bases (Figure 13), rhizoids, tomentum], Proctor (1979) contends that most of the water is held in the larger capillary spaces between the moss shoots. Small amounts of dew that accumulate at the moss tip, *i.e.* the growing region, may be critical to survival (Lange 1969; Kappen *et al.* 1979). Hair points that wrap around the succeeding leaves above (Figure 14) help to deflect light and reduce evaporative loss by creating a diversion for air currents. Proctor (1980) experimented by removing hair points and found that when present they reduced water loss by 35% in *Grimmia pulvinata* and *Syntrichia intermedia*. Thus far, no one has been able to demonstrate that papillae afford any such advantage (Frey & Kürschner 1991).



Figure 13. *Bartramia ithyphylla* illustrating the sheathing leaf base that provides capillary spaces that can hold water. Photo by Michael Lüth.



Figure 14. *Polytrichum piliferum* illustrating leaf hairs that overlap the next leaf and help shield it from light while creating capillary spaces. Photo by Michael Lüth.

The leafy liverwort *Trichocolea* (Figure 15) is highly adapted to take advantage of capillary spaces. Its leaves are highly dissected and **paraphyllia** (leaflike appendages between the leaves; Figure 16) are abundant, permitting this species to act like a sponge. Zehr (1979) observed that it experienced only short-term vapor deficits in its moist habitat and thus was able to grow anytime temperatures were above freezing. Paraphyllia such as those in *Hylocomium splendens* and *Thuidium tamariscinum* create capillary spaces much like a tomentum. Other mosses such as *Mnium* utilize **paraphyses** among the archegonia to conserve water, using the same capillary principle.

Stems and Branches

Most stem and branch arrangements relate to growth form or life form. However, in some cases there is internal or structural modification. For example, Li and coworkers (1992) examined the responses of two closely related *Sphagnum* hummock species, *S. magellanicum* and *S. papillosum*, to distance from water level and related these responses to structural and physiological adaptations of the two species. They found that both species increase growth in length as water becomes more available, *i.e.* as the distance from water level decreases. Likewise, dry mass is maximal under wet conditions, with new branches being a major mass contributor, especially in *S. papillosum*.

Furthermore, while experimenting with effects of distance from water on *S. magellanicum* and *S. papillosum*, Li and coworkers found that dry conditions result in wider stems (Figure 17), with thicker hyaline layers, presumably increasing both absorption and water-holding ability.



Figure 15. *Trichocolea tomentella*, a leafy liverwort with finely divided leaves and paraphyllia. **Top:** dry. Photo by Janice Glime. **Bottom:** wet. Photo by Jan-Peter Frahm. Note the numerous capillary spaces afforded by the filamentous leaves.



Figure 16. *Thuidium recognitum* showing branched paraphyllia on the stem and branches. Photos by Michael Lüth (**upper**) and Paul Davison (**lower**).

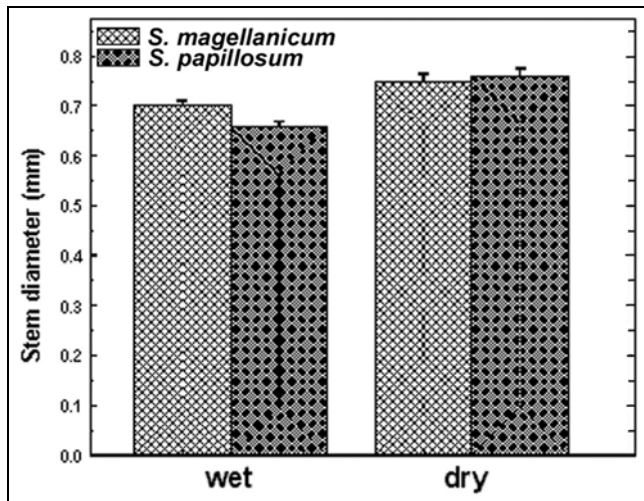


Figure 17. Effect of water level (water availability) on stem diameter in *Sphagnum magellanicum*, a more desiccation-resistant species, and *S. papillosum*, a more desiccation-tolerant species. Wet denotes 0 cm initial distance of capitulum from water; dry denotes 10 cm initial distance. Bars represent standard error; stem diameter in dry treatment is significantly greater in both species. From Li *et al.* (1992).

Sphagnum has pores in its stem, in most species, and has very rapid movement of water externally up the stem by capillary action, adapting it for its annual cycle of being stranded well above water level. Some species of *Sphagnum* have special **retort cells** on the stems for absorbing water (Figure 18).



Figure 18. Retort cell (**arrow**) of *Sphagnum*. Photo with permission from Botany 321 website, www.botany.ubc.ca/bryophyte/LAB8.htm.

Daniels (1989) found that while there is little differentiation between **spreading** and **pendant** branches (Figure 19, Figure 20) among *Sphagnum* plants growing in pools, hummock plants have more closely spaced **fascicles** (groups of branches), comparatively short spreading branches, and thin, closely appressed pendant branches. Pendant branches help to preserve stem water and maintain the wick effect as water level drops. Daniels determined that leaves of pendant branches on submerged plants photosynthesize actively, while those of hummock plants do not. He found that the two species growing in wet hollows or as wet carpets had the highest percentage of unbranched stems. The low hummock species *Sphagnum papillosum*, on the other hand, had up to six **capitula** (terminal clump of branches) per stem; the two species growing in the high-humidity, shaded wet woodland exhibited intermediate degrees of branching.

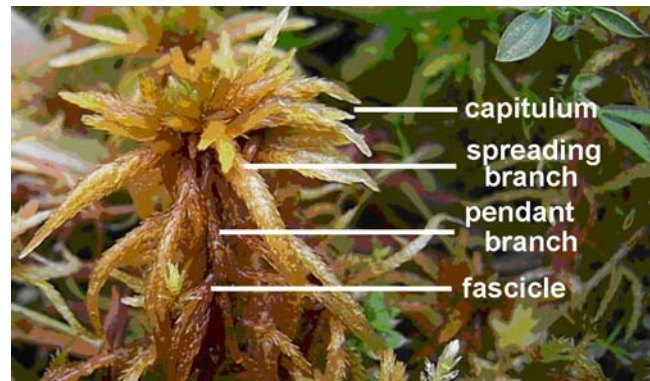


Figure 19. *Sphagnum teres* indicating two major branch types, compact capitulum, and joining of branches into fascicles. Photo by Michael Lüth.



Figure 20. Spreading branches and pendant branches on two hummock *Sphagnum* species. **Left:** *S. magellanicum*. **Right:** *S. magellanicum*. Photos by Yenhung Li.

Sphagnum magellanicum has greater ability to move and hold water than does *S. papillosum* (Li *et al.* 1992). Therefore, when they grow together in the same hummock, *S. magellanicum* will not only stay wet longer, but if it is dominant will keep *S. papillosum* wet (Figure 21). However, it will fail to do so if *S. papillosum* is dominant (Figure 21). This is further supported by lab experiments in which *S. magellanicum* moved water farther externally in 20 hours than did *S. papillosum* (Figure 22; Figure 23)



Figure 21. Predominately *Sphagnum papillosum* (**olive colored**) lower on the hummock causes both species to be dry, whereas predominately *S. magellanicum* (**red**) higher on the hummock causes both species to be wet. Photo by Janice Glime.

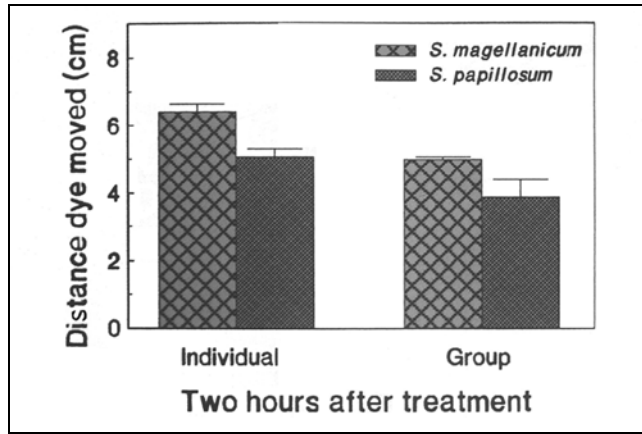


Figure 22. Comparison of distance travelled by dye in two *Sphagnum* species from lower (*S. papillosum*) and higher (*S. magellanicum*) in the hummock after 20 hours. Group refers to those kept together at field density with half of each species. From Li *et al.* (1992).

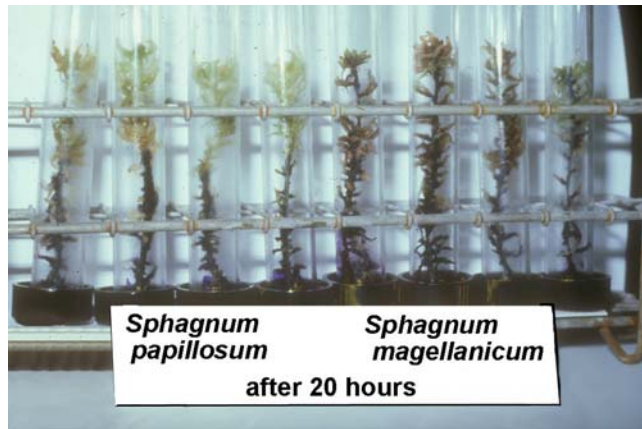


Figure 23. Comparison of upward transport in a low (left) and high (right) hummock species of *Sphagnum*. Movement of water is indicated by purple dye. Photo by Yenhung Li.

Central Strand

In addition to the structural adaptations of stems and branches already described, the vascular system itself may be modified. The **central strand** (Figure 24) is typically composed of hydroids that are elongated and impose fewer cell end walls through which water must travel. Héban (1973) found that variation occurred in the vascular elements, particularly in length and diameter, degree of inclination of end walls, and structure of the walls themselves. For example, whereas walls of hydroids are usually thin, they can be very thick, as in the lateral walls of hydroids in the gametophyte central strand of the Polytrichales or the swollen walls of hydroids in the setae of *Dicranum scoparium*. But insufficient data exist to relate these variations to adaptive function.

Using several references for comparison, Héban (1977) showed that the number of hydroids within the *Polytrichum commune* central strand can vary with habitat, following an apparent moisture gradient. In a pseudo-alpine grassland he reports 900 hydroids in the central strand, peat bog 400, cultivated in artificial peat 280, and cultivated under water 70. There is no clear indication as

to how these numbers affect the rate of conduction, but one would presume that more hydroids conduct more water.

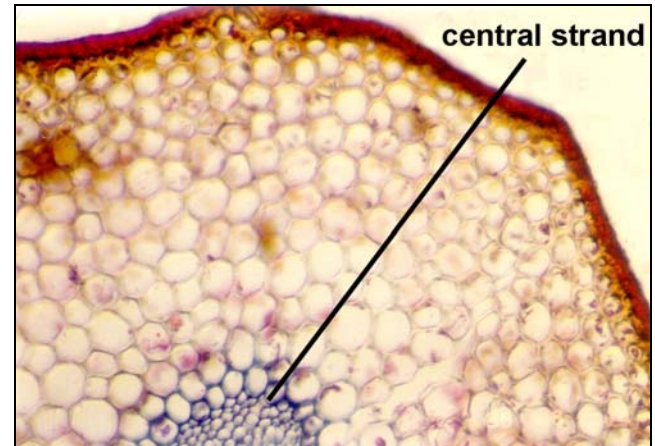


Figure 24. Stem cross section of *Rhizogonium* showing narrow cells of central strand. Photo by Isawa Kawai.

Summary

Bryophytes gain water in their cells both through external (**ectohydric**) capillary movement and internal (**endohydric**) transport. When fully hydrated, their water content is typically high, up to more than 1200% of their dry mass. When dry, they can survive months to many years. Structural adaptations of stems and whole plants such as **growth form, branch and leaf arrangements, rhizoidal tomentum, mucilage, central strand, hydroids, paraphyllia, and ventral scales** aid in moving water, facilitating entry, or reducing loss.

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